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The Seaward Migration of European Eel at a Continental Scale: A Europe-Wide Biotelemetry Meta-Analysis

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ABSTRACT

The European eel (*Anguilla anguilla* L.) has a catadromous life cycle, with a single panmictic population that colonises continental Europe and northern Africa yet migrates 5000 to 9000 km to spawn in the Atlantic Ocean. It is unknown how this continental migration is organised so individual eels arrive in time for spawning with conspecifics. This meta-analysis combined tracking data from 18 water bodies in freshwater and transitional systems distributed along the southwest-northeast axis of Europe, resulting in a dataset of 2306 eels, making it the most comprehensive in terms of geographical coverage and number of eels tagged. The eels were tracked using acoustic telemetry and the Nedap Trail System and allowed us to study the eel's migration phenology at a continental scale. The findings reveal that the day when eels arrive at sea varies significantly with latitude, with northern eels arriving earlier. Migration speed differs between tidal and non-tidal habitats, suggesting that tidal currents facilitate faster movement. However, despite these patterns, we observed substantial variability in arrival at sea time and migration speed within water bodies, suggesting that the eel's migration phenology is considerably plastic. The presence of water regulating structures such as weirs, pumping stations and hydropower plants can impact migration timing and speed, potentially delaying eels, but is likely dependent on local hydrological conditions which can be water body specific.

1 | Introduction

The migratory behaviour of the European eel (*Anguilla anguilla* L.) has baffled scientists for millennia, dating back to the Ancient Greek philosopher Aristotle, who hypothesised on the birthplace of the species (Voultsiadou et al. 2017). Eels have a complex life cycle, spending their growth phase (i.e., the yellow eel phase) in marine, transitional and freshwater habitats before migrating as silver eels to spawn presumably in the Sargasso Sea, an area 5000 km west of continental Europe in the Atlantic Ocean (Schmidt 1923; Tsukamoto et al. 1998; Wright et al. 2022). Based on the sampling surveys for anguillid leptocephali larvae, it is assumed that spawning occurs during a specific period of the year, ca. February–May (Miller et al. 2015). Since the European eel is considered panmictic with a wide distribution from North Africa to northern Europe (Als et al. 2011), it can be assumed that individuals need to time their migration period and/or adjust their speed to be at the spawning grounds together with their conspecifics to maximise their opportunity to spawn successfully (Quintella et al. 2010).

Electronic tracking technology or telemetry can help us gain insight into the spawning migration of European eel (Hussey et al. 2015). In the marine environment, migrating silver eels have been tracked over large geographical scales. Studies have shown that their migration speed ranges between 3 and 47 km day^{-1} and can vary depending on the route taken (Aarestrup et al. 2009; Righton et al. 2016; Verhelst et al. 2022). It has been hypothesised that a proportion of the migrants may arrive at the spawning grounds after a short migration of a few months, whereas others may take longer and arrive a year or more after they started their migration at sea (Righton et al. 2016).

Although many telemetry studies have been conducted in freshwater and transitional areas, these have been relatively limited in space and time and focused on local water bodies (e.g., Frankowski et al. (2019); Monteiro et al. (2020); Trancart, Tétard, et al. (2018); Trancart et al. (2020); Verhelst, Baeyens, et al. (2018); Verhelst, Bruneel, et al. (2018); Verhelst, Buysse, et al. (2018)). The combination of findings from different telemetry studies, together with scientific monitoring programmes on silver eel escapement rates and commercial fisheries data, has led to the current consensus on the main characteristics of silver eel migration in freshwater and transitional areas: silver eels generally migrate from summer to winter, with eels at higher latitudes migrating earlier and larger eels migrating later (Briand et al. 2020; Meyer 1938; Nolte 1938). Nevertheless, numerous observations of eels migrating in spring have been made, illustrating the wide range of the migration season (Aarestrup et al. 2008; Dainys et al. 2017; Verhelst, Baeyens, et al. 2018; Verhelst, Bruneel, et al. 2018).

Eel tracking studies in freshwater often focus on the impacts of water regulating structures (WRS), such as weirs, sluices, shipping locks, water pumping stations and hydropower plants, which can potentially hamper or even block the seaward migration. The impacts of these migration barriers can range from significant delays (Besson et al. 2016; Bolland et al. 2019; Evans et al. 2024; Trancart, Feunteun, et al. 2018; Trancart, Tétard, et al. 2018; Trancart et al. 2020, 2022; van Keeken et al. 2023; Verhelst, Baeyens, et al. 2018; Verhelst, Buysse, et al. 2018) to injuries and mortality by turbine or pumping blades (Bolland et al. 2019; Buysse et al. 2014; Dainys et al. 2018; Winter et al. 2006). While delays due to WRS have been observed at specific study sites, they have not been framed within the larger distribution range of the species nor accounted for the possibility of eels migrating faster when they reach the estuary to compensate for the delay.

Combining seaward migrating silver eel data from different tracking studies in freshwater and transitional areas over a large geographical scale, including the potential impacts of WRS, allows for quantitative and statistical analyses of fundamental migration parameters, such as migration speed and migration period. This will provide a detailed insight into the migration phenology of the species across its distribution and can aid management strategies for improved protection of eels during their spawning migration through fresh and transitional waters. Specifically for the European eel, the insights can be used to improve the implementation of Eel Management Plans (EMPs) developed under the European Eel Regulation (EC 1100/2007) by, for instance, identifying the migration period and therefore the time period when actions for successful silver eel escapement are most desired. Also, knowledge on the migration speeds in systems with and without WRS can help future studies to determine if silver eels are delayed relative to this meta-analysis. Particularly, the regulation imposes a management requirement of at least 40% escapement of the pristine spawning biomass, defined as the best estimate of the theoretical escapement rate if the stock were completely free of anthropogenic influences. Furthermore, the results could inform management measures to protect eels worldwide because of the 19 *Anguilla* species and subspecies, 13 have a threatened status according to IUCN (near threatened, vulnerable, endangered or critically endangered) (Jellyman 2022). Their population declines are attributed, in part, to migration barriers, noting that other anthropogenic factors such as overfishing, habitat degradation, pollution, introduced non-native species and climate change play an important role too (Drouineau et al. 2018; Jellyman 2022; Pike et al. 2020).

When studying animal migration, it is crucial to identify whether or not the animal is definitely in a migratory state because all animals switch between different movement behaviours (such as ranging behaviour, station keeping and migration) at different times of year or in their life cycle (Dingle 2014; Dingle and Drake 2007). These different movement behaviours are often controlled by variations of environmental parameters (Dingle and Drake 2007). Studies of diadromous fish species often consider their test subjects to be in a particular movement state based on the morphological features and environmental contexts, such as the timing and/or location of capture. In European eels, the seaward migrating silver stage of the European eel has very specific characteristics such as enlarged eyes and pectoral fins, a dark grey to metallic blue dorsal side, a silvery-white abdomen and black neuromasts along the lateral line (Acou et al. 2005). This has led to indices to determine if the eel has reached the silver stage or not (Durif et al. 2005; Pankhurst 1982). Although these morphological features are often the only available method to identify whether or not an eel is in a potential migratory state, in the case of telemetry studies, the movements of individuals can provide a more robust approach. Specifically, the movement tracks can help to determine if an eel in freshwater and/or transitional systems is genuinely on its seaward spawning migration or instead simply moving downstream in search of suitable habitat.

In this study, we combined downstream migrating silver eel data from 18 water bodies in nine countries distributed along the southwest–northeast Atlantic axis of Europe and the Baltic Sea. The large sample size used in this study (2306 tagged eels) covering a diversity of freshwater and transitional water body types and geographical locations allowed us to design a migration classification method capable of identifying the eel's migratory state. To gain insight into the eel's phenology, we subsequently investigated if the arrival at sea time and migration speed (to the furthest downstream detection station) differed according to eel size, WRS impact and geographical location at a continental scale for downstream migrating silver eels. Finally, we assessed differences in migration speed between tidal and non-tidal sections of each water body, taking into account the impacts of WRS.

2 | Methods

2.1 | Study Area

Data from 18 water bodies and nine countries distributed along the southwest-northeast Atlantic axis of Europe and the Baltic Sea were combined in this meta-analysis: Portugal ($n=1$), France ($n=2$), the United Kingdom ($n=3$), Belgium ($n=4$), the Netherlands ($n=4$), Germany ($n=1$), Denmark ($n=1$), Lithuania ($n=1$) and Norway ($n=1$) (Figure 1). Water body types included rivers, lakes, estuaries, fjords, canals and polders which flow into the Baltic Sea, the English Channel, the North Sea, the Norwegian Sea and the Atlantic Ocean (Table 1). Thirteen water bodies contained WRS such as weirs, sluices, hydropower plants with turbines, shipping lock complexes and water pumping stations (or a combination thereof), potentially hindering downstream migrating eels, whereas the remaining five had no physical WRS. Maps of each water body, including the WRS, are found in the online Supporting Information (Figures S1–S18).

2.2 | Telemetry and Tagging

In this study, two types of telemetry were used: acoustic telemetry and the Nedap Trail System. Both techniques use detection devices at specific locations that act as detection stations for moving tagged objects, resulting in Eulerian data (Merki and Laube 2012). Acoustic telemetry refers to acoustic transmitters that emit a unique ID in a fish that can be detected by autonomous functioning receivers; here the systems were operated at a frequency of 69 kHz. The detection range is, on average, 200–300 m, but it is influenced by environmental factors (e.g., wind action, currents, bathymetry, sediment type but also the river bank type and embankment (Bruneel et al. 2023; Kessel et al. 2015; Reubens et al. 2019)).

The Nedap Trail System is a type of radio telemetry that relies on inductive coupling between an antenna loop placed on the bottom

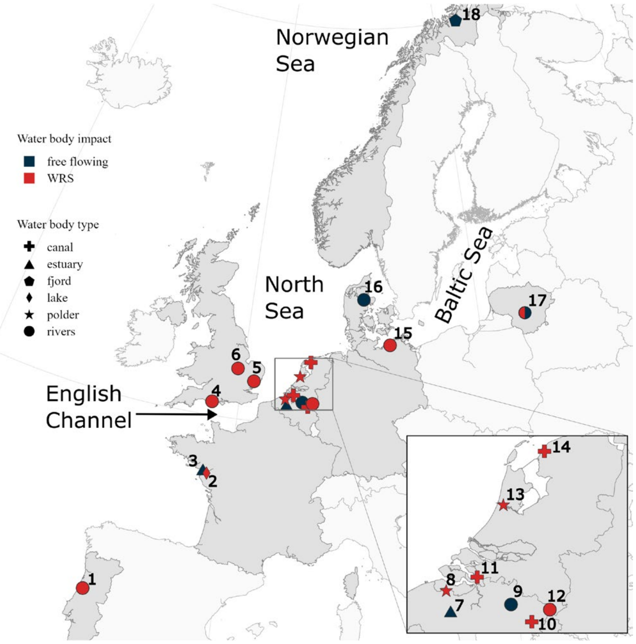

FIGURE 1 | Map of Europe with the nine countries where data were collected indicated in dark grey. The 18 water bodies (1–18) of the different study sites are coloured according to their impact on migration downstream of the eels' release location: Free-flowing systems (black) and systems with water regulating structures (WRS; red). In Lithuania (nr. 17), eels were released in both a free-flowing and a WRS-impacted section of the river basin. The water body type is indicated by a specific symbol at the release locations of the eels. See Table 1 and Figures S1–S18 for more information on each water body.

of the waterbody and the transmitters in a fish. The antenna stations send a signal every 4 s, which activates a transponder when it moves over the antenna. While activated, the transponder sends its unique ID to the receiver of the antenna station (Breukelaar et al. 1998). Breukelaar et al. (1998) stated that the Nedap Trail System performs well with a maximum antenna length of 550 m, a water depth of 15 m, a transponder passing speed of 5–6 m s^{-1} at maximum and a conductivity of $<6000\,\mu$S cm^{-1}.

We compiled data from 18 studies between 2002 and 2021, comprising positional data from 2306 tagged yellow and silver eels that were tracked between a few months and over 3 years. Most of the eels were silver eels and tracked for a few months, whereas some were yellow eels that turned silver during the tracking period as they migrated to the sea later in the study. Eels were captured using methods appropriate to the species, the water body, and season; then those suitable for tagging were identified and tagged under anaesthetic. When anaesthetised, the total length (TL) of the eels was measured to the nearest millimetre and the weight to the nearest gram (eels from the Noordzeekanaal, Markiezaatsmeer and Suderpolder were not weighed). Fifty-nine silver eels were considered males given that their TL was ≤ 450 mm, as Durif et al. (2005) observed that male silver eels did not grow larger than that size and females were never smaller than 450 mm. The transmitters were placed in the abdominal cavity through an incision of 1–3 cm in length. The incision was closed via two or three sutures with surgical thread or commercial-grade

TABLE 1 | Characteristics of the 18 water bodies and the studied eels.

Water body number	Water body name	Water body description	WRS type (number)	Water body class	Country	Range study area (km)	Marine body of drainage	Study period	Fishing method	Kept in captivity > 24 h	Anaesthesia	Number of tagged eels	Number of migratory eels	Number of migratory eels reaching the sea in study period (proportion in %)	TL (mm) migratory eels	W (g) migratory eels	Sex migratory eels: Male	Sex migratory eels: Female
1	Mondego	River into estuary	Weir (6)	B	PT	75	Atlantic Ocean	26/10/2014–04/02/2016	Electrofishing	Yes	0.8 mL/L 2-phenoxy ethanol	40	20	18 (90)	399 ± 99 (328–650)	138 ± 157 (53–566)	17	3
2	Grand Lieu Lake	Lake via canal into estuary	Weir (2) and sluice (4)	B	FR	79	Atlantic Ocean	25/09/2015–01/12/2016	Fyke nets	Yes	150 mg/L benzocaine	48	12	10 (83)	730 ± 37 (683–793)	765 ± 125 (554–1053)		12
3	Loire	Estuary	None	A	FR	104	Atlantic Ocean	25/11/2010–23/03/2012	Stow and trammel nets	Yes	40 mg/L methomidate	89	50	50 (100)	807 ± 85 (581–1030)	976 ± 349 (355–2170)		50
4	Frome	River into estuary	Weir (4)	B	UK	14	English Channel	21/10/2014–09/01/2015	Eel rack	No	0.4 mL/L 2-phenoxy ethanol	50	47	46 (98)	467 ± 91 (342–671)	215 ± 133 (75–560)	21	26
5	Stour	River into estuary	Weir (5)	B	UK	24	North Sea	19/11/2013–26/02/2015	Fyke nets	Yes	200 mg/L benzocaine	86	81	78 (96)	620 ± 76 (500–884)	461 ± 194 (208–1498)		94
			Weir (3)	B								14	13	13 (100)				
6	Nene	River into estuary	Weir (9)	B	UK	81	North Sea	31/10/2014–28/12/2014	Eel rack	Yes	200–300 mg/L benzocaine	19	19	15 (79)	785 ± 79 (610–884)	1231 ± 388 (709–1928)		19
7	Scheldt	Estuary	None	A	BE—NL	162	North Sea	17/04/2015–15/01/2021	Fyke nets	No	0.2–0.3 mL/L clove oil	126	86	76 (88)	707 ± 75 (575–920)	734 ± 238 (417–1318)		86
8	Leopold canal	Polder into estuary	Pumping station (1) and sluice (1)	E	BE—NL	51	North Sea	03/07/2012–29/10/2015	Fyke nets	No	0.3 mL/L clove oil	96	54	34 (63)	682 ± 75 (556–874)	671 ± 262 (310–1615)		56
			weir (1)	B									2	2 (100)				
9	Grote Nete	River into estuary	None	A	BE—NL	169	North Sea	02/10/2019–27/02/2021	Fyke nets	No	0.2–0.3 mL/L clove oil	39	34	33 (97)	673 ± 86 (423–798)	582 ± 216 (141–1075)	1	33
10	Albert canal	Shipping canal into estuary	Shipping lock (5)	D	BE–NL	288	North Sea	18/10/2013–24/08/2018	Fyke nets	No	0.2–0.3 mL/L clove oil	12	4	0 (0)[a]	842 ± 69 (620–1020)	1235 ± 312 (522–2241)		132
			Shipping lock (6)	D								5	5	4 (80)[a]				
			Shipping lock (7)	D								127	123	21 (17)[a]				

(Continues)

TABLE 1 | (Continued)

Water body number	Water body name	Water body description	WRS type (number)	Water body class	Country	Range study area (km)	Marine body of drainage	Study period	Fishing method	Kept in captivity > 24 h	Anaesthesia	Number of tagged eels	Number of migratory eels	Number of migratory eels reaching the sea in study period (proportion in %)	TL (mm) migratory eels	W (g) migratory eels	Sex migratory eels: Male	Sex migratory eels: Female
11	Markiezaatsmeer	Shipping canal into estuary	Sluice (2)	B	NL	83	North Sea	11/01/2018–14/05/2019	Fyke nets	No	0.9 mL/L 2-phenoxy ethanol	25	14	11 (79)	679 ± 32 (632–756)	NA		14
12	Meuse	River into estuary	Hydropower (7)	C	NL	272	North Sea	04/09/2002–23/12/2017	Fyke nets	Yes	0.9 mL/L 2-phenoxy ethanol	895	584	283 (48)	817 ± 80 (532–1060)	1141 ± 336 (520–2567)		584
13	Noordzeekanaal	Shipping canal and polder	Shipping lock (1)	D	NL	76	North Sea	29/09/2017–27/03/2018	Fyke nets	Yes	0.9 mL/L 2-phenoxy ethanol	125	78	56 (72)	821 ± 88 (537–1130)	NA		142
			Shipping lock (2)	D								64	21	14 (67)				
			Pumping station (1) and shipping lock (1)	E								115	43	20 (47)				
14	Suderpolder	Shipping canal	Shipping lock (1)	D	NL	12	North Sea	11/06/2018–15/05/2019	Fyke nets	Yes	0.9 mL/L 2-phenoxy ethanol	25	3	0 (0)	652 ± 63 (597–721)	NA		3
15	Warnow	River	Weir (1)	B	DE	46	Baltic Sea	18/06/2011–19/04/2012	Stow nets	Yes	0.1 mL/L clove oil	143	108	87 (81)	746 ± 85 (600–1010)	829 ± 304 (457–1750)		107
16	Gudena	River	None	A	DK	51	Baltic Sea	10/05/2004–28/04/2006	Wolf trap	Yes	5 mg/L methomidate	68	59	20 (34)	676 ± 88 (570–900)	583 ± 237 (301–1274)		59
17	Nemunas (and tributaries Sventoji, Neris and Zeimena)	River	None	A	LT	567	Baltic Sea	20/05/2014–05/01/2015	Fyke nets	No	0.8 mL/L 2-phenoxy ethanol	45	22	12 (55)	744 ± 70 (600–880)	777 ± 234 (411–1376)		33
			Hydropower (1)	C								25	11	10 (91)				
18	Alta	River into fjord	None	A	NO	36	Norwegian Sea	03/10/2007–09/11/2007	Wolf trap	Yes	40 mg/L methomidate	25	22	22 (100)	643 ± 55 (480–725)	437 ± 117 (204–681)		22

Note: A brief description per water body is given, including the type of water regulating structures (WRS), water body class (class A: free-flowing water bodies without WRS; class B: rivers, lakes and canals regulated by weirs and sluices; class C: rivers with hydropower plants and weirs; class D: shipping canals with shipping locks; class E: polders with water pumping stations), its studied length, marine area in which the water body drains and the study period. The fishing method is given and whether the eels were kept in captivity for more than 24 h, together with the applied anaesthesia. Both the total number of tagged eels as the number of migratory eels are reported. Of the migratory eels, the number and proportion (in %) are given, the mean ± SD (min–max) total length (TL) and weight, and the sex.

[a]Potential underestimation of eels from the Albert Canal reaching the North Sea since the route to the River Meuse was not completely covered and therefore the success of Meuse migrants was impossible to estimate. Yet, the study on the River Meuse showed that only 48% of the eels were able to reach the sea.

cyanoacrylate adhesive (Baras and Jeandrain 1998; Thorstad et al. 2013). In one study (the River Frome), eels were instead tagged by gastric implantation. At some sites, eels were tagged and released upon capture, while at others they were kept in holding facilities for > 24 h to monitor tagging survival and wound healing. Full details on fishing and handling methods, the anaesthetics used, the number of eels tagged per water body and other information are given in Table 1. The release locations, position of the detection stations and both transmitter and detection station specifications per water body are found in the online Supporting Information (Figures S1–S18; Table S1).

The ratio of transmitter weight to fish body weight did not exceed 5%. While we do not have weight information for 400 eels, the minimum weight of those eels was estimated to be 220 g based on the length-weight relationship of the other 1906 eels (Figure S19). Hence, we assumed that the 5% ratio was not exceeded given the documented TL and the weight of the implanted transmitters. Although this 5% ratio is higher than the commonly applied 2% rule (Winter 1983), the studies have shown that fish can tolerate higher tag weights in relation to the total body weight (Brown et al. 1999; Childs et al. 2011; Jepsen et al. 2004).

2.3 | Classifying Migratory State

A three-stage expert validation procedure was applied to identify if eels were in a migratory state. First, eels that did not move more than a net distance of 4 km during the total tracking period were excluded, as several studies have shown that the average home range of non-migratory, foraging yellow eels is 4 km or less (Baras et al. 1998; Verhelst, Reubens, et al. 2018; Walker et al. 2014). Consequently, it is difficult to distinguish between migratory and non-migratory movements in these cases. Second, we used expert judgement to classify the date eels became migratory by looking at detection positions over time and identifying a 'migratory event' or migration. An eel was considered migratory from that moment onwards until it reached the sea or its most downstream detection (Figure 2). The rationale behind this is that eels may temporarily halt their migration due to environmental factors (e.g., reduced migration cues) or search behaviour near the WRS (Besson et al. 2016; Stein et al. 2016; Trancart, Feunteun, et al. 2018; Trancart, Tétard, et al. 2018; Trancart et al. 2022; Verhelst, Buysse, et al. 2018). Third, to validate the expert judgement, we used two threshold criteria to classify the onset of migration: movement distance and speed. We tested combinations of values of these two thresholds (i.e., distance thresholds of 1 km, 3 km, 4 km, 5 km and 7 km, and speed thresholds of 0.01 m s^{-1}, 0.05 m s^{-1} and 0.10 m s^{-1}) to classify the migratory state (Figure S20).

In stage three, the thresholds of 4 km and 0.01 m s^{-1} were the best criteria as they resulted in the lowest number of misidentifications between the expert judgement of stage two and the analytical approach; see Figure S20 for an overview of misidentifications per combination of movement distance and speed threshold checked. There were two types of misidentifications: eels that were analytically identified as migrants but not by expert judgement ('overselected' migrants) and eels that were not analytically identified as migrants but were by expert judgement ('underselected' migrants). Overselected eels did not show a downstream migration pattern, but rather ranging behaviour over a large area with even seasonal movements (e.g., eel A69-1601-52665 in Figure S21). Underselected eels were classified as migrants in the expert review stage because, although their behaviour did not trigger the thresholds, they reached the sea or travelled a significant distance downstream (i.e., > 10 km).

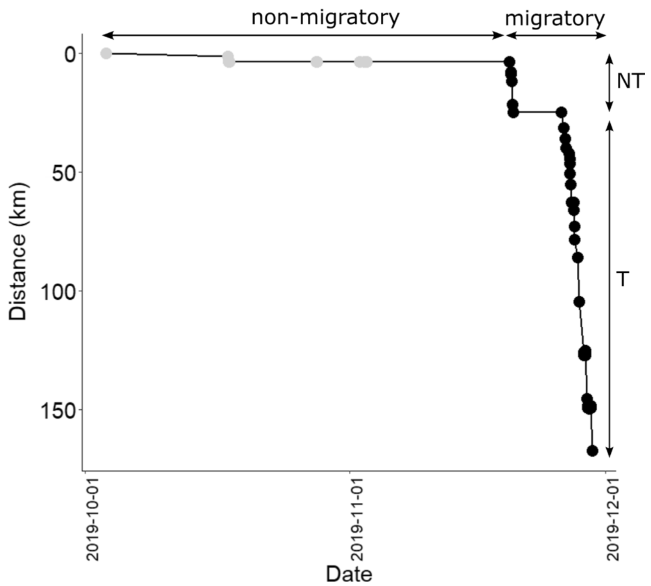

FIGURE 2 | Example of an eel track (ID: A69-9006-3976) from the River Grote Nete (Belgium) with dots indicating the detections at detection stations. The *y*-axis shows distance from release position of the tagged eel, where distances illustrate downstream movement. The eel was tagged and released on 3 October 2019 but was only identified as migratory from 19 November 2019 onwards until its last detection at the mouth of the Scheldt Estuary on 29 November 2019 (black dots); the non-migratory part of the track is indicated with grey dots. The part of the trajectory in a non-tidal, freshwater river is indicated by 'NT' and the part in a tidal habitat by 'T'.

Nine overselected migrants (1% from migratory eels using the identification method) from the Scheldt Estuary were excluded from the analysis (Figure S21). The 75 underselected migrants (5% from the migratory eels based on expert judgement) were also excluded from the analysis. Consequently, of the 2306 tagged eels, we judged 1589 migrated downstream and the identification method retained 1514 eels to include in the analysis (Table 2).

2.4 | Data Analysis

To gain insight into the eel's phenology, two response variables were studied: the arrival at sea time (reflecting the migration period) and the migration speed (measured from first to last detection during the migratory phase). For the analysis of migration speed, we split the water bodies into tidal ($n = 13$)

TABLE 2 | The number of identified downstream migratory eels based on expert judgment and the identification method according to the water body.

Water body	Number of tagged eels	Number of migratory eels—expert judgement	Number of migratory eels—identification method	Overselected migrants	Underselected migrants	Identification accuracy (%)
Mondego	40	21	20		1	95
Grand Lieu Lake	48	12	12			100
Loire	89	50	50			100
Frome	50	47	47			100
Stour	100	94	94			100
Nene	19	19	19			100
Scheldt	126	86	95	9		110
Leopold canal	96	57	56		1	98
Grote Nete	39	35	34		1	97
Albert canal	144	134	132		2	99
Markiezaatsmeer	25	14	14			100
Meuse	895	627	584		43	93
Noordzeekanaal	304	165	142		23	86
Suderpolder	25	5	3		2	60
Warnow	143	108	107		1	99
Gudena	68	60	59		1	98
Nemunas (and tributaries Sventoji, Neris and Zeimena)	70	33	33			100
Alta	25	22	22			100

Note: The number of over- and underselected migrants is indicated as well as the identification accuracy of the method.

and non-tidal habitats ($n = 15$) (Figure 3). Because the Baltic Sea has a very limited tidal amplitude (max 23 cm) (Medvedev et al. 2016), rivers draining into it were considered non-tidal. The response variables were statistically related to eel size (i.e., TL), geographical location, and the impact by WRS. We used release latitude as a proxy for the geographic location of eels (release latitude and longitude were strongly correlated (Pearson cor = 0.75)). To assess the impact by WRS, we categorised the water bodies of non-tidal habitats into five classes depending on the WRS type (Table 1). The number of water bodies per class is indicated between brackets.

Class A: free-flowing water bodies without WRS ($n = 3$)

Class B: rivers, lakes and canals regulated by weirs and sluices ($n = 8$)

Class C: rivers with hydropower plants and weirs ($n = 2$)

Class D: shipping canals with shipping locks ($n = 3$)

Class E: polders with water pumping stations ($n = 2$)

To analyse the impact of the WRS on tagged eels, we only considered those WRS in the water body within the range of the tracking network. All data processing and analyses were conducted using the free R-software environment (R Core Team 2023).

2.4.1 | Arrival at Sea Time

The arrival at sea time was defined either as the day on which successful migrants were detected in the lower section of the tidal area, or as the day of a detection at a station downstream of a tidal WRS in cases where there was no extensive tidal area included in the acoustic receiver network (i.e., Noordzeekanaal, Suderpolder and a particular route taken by two eels in the Leopold Canal). We made an exception in the case of the Scheldt Estuary: eels were considered successful if they were detected at the border between the Netherlands and Belgium, which is halfway along the estuary (Figure S7). Beyond the border, the distance between the detection stations exceeded the average detection range

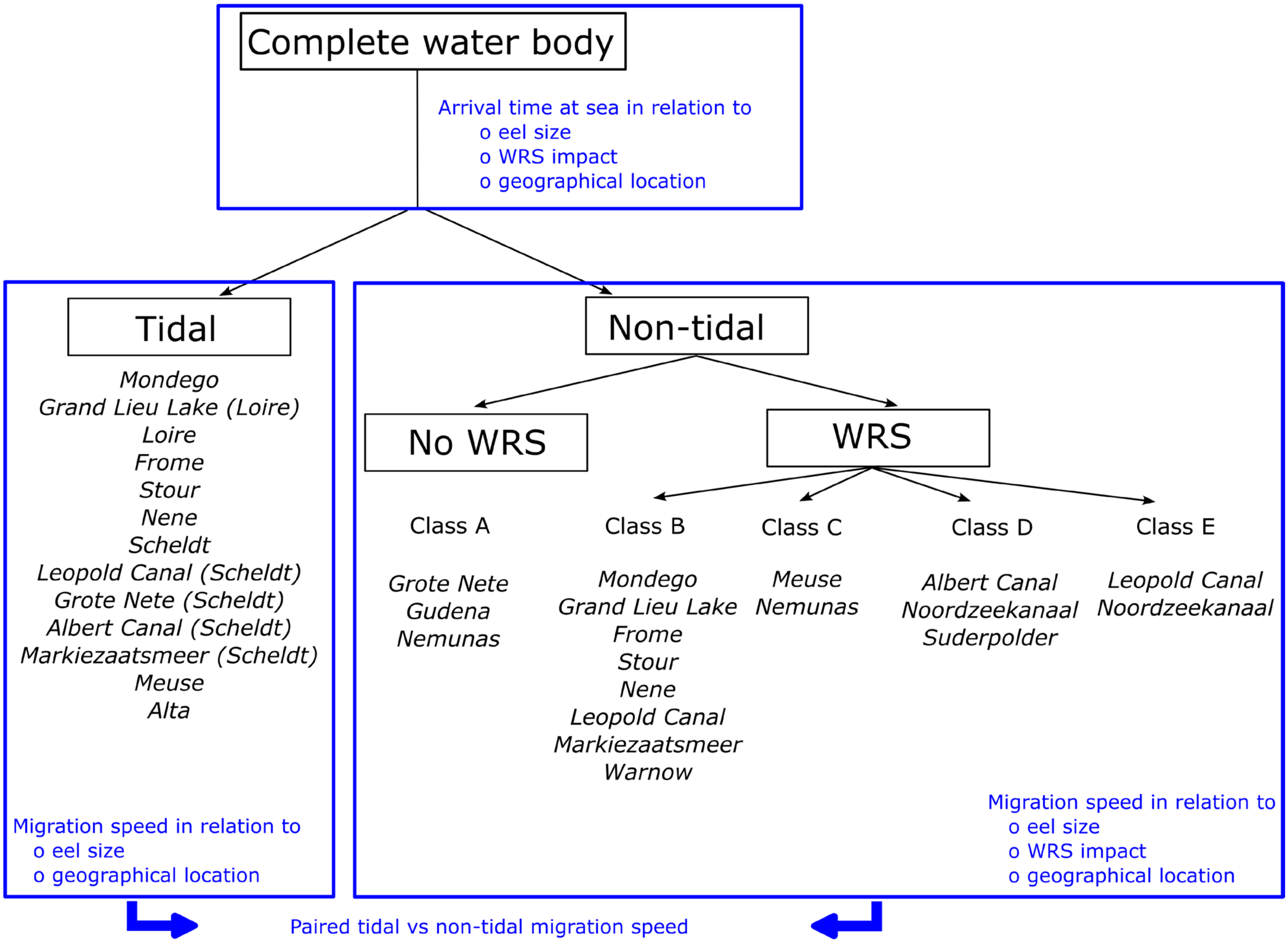

FIGURE 3 | Overview of the data analysis flow. Tracking data from the complete water body were used to analyse the arrival at sea time in relation to eel size, water regulating structures (WRS) impact and geographical location. Next, we split the water bodies into their tidal and non-tidal habitats to analyse the migration speed in relation to eel size, geographical location and the impact of WRS in the non-tidal part. The estuary name is given between brackets in case its name differed from the water body where the eels were released. Finally, we compared the migration speed in tidal and non-tidal habitats within the same water body. The WRS impact was taken into account by categorising the water bodies into five classes according to the presence of WRS: A = no WRS, B = weirs and sluices, C = hydropower plants with weirs (and in case of the River Meuse shipping locks), D = shipping canals with shipping locks and E = polders with water pumping stations.

(> 300 m), making it plausible that some eels passed undetected (Verhelst, Bruneel, et al. 2018), in particular because dynamic tidal currents and waves can significantly reduce the detection range (Bruneel et al. 2023; Edwards et al. 2024; Merk et al. 2023; Reubens et al. 2019). The arrival day at sea was calculated as the day after 1 June to centralise the main migration period given autumn and winter are the general migration periods for silver eels in the largest part of the considered study area.

The arrival at sea time was fitted as the response variable into a linear mixed model (LMM) with eel size, latitude of release as a proxy for geographic location, and water body class as explanatory variables in the fixed effects part of the LMM. Eel size was nested within the water body as a random slope because there was a significant dependence between both variables (Kruskal–Wallis test, $\chi^2 = 735.94$, df = 16, $p < 0.0001$). Hence, the full LMM had the following structure:

$$\text{arrival at sea time} \sim \text{eel size} + \text{releaselatitude} + \text{waterbodyclass} + (\text{eel size} \mid \text{waterbodyname})$$

We applied a stepwise backward selection procedure and retained the model with the lowest AIC, indicating the best fit without too much complexity. This resulted in the removal of the variable ‘water body class’. The ‘nlme’ R package was used to apply the LMM (Pinheiro et al. 2000; R Core Team 2023).

2.4.2 | Migration Speed

The migration speed was calculated as the distance moved along the water body from the most upstream detection station to the most downstream station divided by the time, once an eel was considered to be migrating. We calculated this speed for the tidal and non-tidal habitats per water body. For each habitat, a LMM was constructed with eel size nested within the water body as a random slope because of the dependency between both variables. Migration speed in the LMMs was tested against eel size and release latitude as a proxy for geographical location, while the water body classification was also added to the non-tidal LMM as only the non-tidal part of the water bodies had WRS. Note that the number of water bodies within each water body classification differed (Figure 3). The migration speed was log-transformed for both the tidal and non-tidal LMMs to improve the normal distribution and homogeneity of variances of the model residuals. The full LMM for the tidal and non-tidal habitats was as follows:

$$\text{Tidal: log(migrationspeed)} \sim \text{eel size} + \text{releaselatitude} + (\text{eel size} \mid \text{waterbodyname})$$

$$\text{Non} - \text{tidal: log(migrationspeed)} \sim \text{eel size} + \text{releaselatitude} + \text{waterbodyclass} + (\text{eel size} \mid \text{waterbodyname})$$

After a stepwise backward selection based on AIC, eel size was removed from the tidal LMM and release latitude from the non-tidal LMM. For the latter model, a Tukey multiple comparison test was used to compare the different groups (i.e., water body classes) using the 'multcomp' R package. The 'nlme' R package was used to apply the LMM (Pinheiro et al. 2000).

Finally, for each water body separately, we analysed if the migration speed of eels in non-tidal and tidal habitats differed using paired samples *t*-tests. Eels were tracked through both habitat types in 10 water bodies, i.e., the Mondego, Grand Lieu Lake, Frome, Stour, Nene, Leopold Canal, Grote Nete, Albert Canal, Markiezaatsmeer and Meuse.

3 | Results

3.1 | Arrival at Sea Time

Across all water bodies studied, the average ± SD period when eels arrived at sea was 142 ± 98 days after 1 June (or 21 October) (range: 30–360 days) (Figure 4). While the time period of escapement was relatively well defined (range < 90 days) for the majority of the water bodies, almost a year-round arrival at sea was observed for the rivers Warnow and Meuse, and the Albert Canal. The final LMM indicated that eels from higher latitudes arrived at sea significantly earlier, with each degree of increasing latitude corresponding to an arrival approximately 4 days earlier. In consequence, there was a difference of between two to 3 months in the escapement time of eels from northern Norway and rivers draining into the Baltic Sea compared with eels leaving rivers that drain into the Atlantic Ocean (Figure 4 and Table 3; see Figure S22 for model diagnostics). There was a small but significant positive effect of eel size, meaning that larger eels tended to migrate later.

3.2 | Migration Speed

3.2.1 | Migration Speed Within Tidal and Non-Tidal Habitats

The highest migration speeds were observed in tidal systems with an average ± SD of $0.45 \pm 0.93\,\mathrm{m\,s^{-1}}$. Eel size and geographical location did not affect the speeds as the LMM for tidal habitat did not retain eel size after the stepwise backward selection, and the geographical location was not significant (LMM, t-value $= -0.46$, $p = 0.65$) (see Figure S23 for model diagnostics). The migration speed in non-tidal habitat was on average $0.15 \pm 0.25\,\mathrm{m\,s^{-1}}$. Eel size did not have a significant effect either according to the LMM for non-tidal habitat, but the water body class did (Table 4; see Figure S24 for model diagnostics). Furthermore, the Tukey's multiple comparison test indicated that the migration speeds of eels from water body classes A to D were significantly faster than those of eels from water body class E (Table 5; see Figure S25 for the 95% confidence intervals).

Migration speed summary values such as the mean, median and range in tidal and non-tidal habitats, with the latter divided into the five water body classes A–E, are shown in Table 6. An overview of the migration speeds for the different water bodies in non-tidal habitats according to the water body classes is found in Figure S26.

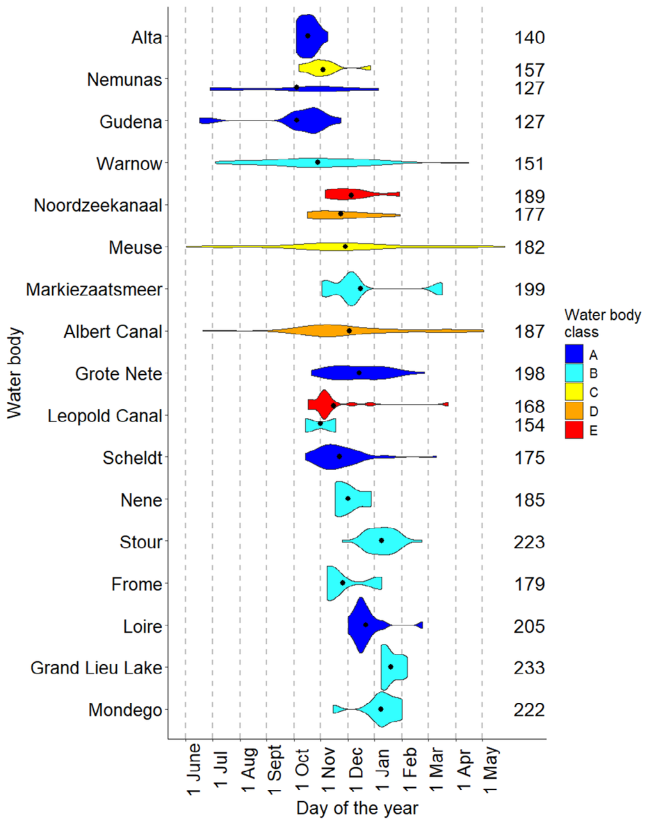

FIGURE 4 | Violin plots illustrating the relative number of eels per water body and water body class arriving at sea throughout the year. The water bodies are ranked according to their latitude (highest at the top and lowest at the bottom) and the water body classes are given a specific colour. The black dots and values on the right side of the plot represent the mean day of arrival at sea after 1 June for each water body.

TABLE 3 | Fixed effects output of the final linear mixed model of the arrival at sea time in relation to the geographical location (i.e., release latitude) and eel size.

Variable	Estimate	SE	df	*t*-value	*p*
Intercept	355.08	59.08	913	6.01	**< 0.0001**
Release latitude	−4.14	1.05	913	−3.96	**0.0001**
Eel size	0.05	0.02	913	2.28	**0.02**

Note: The output shows the model estimates with their standard error (SE), as well as the number of degrees of freedom (df), *t*-value, and *p*-value. Significant ($p < 0.05$) differences are indicated in bold.

TABLE 4 | Fixed effects output of the final non-tidal linear mixed model of the log-transformed migration speed in relation to eel size and water body classes (B–E).

Variable	Estimate	SE	df	*t*-value	*p*
Intercept	−3.50	0.50	1323	−6.95	**< 0.0001**
Eel size	0.001	0.001	1323	1.84	0.07
Class B	−0.08	0.47	1323	−0.17	0.86
Class C	0.03	0.43	1323	0.07	0.94
Class D	−0.95	0.56	1323	−1.68	0.09
Class E	−2.10	0.57	1323	−3.66	**< 0.001**

Note: The output shows the model estimates with their standard error (SE), as well as the number of degrees of freedom (df), *t*-value, and *p*-value. Significant ($p < 0.05$) differences are indicated in bold.

TABLE 5 | Output from the Tukey's multiple comparison test following a significant linear mixed model on the log-transformed migration speed of eels in non-tidal habitat according to water body class (A–E).

Group comparison	Estimate (log-scale)	SE	*z*-value	*p*
Class A—class B	−0.01	0.47	−0.17	1.00
Class A—class C	0.03	0.43	0.07	1.00
Class A—class D	−0.95	056	−1.68	0.42
Class A—class E	−2.09	0.57	−3.66	**< 0.01**
Class B—class C	0.11	0.48	0.23	1.00
Class B—class D	−0.87	0.46	−1.88	0.31
Class B—class E	−2.01	0.46	−4.32	**< 0.001**
Class C—class D	−0.98	0.58	−1.69	0.42
Class C—class E	−2.12	0.58	−3.63	**< 0.01**
Class D—class E	−1.14	0.26	−4.39	**< 0.001**

Note: The output shows the model estimates with their standard error (SE), as well as the *z*-value and *p*-value. Significant ($p < 0.05$) differences are indicated in bold.

3.2.2 | Migration Speed Between Tidal and Non-Tidal Habitats

Finally, we analysed if the migration speed in tidal and non-tidal habitats differed within each water body. Of the 10 water bodies where eels moved through both habitats, four had a significantly higher migration speed in the tidal habitat compared with the non-tidal habitat (Figure 5 and Table 7). One of these water bodies was the River Frome, and the other three (i.e., Leopold Canal, Albert Canal and Markiezaatsmeer) were all water bodies draining into the Scheldt Estuary; the River Frome drained into the Frome Estuary.

4 | Discussion

4.1 | Migration Identification Method

Telemetry studies have shown that tagged silver eels do not always migrate immediately after release, which can be caused by various effects such as the tagging procedure itself (i.e., recovery time), or because the appropriate migration conditions are no longer met, such as an increased river water flow and decreased water temperatures (Bultel et al. 2014; Verhelst, Bruneel, et al. 2018; Vøllestad et al. 1986, 1994). Consequently, considering external morphometrics alone to classify eels as migrants in a telemetry study may result in underestimates of migration speeds and escapement rates to the sea. Therefore, an identification method that selects the migration behaviour based on behavioural characteristics is much more likely to provide accurate results. Such a method can also be applied to eel species for which the silvering characteristics are less clear, such as tropical species (Hagihara et al. 2012).

Movement-based identification methods have previously been applied to identify whether the tracked eels are migratory or not. These methods include passing through a defined number of sequential detection stations, a specific distance covered, or based on residence time (Stein et al. 2016; Trancart et al. 2022; Verhelst, Bruneel, et al. 2018; Verhelst, Buysse, et al. 2018). However, the use of different identification methods between studies can make it difficult to compare results. Consequently, the application of a general movement-based identification method can be valuable for future telemetry studies but requires a definition of what is considered migratory. In this meta-analysis, we applied different distance and speed thresholds to a pan-European tracking dataset of 2306 tagged yellow and silver eels. We found that when eels started migrating a minimum distance of 4 km at a speed of $0.01\ \mathrm{m\,s,}^{-1}$ this matched well to the expert judgement applied in the identification method, with an identification agreement of 95%. Use of these criteria resulted in the selection of 1514 migratory eels. When a lower distance threshold was used, the algorithm selected eels that were not migratory (i.e., overselection) and were likely moving within a home range, as the average home range of eels can be 4 km or less (Baras et al. 1998; Verhelst, Reubens, et al. 2018; Walker et al. 2014). In contrast, when the distance threshold was > 4 km or the speed threshold $> 0.01\ \mathrm{m\,s^{-1}}$, a lower number of migratory eels was selected (i.e., underselection).

The underestimation by ‘underselected’ migrants was often caused by a relatively sparse detection network. When the detection stations were too far apart (ca. every 15 km or more), they were unlikely to pick up direct downstream movements, but rather downstream movements including pauses in migration, resulting in an underestimation of the progression speed

TABLE 6 | Summary values of the mean with standard deviation (SD), median, minimum and maximum migration speeds (m s^{-1}).

	Mean	SD	Median	Minimum	Maximum
Tidal habitat	0.45	0.93	0.11	< 0.01	5.99
Non-tidal habitat	0.15	0.25	0.04	< 0.01	1.61
Class A	0.11	0.16	0.04	< 0.01	0.79
Class B	0.15	0.19	0.03	< 0.01	0.74
Class C	0.20	0.31	0.06	< 0.01	1.61
Class D	0.08	0.14	0.02	< 0.01	1.01
Class E	0.02	0.03	0.01	< 0.01	0.14

Note: For non-tidal habitats, both the overall values are given as well as the values specific to each water body class (A–E).

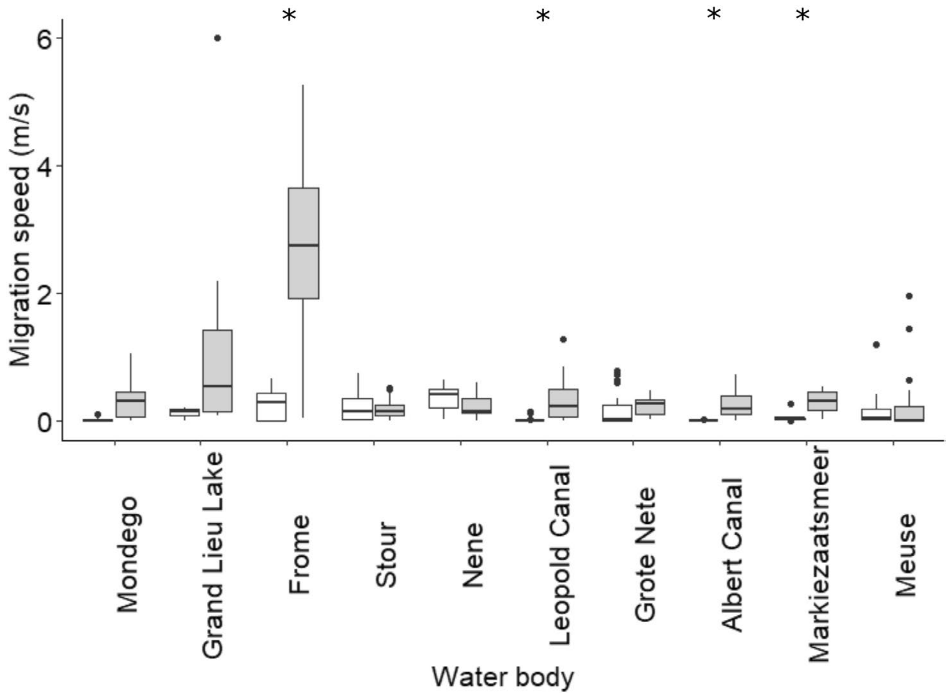

FIGURE 5 | Migration speeds of eels in non-tidal (white) and tidal (grey) habitats per water body. Significant differences ($p < 0.05$) are indicated with asterisks on top of the bar plots.

TABLE 7 | Output of the paired samples *t*-tests per water body showing the estimated difference, *t*-values, degrees of freedom (df), 95% confidence intervals (CI) and *p*-values of the migration speed.

Water body	Estimate	*t*-value	df	95% CI	*p*
Mondego	0.33	2.11	5	[−0.07, 0.74]	0.09
Grand Lieu Lake	1.26	1.56	6	[−0.72, 3.25]	0.17
Frome	2.45	12.39	43	[2.05, 2.85]	**< 0.0001**
Stour	−0.02	−0.6	84	[−0.07, 0.04]	0.55
Nene	−0.11	−1.85	16	[−0.25, 0.02]	0.08
Leopold Canal	0.31	5.03	28	[0.18, 0.43]	**< 0.0001**
Grote Nete	0.07	1.49	33	[−0.02, 0.16]	0.15
Albert Canal	0.26	6.76	25	[0.18, 0.33]	**< 0.0001**
Markiezaatsmeer	0.25	4.62	8	[0.12, 0.37]	**< 0.01**
Meuse	0.07	0.7	29	[−0.13, 0.27]	0.49

Note: Significant ($p < 0.05$) differences are indicated in bold.

and hence failure to select the eels as migrants. Therefore, we suggest deploying detection stations at least every 10 km to have a good migration behaviour resolution when applying this method. Obviously, this method will not classify eels that are tracked over distances <4 km. Importantly, when eels are tracked in relation to WRS they must be released at least 4 km upstream of the structure (preferably more) so that the movement-based identification method can determine whether the eel was considered migratory before approaching the WRS. Indeed, this was not always the case in our dataset (e.g., the Grand Lieu Lake, the Noordzeekanaal and River Nemunas), so it is likely that some of the 792 eels not selected as migratory were migrating but not identified as such because their migration was abruptly stopped by a WRS, such as a pumping or hydropower station, less than 4 km upstream, causing mortality.

4.2 | Arrival at Sea Time

There was a large variability within water bodies, illustrating considerable plasticity in eel migration timing. The mean arrival at sea time spanned 4 months in autumn and winter (October–January), with eels from northern Europe arriving at sea earlier than conspecifics in the south: eels from the Baltic and Scandinavia arrived at sea 2 to 3 months earlier (October–November) than eels from southern locations, such as Portugal and France (December–February). A large migration period has also been observed for other temperate eel species like the American eel (*A. rostrata*) (Béguer-Pon et al. 2014), Japanese eel (*A. japonica*) (Sudo et al. 2017), the Australian short-finned eel (*A. australis*) and the New Zealand longfin eel (*A. dieffenbachii*) (Todd 1981; Koster et al. 2024). However, although there is limited knowledge on the downstream migration of tropical eels, the few studies suggest that these species migrate all year round (Arai and Abdul Kadir 2017; Hagihara et al. 2018). This indicates that the large plasticity in migration timing could be a common feature among Anguillids.

Particularly water bodies severely impacted by WRS showed an almost year-round arrival at sea, such as the River Meuse and the Albert Canal. Eels that are substantially delayed during their migration may try to continue leaving a water body during periods other than autumn–winter. For instance, in the Albert Canal it was previously observed that eels showed two migration peaks throughout the year, i.e., in autumn and in spring (Verhelst, Bruneel, et al. 2018). An almost year-round arrival period at sea was also observed in the River Warnow, which has a relatively limited water regulating impact. In contrast to the River Meuse and the Albert Canal, the River Warnow is regulated by a single (tidal) weir, which is not expected to have a substantial impact on downstream migrating eels. In fact, eels from other water bodies with multiple weirs had a rather well-defined arrival time period at sea (e.g., eels from the rivers Mondego, Frome and Nene), suggesting a low impact of these weirs. The year-round arrival at sea may be related to the river's hydrology or its geographical location, as eels from other rivers draining into the Baltic Sea also had a relatively long arrival at sea time period, i.e., ca. 5 months for eels from the River Gudena and ca. 6 months for eels from the River Nemunas.

It is unlikely that the differences in arrival at sea times across the geographical distribution of eels are orchestrated to join conspecifics from lower latitudes at sea on their way to the spawning grounds (Als et al. 2011). Therefore, the timing of arrival at sea is probably affected by local environmental variables, including interactions by WRS. Silver eel migration has mainly been linked to increases in river discharge caused by precipitation, decreasing water temperatures and decreasing photoperiod (Reckordt et al. 2014; Travade et al. 2010; Verhelst, Buysse, et al. 2018; Vøllestad et al. 1986, 1994). In particular, water temperature and photoperiod follow a latitudinal trend with lower values occurring earlier in the year at higher latitudes. It is therefore reasonable to assume that these variables cause the seasonal geographical pattern in the migration period and the arrival at sea time. As increased discharge is considered one of the main factors stimulating silver eel migration, the strength of its effect could increase as water temperature and photoperiod become more favourable for silver eel migration.

Furthermore, eels may not reach the spawning grounds for the spawning event estimated to occur in February–May following their departure from continental waters (Miller et al. 2015). The migration speed in the North Sea and adjacent seas is approximately 20 km day^{-1} (the speed ranges between 3 and 47 km day^{-1} (Righton et al. 2016; Verhelst et al. 2022)). Hence, if eels arrive at sea in autumn–winter and they need to migrate 5000–9000 km to reach the spawning grounds, even at a marine speed of 40 km day^{-1} some of them would not arrive by the next spawning season, and at 20 km day^{-1} it will take them approximately 8 to 15 months. Additionally, the lower end of the observed marine migration speed indicates that it will take at least 2 years for some eels to arrive at the spawning grounds. The high variability in arrival time period at sea illustrates a large plasticity and is in accordance with the mixed migratory strategy proposed by Righton et al. (2016) with eels arriving at different times at the spawning grounds rather than as a single cohort. Such a strategy may make the species more resilient to environmental change, especially in continental waters and hence increase the reproductive fitness of the population. Furthermore, as eels may arrive at different moments at the spawning sites, they may wait for a period of time between arrival at the spawning grounds and actual spawning when the density of conspecifics reaches a critical number or when specific environmental characteristics are met. Prespawning waiting behaviour is common in anadromous salmonids which can wait from weeks to months to spawn following arrival at the spawning grounds (Dahl et al. 2004; Hoopes 1972; Morbey and Ydenberg 2003).

4.3 | Migration Speed

The migration speed was highly variable, but overall a slow process, which has also been concluded for other Anguillid species (Béguer-Pon et al. 2014; Noda et al. 2021). Particularly, swim speeds have been reported over 1 m s^{-1}, with optimal speeds around 0.61–0.68 m s^{-1} (Palstra et al. 2008). The observed slow ground migration speeds suggest that eels can take pauses during their downstream migration, as observed in previous studies, or migrate at a pace below the optimal speed (Stein et al. 2016; Verhelst, Bruneel, et al. 2018). The migration speed did not differ according to eel length and was not influenced by the geographical position of the water bodies. However, there were environmental impacts on migration speeds, with speeds in tidal habitats over twice as fast as in non-tidal habitats. When comparing speeds of eels in tidal versus non-tidal habitats within the same water body, 4 of 10 water bodies showed eels with significantly higher speeds in the tidal part. Three water bodies were severely regulated freshwater systems with relatively slow migration speeds, draining into the Scheldt Estuary characterised by strong tidal currents (maximum tidal amplitude of 6 m (Seys et al. 1999)). As with arrival at sea time, it is likely that migration speed is driven by local environmental factors, particularly increased river discharge resulting in higher migration speeds (e.g., Reckordt et al. (2014); Vøllestad et al. (1986)). Various studies have suggested that eels drift passively or semi-passively with the current (Drouineau et al. 2017; Merk et al. 2023). It has been shown that silver eels use selective tidal stream transport in tidal habitats, suggesting that they mainly migrate during the ebb tide to reach the sea (Merk et al. 2023; Verhelst, Bruneel, et al. 2018). Consequently, the migration speeds in tidal habitats might be dependent on the tidal current strengths. However, we did not have information on the tidal current strengths of the different water bodies to link to the observed migration speeds. Despite resting ca. half of the day during the incoming tide, tidal currents can be strong, resulting in high migration speeds during the outgoing tide in estuaries. Particularly, the highest migration speed observed in this study (i.e., 5.99 $m\,s^{-1}$) was from the Frome Estuary. This estuary drains almost completely through very strong ebb currents, making such speeds plausible rather than considering them outliers.

The results of this meta-analysis indicated that the migration speed in non-tidal water bodies is relatively slow, with ground migration speeds ranging from 0.02 to 0.20 $m\,s^{-1}$ and differing between the water body classes. Surprisingly, we only found significant differences in migration speeds between free-flowing water bodies (class A), water bodies with weirs and sluices (class B), rivers with hydropower plants (class C) and shipping canals with shipping locks (class D) to polders with water pumping stations (class E). The reason for this is twofold. The first relies on the methodology: despite analysing 1589 migratory eel tracks, classifying the water bodies results in a low number of replicates between each water body class, with a low number of case studies for classes A ($n=3$), C ($n=2$), D ($n=3$) and E ($n=2$). In addition, although we aimed to classify water bodies, each case study is likely to have a unique (seasonal) hydrodynamic regime but is also dependent on local water management. This is likely at the basis of the immense variability of the observed migration speeds both within and between the water bodies, as silver eel migration speed is likely to be influenced by the strength of water current (Figure S26). Second, not all barriers impacted silver eel migration speed in the same way. It can be argued that weirs and sluices (class B) are not absolute migration barriers for downstream migrating eels as they are opened during peak discharges, i.e., when silver eels are migrating. Hydropower plants (class C), on the other hand, can have severe impacts on downstream migrating eels, such as eel survival and escapement success rate on numbers reaching the sea (e.g., Trancart, Tétard, et al. (2018); Winter et al. (2006)). The two rivers with hydropower turbines included in this study still had natural, seasonal discharge fluxes with water either passing through the turbines or over associated weirs. Yet this study shows that the overall migration speed in these two rivers in our meta-analysis did not differ significantly from the free-flowing rivers and rivers with weirs and sluices. However, this may not be the case for other rivers with hydropower due to differences in water management regimes, hydropower turbine types, downstream passage systems and debris racks. For instance, rivers with large hydropower dams leading to almost lentic systems could cause large delays and, hence, lower migration speeds as it is more difficult for eels to detect the current they use to escape to the sea (Trancart et al. 2020).

The results of the migration speeds for shipping canals (class D) and polders (class E) should also be interpreted with caution, as the hydrodynamics can vary considerably. Silver eel passage and hence migration speed is dependent on shipping lock and water pump operation, which can differ within and between water bodies (e.g., Evans et al. (2024); van Keeken et al. (2020)). If the water flow in the shipping canal or polder is therefore very low, resulting in a weak migration cue for the silver eels, so will their speed (Bolland et al. 2019; Vergeynst et al. 2021; Verhelst, Baeyens, et al. 2018; Verhelst, Buysse, et al. 2018). For instance, shipping locks in canals with intense commercial boat traffic likely open more frequently compared with canals with recreational shipping, and in some canals, the shipping locks are not operated at night, when silver eels mainly migrate (van Keeken et al. 2023). Conversely, sluice operation at pumping stations can be manipulated to maximise safe and timely passage (Carter et al. 2023).

Consequently, the downstream migration speed is likely strongly determined by the hydrodynamics of the water body as observed by numerous studies (e.g., Reckordt et al. (2014); Verhelst, Buysse, et al. (2018); Vøllestad et al. (1986)) and suggested by this analysis, with water bodies that have natural seasonal discharge fluxes and uninterrupted directional currents not causing significant delays in eel migration speed. Because hydrodynamics are water body specific, particularly when they are strongly regulated, it is difficult to assess which water body class causes significant delays. Importantly, a lack of or limited delay does not indicate unhampered downstream migration. Successful escapement to the sea can be strongly affected by migration barriers although the eels' downstream migration speed is not (Besson et al. 2016; Bolland et al. 2019; Buysse et al. 2014; Trancart, Feunteun, et al. 2018; Trancart, Tétard, et al. 2018; Trancart et al. 2020; Verhelst, Baeyens, et al. 2018; Winter et al. 2006). The migration identification method only takes into account the migration speed between the considered onset of migration until the furthest downstream detection. Hence, if an eel is not able to escape into the sea, its migration success is obviously affected, but the speed during the considered migration event could still be similar to other systems with less impacting or no WRS. We did not analyse the escapement success rate in this study, because the study set-up would require too many assumptions, such as fishing intensity (quantitative data not available), and requires eels to be released a minimum of 4 km upstream of the first barrier for the movement-based identification method to identify an eel as migratory. Moreover, the distribution of tagged and released silver eels over the course of a water body might not reflect the true, mostly unknown, underlying distribution of silver eels in that water body starting their seaward migration (Winter et al. 2007). These lead to uncertainties, and perhaps biases, in assessing overall escapement of silver eels to the sea from telemetry studies. In addition, the effects of delays on the eels' physiology and reproductive success are still unknown. It is accepted that silver eels stop feeding as their digestive system degenerates (Chow et al. 2010), suggesting that delayed eels lose precious energy for their trans-Atlantic migration. However, silver eels have been observed to return into a yellow stage in freshwater, probably recommencing feeding as a response to depleted energy reserves (Feunteun et al. 2000).

Nonetheless, to minimise delay for migratory silver eels, management needs to strive for a continuous water current during the peak season of eel migration (i.e., autumn–winter throughout most of the range) and in case of hazardous structures like hydropower turbines and water pumping stations, obviously a safe (i.e., non-lethal and without injuries) passage.

4.4 | Prospects for Future Research to Cover Knowledge Gaps

This continental-scale meta-analysis of downstream silver eel migration is the most comprehensive in terms of geographical coverage and number of eels tagged. The results provide a quantitative overview of the arrival at sea time at a European-wide geography and of downstream migration speeds of eels in five different water body classes, according to the type of WRS. The study therefore provides a reference for the time of arrival at sea and the migration speed, allowing future research to compare and qualitatively assess how much the eels might be delayed. However, despite the comprehensive nature of this study, the number of water bodies within the five WRS classes is limited. Knowledge of delays in water bodies with specific WRS is therefore still needed, together with the potential effects of delays on individual eels, such as migration speed and success of onward migration, and the population. In addition, to investigate escapement success despite the cumulative mortality risks of multiple stressors acting in concert, e.g., impact of fisheries, shipping, different types of WRS and predation, further data mining and analyses of existing datasets for these factors for the different water bodies is warranted, as are more telemetry studies on silver eels to further complement the current large dataset. Such a meta-analysis would allow the relative impacts of these different natural and anthropogenic stressors to be compared and assessed with a level of discrimination that is not possible within individual case studies alone.

There are also major knowledge gaps on the migration behaviour of male silver eels, which are largely absent in current telemetry studies: only 39 of the 1514 migratory eels in this meta-analysis were males due to the female dominance in most of the studied water bodies (Table 1). It has been hypothesised that male silver eels migrate earlier in the season than females to compensate for their assumed slower migration speed due to their smaller size, thus enabling both sexes to arrive at spawning grounds at the same time (Quintella et al. 2010).

Finally, despite the vast distribution area of the European eel, electronic tracking is mainly conducted in the Atlantic region, North Sea, and Baltic Sea. Studies tracking eels from freshwater and transitional systems into the Black Sea and Mediterranean are lacking. There are, however, a handful of studies on marine migration in the Mediterranean Sea (Amilhat et al. 2016; Westerberg et al. 2021) and studies investigating migration in inland systems using cameras (Lagarde et al. 2023). Further research in these regions is encouraged.

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Ethics Statement

All tagged eels comply with the animal welfare regulations of the respective countries. The study in the River Mondego (Portugal) was carried out in strict accordance with the recommendations present in the Guide for the Care and Use of Laboratory Animals of the European Union 62/2010—in Portugal under DL n° 129/92, Portaria n° 1005/92 and DL 113/2013. In the Belgian case studies (i.e., Leopold Canal, Albert Canal and Scheldt Estuary), the tagging method was approved by the Ethical Committee of the Research Institute for Nature and Forest (licences ECINBO05, ECINBO09 and ECINBO11, respectively). The studies in the UK (i.e., Rivers Frome, Stour and Nene) were carried out under the Home Office Project Licence numbers PPL 70/7958 and PPL 30/2684. Also, the studies in the Netherlands used in this paper were in accordance with the use of experimental animals complied with the Dutch animal welfare laws, guidelines and policies as approved by the 'Central Committee Animal experiments'. In the River Warnow (Germany), eel tagging was carried out in compliance with regulations approved by the State Office for Agriculture, Food Safety and Fisheries of MV under docket number 7221.3-1.1-044/10. In the River Gudena (Denmark), eels were tagged in accordance with the guidelines described in permission (2005/561-987) from the Danish Ministry of Justice. In Lithuania, the permit to collect and tag eels was issued by the Environmental Protection Agency under the Ministry of Environment of the Republic of Lithuania (No. 025, issued on May 8, 2014). In the River Alta (Norway), fish tagging was approved by the Norwegian Food Safety Authority (permission no. S-2007/46662). For France, however, the eel telemetry studies (i.e., the Loire Estuary and the Grand Lieu Lake) date from a period before the country had an ethical committee, hence there are no licences available for these studies.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All detection data used in this study are deposited in Verhelst (2025). These data were derived from 18 source studies/datasets. Sixteen of these datasets are maintained in the European Tracking Network database (http://www.lifewatch.be/etn/), developed by the Flanders Marine Institute (VLIZ) as part of the Flemish contribution to LifeWatch, and were extracted using the 'etn' R package (Huybrechts et al. 2025). Two additional datasets (River Meuse and River Stour) were provided by their data owners. Analysis code used to process these data is deposited in Verhelst & Oldoni (2025).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.