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Animal behaviour

Migrating silver eels return from the sea to the river of origin after a false start

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The European eel's singular spawning migration from European waters towards the Sargasso Sea remains elusive, including the early phase of migration at sea. During spawning migration, the movement of freshwater resident eels from river to sea has been thought to be irreversible. We report the first recorded incidents of eels returning to the river of origin after spending up to a year in the marine environment. After migrating to the Baltic Sea, 21% of the silver eels, tagged with acoustic transmitters, returned to the Narva River. Half returned 11–12 months after moving to the sea, with 15 km being the longest upstream movement. The returned eels spent up to 33 days in the river and migrated to the sea again. The fastest specimen migrated to the outlet of the Baltic Sea in 68 days after the second start—roughly 1300 km. The surprising occurrence of returning migrants has implications for sustainable management and protection of this critically endangered species.

1. Introduction

The European eel *Anguilla anguilla* (L., 1758) stands out among other fish species by its unique spawning migration. The route from European waters to the Sargasso Sea, its likely spawning ground, stretches from 5000 to 10 000 km, which is the longest distance among anguillid eels [1–3]. Eels are semelparous, meaning they have a chance to spawn only once in a lifetime. The realization of reproductive potential for which eels have invested much energy and time (approximately 10 to 20, even 44 years; [4,5]) is determined by the success of a long and dangerous spawning migration [3].

European eel stocks have collapsed in recent decades; juvenile eel abundance has decreased by over 90% [6]. The species is considered critically endangered [7]. Their decline is associated with the drastic negative effect of habitat loss, hydropower, overfishing, climate change, pollution, parasites and diseases on spawning stock size [7,8]. Eel spawning stock is determined by the number of migrating silver eels (escapement) from the waters of North Africa to the northern tip of Scandinavia [9,10]. In the first decade of the 2000s, European Union countries established a common eel-recovery strategy [11]. The main recovery measure is increasing the escapement of silver eel biomass to at least 40%, relative to the best estimate of escapement that existed before anthropogenic impacts to the stock. In addition to the number or biomass of escaping silver eels, the size of the spawning stock depends on the success of silver eel spawning migration, which is also important when planning appropriate conservation measures for the species.

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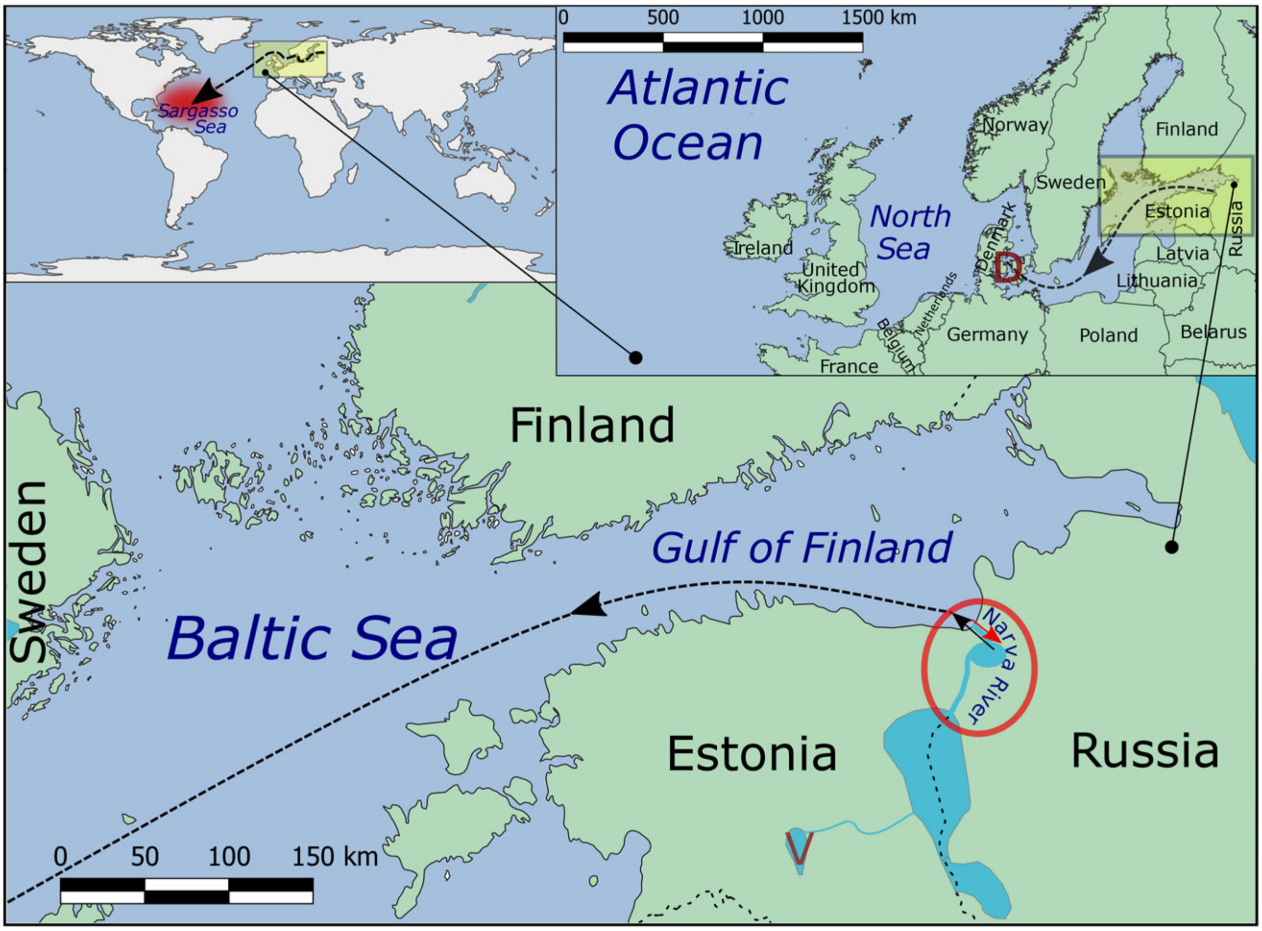

Figure 1. Study area. European eel migration from freshwater areas towards spawning areas in the Sargasso Sea (dashed line on top left) was studied with acoustic telemetry during its first quarter of migration (dashed line on top right). Acoustic receivers were located in Danish Straits (D), Narva reservoir and the Narva River (red ellipse bottom right). The experimental fish were caught in Lake Võrtsjärv (V).

Many studies indicate that the success of spawning migration depends on the route and timing of migration ([12] and references therein). The right timing assures that in every phase of the migration, eels are in suitable physical condition, environmental factors (water temperature, currents, salinity, etc.) are favourable and the predation risk is minimal [4]. Failures in migration timing, including delays caused by man-made obstacles, can be costly [8]. It has been shown that the timing of migration is adjusted according to the conditions in freshwaters, estuaries and marine waters [12–16].

Eels that have migrated to the sea from freshwater might not start swimming directly towards the Sargasso Sea. Recent findings suggest that silver eels, after descent to saltwater, may remain temporarily in coastal areas or fjords, thereby performing a two-step migration [12,13,17–20]. Such an extended residence prior to seaward migration appears to be characteristic not only for the European eel but also for other species, such as *Anguilla australis* and *Anguilla rostrata* [12,21]. This halt might even continue for years [22,23], resulting in considerable delay in the spawning migration of eels. The effects of such delays during spawning migration on successful passage to the Sargasso Sea are unclear (see e.g. [17,24,25]). It is demonstrated that eels can also stop or make temporary upstream movements inside an estuarine habitat [14]. However, return from the sea to a freshwater part of a river by silver eels has not previously been scientifically documented.

In the context of the Baltic Sea, silver eels migrating towards the Atlantic Ocean may cover the distance from the Narva River to the ocean, i.e. Danish Straits (approx. 1300 km) in five months; however, the journey often lasts longer [26], implying a pause in migration. Although fish can theoretically stop or rest at any point along with this phase of migration, presumably it might occur near the river mouth. This study was initially designed with a focus on the downstream migration of eels and an exit from the Baltic Sea during an extended time period. Using tags with an extended operating lifetime made it possible to detect the phenomenon of eel return from the sea to the river. The present paper sought to improve comprehension of silver eel migration between the river and the sea and to see whether any delays in migration or unseen patterns of movements from one environment to another exist during two main migration seasons.

2. Methods

(a) Study area

To study silver eels' behaviour, fish were tracked in riverine and marine environments during their migration from the Narva River reservoir towards an outlet of the Baltic Sea to the North Sea. The Narva River discharges (400 $m^3\ s^{-1}$) to the Gulf of Finland in the Baltic Sea (figure 1). The Baltic is a brackish sea with a limited connection to the open ocean and its salinity is controlled by freshwater outflow from rivers and inflow of saline waters from the North Sea [27]. The salinity of the Baltic Sea decreases along with a notional line from west (Kattegat) to east (Gulf of

Table 1. Environmental data during the first migration of the European eel from the Narva River to the Baltic Sea (ordered by the date of the first descent). Fish returning to the river after descending to the sea are in bold. The significance of environmental predictors for the probability of eel return was assessed using the LRT. The water temperatures and discharges during fish entering the sea are based on daily averages of River Narva. Moon phase during entering the sea is expressed as moon illumination rate (at New Moon and Full Moon the per cent illuminated is 0 and 100%, respectively). Dates of leaving the Narva Reservoir and reaching the Danish Straits are provided. * represents the fish caught in the sea *ca* 50 km northeast from the river mouth on 20 October 2019.

Eel ID	date entering the sea	date leaving the Narva Reservoir	temperature (°C)	discharge ($m^3 s^{-1}$)	moon phase (%)	date reaching the Danish Straits
166	25.10.18	24.10.18	8.2	412	99	
179	**″**	**″**	**″**	**″**	**″**	
183	″	″	″	″	″	
188	″	″	″	″	″	
176	″	25.10.18	″	″	″	
182	26.10.18	24.10.18	7.7	334	96	
189	″	25.10.18	″	″	″	
193	27.10.18	26.10.18	7.3	316	91	
200	″	24.10.18	″	″	″	
208	″	25.10.18	″	″	″	30.09.19
162	28.10.18	27.10.18	6.5	317	84	
173	**″**	**26.10.18**	**″**	**″**	**″**	**06.02.20**
181	″	27.10.18	″	″	″	
192	″	28.10.18	″	″	″	
206	″	25.10.18	″	″	″	
184	31.10.18	30.10.18	4	307	53	02.12.19
172	**04.11.18**	**03.11.18**	**5.4**	**463**	**13**	
168	05.11.18	04.11.18	5.4	456	6	
191	**″**	**04.11.18**	**″**	**″**	**″**	
190	10.11.18	09.11.18	6.1	358	8	
201	**11.11.18**	**11.11.18**	**5.7**	**357**	**14**	
163	**12.11.18**	**″**	**5.5**	**369**	**22**	**30.12.19**
171	″	″	″	″	″	
174	″	″	″	″	″	
178	″	″	″	″	″	
198	″	″	″	″	″	
177	13.11.18	12.11.18	5	413	30	
197	″	″	″	″	″	11.12.19
195*	″	13.11.18	″	″	″	
212	14.11.18	11.11.18	4.9	437	39	
213	19.11.18	12.11.18	4.6	449	84	
167	05.05.19	27.04.19	8.3	437	0	21.11.19
161	**27.05.19**	**22.04.19**	**15.2**	**229**	**43**	**19.01.20**
209	15.06.19	30.04.19	19.5	394	96	15.02.20
175	20.06.19	12.05.19	21.4	425	91	
205	**30.06.19**	**18.04.19**	**19.3**	**449**	**7**	
164	25.09.19	20.04.19	10.4	311	16	
196	23.10.19	28.10.18	8.7	296	29	
average values for the returners (mean)	**29.12.18**		**8.9**	**382**	**36**	**18.01.2020**
average values for the rest fish (mean)	16.12.18		7.5	368	60	04.12.2019

(*Continued*.)

Table 1. (*Continued.*)

Eel ID		date entering the sea	date leaving the Narva Reservoir	temperature (°C)	discharge ($m^3\ s^{-1}$)	moon phase (%)	date reaching the Danish Straits
statistics of LRT	χ^2			0.64	0.37	2.79	
	d.f.			1	1	1	
	P			0.42	0.54	0.10	

Finland) with the mean value of 6‰ [28]. The average depth of the Baltic Sea and the Gulf of Finland area is 55 m and 38 m, respectively. The distance from the Narva River mouth to the Danish Straits is approximately 1300 km.

(b) Fish, tagging and tracking

An acoustic telemetry method was used to track the movements of 38 silver eels migrating to and through the Baltic Sea from the Narva River. The experimental fish were caught in Lake Võrtsjärv, situated in the Narva River catchment area, *ca* 250 km from the sea. The eels in the lake are all restocked as glass eels or elvers. The tagged fish were of silvering appearance with a length of 604 to 896 mm (mean total length ± s.d.: 700 ± 78 mm), a weight of 371 to 1495 g (mean total weight ± s.d.: 680 ± 261 g), and with silvering stages of FIII to FV ([29]; electronic supplementary material, table S1). Before tagging, the eels were anaesthetized in an aqueous solution of metomidate (40 mg l^{-1}; Aquacalm, Syndel Laboratories Ltd., Canada). Coded acoustic transmitters 9 × 27.5 mm (d × l) were surgically implanted into the body cavities (Vemco, Nova Scotia, Canada, V9-2 L-A69-1602 tags, with a random pulse delay of 40–80 s, 476 days). Eels were released into the Narva River reservoir (water temperature 8.5°C), 20 km from the river mouth on 24 October 2018. The fish were transported by car in 1 m^3 aerated tanks.

In the river and reservoir, the fish were monitored by eight stationary Vemco VR2 W automatic receivers (electronic supplementary material, figure S1). To confirm the descent of the eels from the river to the sea, manual tracking (Vemco VR100) was performed nine times in the 5 km long river mouth area.

A total of 45 acoustic receivers were deployed in the Danish Straits during August and September 2019 (electronic supplementary material, figure S2). The receivers covered all three natural exits from the Baltic Sea to the Kattegat/North Sea. Receivers were mounted on bridges ($N = 35$) or with Desert Star ARC-1XD acoustic release systems on the sea floor ($N = 10$). Receivers mounted on bridges and, on sea floor moornings, were deployed with a distance of 410–440 and 300–550 m between receivers, respectively. Due to severe storms in November to December 2019, one natural exit was covered partially.

(c) Data analysis

Statistical tests were performed using the program R v. 4.0.2 [30].

The Clopper–Pearson method was used to calculate the binomial 95% confidence interval (CI) for the point estimate of the proportion of returning eels.

The probability of tagged eels returning to the river from the sea was calculated by logistic regression models, with biological fish parameters and environmental parameters as predictors (table 1; electronic supplementary material, table S1). As several explanatory parameters correlated with each other, single-predictor models were used. Statistical significance of the predictors was assessed using the likelihood ratio test (LRT).

Environmental data were obtained from the hydrometric and meteorological stations located in the Narva River area (Estonian Environment Agency).

3. Results

European eels ($N = 38$), tagged with coded acoustic transmitters, were tracked with stationary receivers in riverine and marine environments during their spawning migration. Eight of the 38 specimens (21%) that migrated to the Baltic Sea from the Narva River reservoir returned to the Narva River (95% CI 10–37%; figure 2; tables 1 and 2; electronic supplementary material, table S1). All eels that returned to the Narva River migrated back to the sea after a period spent in the river. Three of the eight eels were subsequently detected beyond the Baltic Sea in the Danish Straits. The migration of these fish took 68 to 199 days, starting with the second descent to the Baltic Sea in 2019 (July, October and November) and lasting until detection in the Danish Straits (about 1300 km from the river) during the following winter (tables 1 and 2).

Most eels reached the sea for the first time in October and November 2018 (30 individuals; table 1), i.e. soon after release on 24 October. No eels descended during the subsequent winter, and the remaining eight eels reached the sea later, between April and October 2019.

The probability of tagged individuals ascending back to the river from the sea did not depend on fish phenotypic characteristics or environmental factors (LRT; all $p \geq 0.1$; tables 1 and 2; electronic supplementary material, table S1).

Of the 30 fish that did not return to the river, five were subsequently detected in the Danish Straits (table 1). The sizes and maturation indexes of these fish were diverse. One tagged fish was recaptured in the Gulf of Finland (Luga Bay) 50 km northeast of the Narva River outflow in October 2019 (table 1).

Movement patterns of the individuals that returned to the river are described schematically in figure 2 (see also table 2). Fish typically returned to the river 11 to 12 months after first descending to the sea in October and November 2019. Other fish returned earlier. Environmental factors, such as temperature, discharge, moon phase and precipitation, varied widely depending on the time of arrival (table 2). The longest upstream migration was to an impassable barrier located 15 km upstream from the river mouth. The returning eels spent up to 33 days in the river before returning to the sea.

4. Discussion

Our results reveal that silver eels migrating to spawn may show unexpected behaviour after descending to the sea. Instead of starting to move towards the ocean, some fish returned to freshwater after spending a period in the marine environment before subsequently moving to the sea again. This kind of behaviour was exhibited by 21% of the tagged specimens in the study. This is an impressive case in animal ecology, showing how a semelparous species, which invests heavily in building its reproductive potential and faces a particularly challenging

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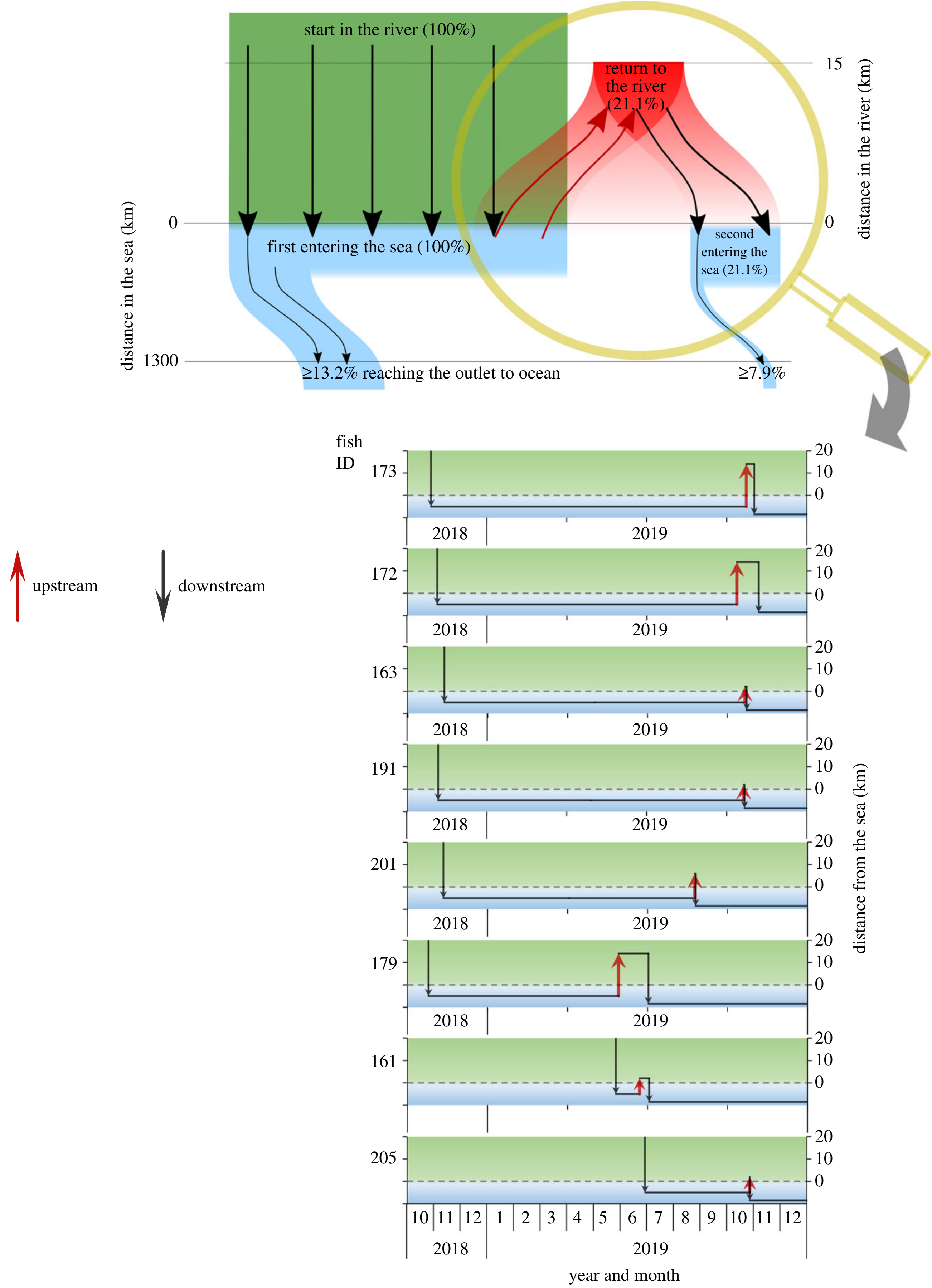

Figure 2. Migration patterns of telemetrically tagged silver European eels. Upper panel: arrows on green background indicate fish ($N = 38$) first descending from the Narva River to the Baltic Sea, arrows on red ascending back to the Narva River with the second migration to the sea, arrows on blue migration in the sea to the Danish Straits (outlet to the ocean). Lower panel: schematic description of the silver European eel individuals moving to the Baltic Sea, back to the Narva River and again to the sea. Movements to the sea are indicated with black arrows, movements to the river with red arrows. The horizontal continuous lines between arrows indicate the duration of freshwater or brackish water phases. The spatial extent of movements in the sea is not known (except for fish with ID nos. 161, 163 and 173 after second descent to the sea).

Table 2. Tracks of the riverine movements of silver European eels after returning to the Narva River from the Baltic Sea and environmental data. The water temperatures and discharges during the fish return to the river are based on daily averages of River Narva. Moon phase during return to the river is expressed as moon illumination rate (at New Moon and Full Moon the per cent illuminated is 0 and 100%, respectively). See the location of each receiver on the map (electronic supplementary material, figure S1).

eel ID	date returning from the sea to the river	length of upstream movement in the river (km)	number of stationary receivers	date reaching to the most upstream location	date leaving the most upstream location	date of second entering the sea	temperature (° C)	discharge ($m^3 s^{-1}$)	moon phase (%)	perticipation (mm day^{-1})
161	23.06.2019	1	1	25.06.2019	02.07.2019	04.07.2019	21.6	348	69	0.0
163	21.10.2019	1	1	22.10.2019	22.10.2019	23.10.2019	8.8	407	51	0.3
172	12.10.2019	15	5	21.10.2019	23.10.2019	06.11.2019	8.5	404	98	12.2
173	23.10.2019	14	4	24.10.2019	24.10.2019	01.11.2019	8.7	431	29	0.1
179	30.05.2019	14	4	03.06.2019	03.06.2019	03.07.2019	14.9	438	17	0.0
191	20.10.2019	1	1	21.10.2019	21.10.2019	21.10.2019	8.5	333	62	4.8
201	25.08.2019	5	2	25.08.2019	26.08.2019	26.08.2019	19.1	203	32	0
205	27.10.2019	1	1	27.10.2019	27.10.2019	27.10.2019	8.9	447	1	20

migratory route, could develop sophisticated strategies for regulating its migration. In addition to adjusting the timing of migration, eels can temporarily migrate in the opposite direction of their spawning migration target in the Sargasso Sea. Recognition of this behaviour may be important for better understanding of spawning migration and has a potential impact on the management and conservation of the species.

Movements from the sea into freshwater are common for eels during their growth phase (for yellow eels, [31–34]), but has not been previously documented for the post-feeding stage (silver eels). In our study, factors that could determine the temporary return of silver eels to the river remain obscured. After first descending to the sea, the interruption of eel spawning migration at sea could be linked to the restart of feeding [17,24] or some other factor (e.g. orientation problems, [23]). Nevertheless, the temporary return of silver eels to the river is probably not associated with feeding in the riverine environment, as the feeding activity of eels ceases when the water temperature is less than 10°C [35]. Half the returns occurred at lower water temperatures (8.5–8.9°C). In addition, the standard phenotypic characteristics (size, maturation, etc.) or environmental factors (temperature, discharge, etc.) tested in logistic regression models failed to account for the returning behaviour. Eels in this study were restocked as elvers or glass eels. Therefore, the temporary return can be inherent to eels of some specific ecotype and may be revealed in situations in which fish are removed from their natural habitats and translocated to an area with different environmental conditions (see also [36–38]). Although the reasons why it takes a long time for eels to navigate through the Gulf of Finland and the Baltic Sea on their way to the ocean, and why some fish behaved as 'false starters' remain unresolved, the migration pattern found is an important addition to the description of the plastic behaviour of eels, especially at the beginning of the complex marine phase of their spawning migration (e.g. [12,17,19,20]).

From a management perspective, it is important to note that the fish in this study returned to the river mainly in October and November of the following year, which is known as the main spawning migration season [39,40]. This means these returning eels may join those that are migrating towards the sea for the first time. If the estimation of silver eel escapement relies on direct fishing or counting the migrating specimens and does not consider the possibility of returning specimens, the tally of migrating eels may be incorrect. As a result, escapement may be overestimated, as individuals are counted twice. Rather than counting eels from the same escapement year, specimens from the previous year may be included in the count. In addition, the returning silver eels are once more subject to local fishing and predation (by seals, cormorants or other fish species [41,42]), likely increasing their mortality. Taking such a subgroup of returning silver eels into account and regulating fisheries accordingly can help decrease the mortality and increase the success of migrating silver eels reaching spawning grounds.

We have shown that there may be an undiscovered component in the chain of events guiding eels from the coastal sea to the spawning grounds—a temporary return to the river. We need to be aware that the behaviour of eels can be very diverse in the early stages of spawning migration. Subgroups with different migration strategies can increase the plasticity of the population, which can be particularly important in a changing environment. In order to protect critically endangered European eels, it is necessary to consider the specific needs of the subgroup described in this study and to adapt relevant conservation measures. The 'false starts' of silver phase eels may be more common in anguillid eels than thought and continued research on this phenomenon on stocked and naturally invading eels is needed.

Ethics. Fish tagging and release were carried out in accordance with License 1-3/19/1363 (Environmental Board of Estonia).

Data accessibility. Data supporting the current study are provided in the electronic supplementary material [43].

Authors' contributions. All authors participated in fieldwork and article preparation. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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