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Using ‘trap and transport’ to facilitate seaward migration of landlocked European eel (*Anguilla anguilla*) from lakes and reservoirs

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ABSTRACT

‘Trap and transport’ (T&T) is employed to facilitate the seaward migration of European eel (*Anguilla anguilla*) past obstacles such as hydropower facilities. Hence, previous studies assessing its efficacy have focussed on disrupted fluvial systems. The transferability of findings from lotic to lentic systems is uncertain because many of the environmental cues that trigger eel migration in rivers are lacking from reservoirs and lakes, particularly those with limited flow connection to the surrounding catchment. We used acoustic telemetry to compare the migration behaviour of T&T adult *A. anguilla* which were fyke netted and transported from two disconnected reservoirs ($n = 80$) to a control group of resident river eel ($n = 30$) during their migration through the lower River Stour, UK, to the North Sea. Migration patterns and behaviour were broadly similar between the reservoir T&T eel and river eel with 86 and 90 % of each group successfully reaching the sea, respectively. Reservoir eel were larger and at a more advanced stage of migratory readiness (silvering) and commenced migration sooner after release than the river eel, but they descended the catchment at a slower rate. Behaviour in the estuary was highly variable between individuals with residence times ranging from 5 h to 83 days (median = 1.4 days) across all groups. Only one individual failed to migrate through the estuary and most (75 %) reached the sea within five days of entering the estuary. Findings indicate that T&T of adult eel from reservoirs represents a feasible method to allow landlocked individuals to migrate and potentially contribute to the spawning stock, either now or in the future. Results also highlighted the high capture effort that may be required to implement an effective T&T programme. Gaining a thorough understanding of eel abundance and population structure in the source waterbody is desirable before implementation.

1. Introduction

The European eel (*Anguilla anguilla*) displays considerable behavioural plasticity in habitat use and is found in a broad range of habitats including rivers, lakes, canals and estuaries (Daverat et al., 2006). Lentic systems, such as lakes and reservoirs, can provide productive eel growing habitats and accordingly support high densities and biomass (Deelder, 1954; Poole and Reynolds, 1996; Trancart et al., 2018). For example, in a shallow (< 0.5 m depth) boulder-covered area of Lake Constance eel density and biomass reached a maximum of 62 individuals 100 m^{-2} and 40 kg 100 m^{-2}, respectively (Fischer and Eckmann, 199s7). The annual combined harvest of yellow (> 300 mm length) and silver eel from Lough Neagh, Northern Ireland, a 400 km^2 freshwater lake that supports the largest wild adult eel fishery in Europe, is 297–434 t, although it relies on stocking and assisted migration (trap and transport) of 0.4–3.4 t, of juveniles each year (2006 to 2018 data) (ICES, 2019). In addition to stocking (Wickström et al., 1996), juvenile eel may enter lakes and reservoirs through natural upstream migration (Poole et al., 1990) and within pumped water inputs (Patrick and McKinley, 1987). After a typical freshwater growth phase of 8 to 15 years (females) and 3 to 12 years (males), eel undergo the onset of sexual maturation (silvering) (Aprahamian, 1988; Feunteun, 2002). To complete their lifecycle, they must undertake seaward migration and an oceanic journey of up to 9000 km to spawning grounds in the Sargasso Sea (Righton et al., 2012).

Artificial reservoirs and many naturally-formed lakes are subject to flow regulation for the purposes of water abstraction, hydropower generation or flood risk management. Flow connectivity with the surrounding catchment may consequently be rendered limited or even absent, thereby reducing opportunity for seaward migration of

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maturing (silver) eel that likely entered as juveniles within pumped inputs or ascended the spillway by climbing. Often the only means of egress from these temporally disconnected waterbodies is within dam overspill or controlled discharge, which can be minimal and erratic (e.g. Acou et al., 2008). Alternatively, eel may exit through pipework and pumps when water is abstracted. However, pumped routes for potable or irrigation supply rarely reconnect with a viable migration path (Acou et al., 2008; Besson et al., 2016; Trancart et al., 2018) and eel are highly susceptible to damage and mortality caused by both pumps and their associated screens (Buysse et al., 2014; Calles et al., 2010). In the absence of a feasible migration route to the sea, adult eel in temporally disconnected waterbodies are prevented from contributing to the spawning stock.

There are legislative drivers in place in Europe to reverse the post-1980s severe recruitment decline in *A. anguilla* by enhancing protection and passage (ICES, 2011). Under the EU Recovery Plan (Council Regulation 1100/2007/EC), Member States are required to detail actions to meet the target to permit with high probability the escapement to sea of at least 40% of the silver eel biomass relative to the best estimate of escapement that would have existed if no anthropogenic influences had impacted the stock. In the UK, The Eels (England and Wales) Regulations 2009 aim to prevent the ingress of eel into potentially harmful water abstraction points (those capable of pumping ≥ 20 m^3/day) by screening (2–20 mm gap spacing, dependent on lifestages present), a measure that will restrict the recruitment of juvenile eel into reservoirs via pumped inputs. Nevertheless, the substantial eel biomass already present in many disconnected lotic waters could represent a significant contribution to catchment-based conservation targets if migratory silver eel from these landlocked populations were able to reach the sea. For example, in the East Anglian region of the UK, the four largest potable water reservoirs represent 19.6 km^2 of potential eel habitat, yet none have a feasible route of egress for eel (unpublished data). Moreover, given the suspected contribution of habitat reduction in the eel decline (Feunteun, 2002), enhancing recruitment to currently disconnected waterbodies either through restoring natural ingress or stocking, coupled with provision of a safe means of adults reaching the sea, offers potential to utilise these large areas of habitat to increase future spawner output.

One proposed means of facilitating the adult spawning migration of landlocked eel is through their capture and translocation to a location with good seaward connectivity. This ‘trap and transport’ (T&T) (or ‘trap and haul’) approach has been applied to other diadromous fish species such as Pacific salmonids for several decades with some success (Ward et al., 1997). Each year, millions of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) are captured in the lower Snake and Columbia Rivers and moved downstream of major obstacles using barges and trucks (Lusardi and Moyle, 2017), although there are known issues of stress-induced physiological changes and elevated predation risk among transported individuals (Kemp, 2015). T&T may be associated with lower capital costs than restoring connectivity through the installation of fish passes or other passage solutions and, for seaward-migrating eel, the availability of effective designs for downstream passage facilities is limited. Consequently, T&T is increasingly being used to mitigate eel migration delay and mortality caused by hydropower facilities and pumping stations in rivers (e.g. MacNamara, 2012). In the Dutch polders, T&T is the principal method of achieving national escapement targets, enabling migration from these heavily regulated systems for which the only alternative is passage via pumps (van der Meer, 2012). A five-year study of a T&T programme for American eel (*Anguilla rostrata*) on the St Lawrence River, Canada, suggested it was an effective means to reduce mortality at hydropower facilities with ‘acceptable’ capture rates (up to 2200 individuals per year) and no reported differences in migration rate or maturation indices between transported eel and wild migrants (Stanley, 2014).

Studies that demonstrate the successful application of T&T to seaward-migrating eel have focussed on fluvial systems disrupted by engineered structures (e.g. Béguer-Pon et al., 2018; McCarthy et al., 2014; Stanley, 2014). Its applicability to eel in lentic waterbodies is largely unknown, with key knowledge gaps regarding the effort and methods required to effectively capture maturing adults, their ability and propensity to migrate post-release, and their spawning viability. Some key triggers to the onset of seaward migration in lotic systems, such as increased flow and pulses of high turbidity (Haro, 2003), are severely reduced or completely absent in lakes. A recent study in Grand-Lieu Lake, France, showed silver European eel movements were independent of environmental factors such as water temperature, atmospheric pressure and current velocity, with escapement from the lake dependent on water levels and sluice operation (Trancart et al., 2018). When migratory delay in rivers (e.g. due to a barrier) persists beyond the migration window, sexually maturing eel may revert to the pre-maturation yellow phase until conditions allow passage (Durif et al., 2003; Feunteun et al., 2000). While eel in lentic waterbodies do undergo the physical changes associated with silvering, such as enlargement of the eyes and pectoral fins (Svedäng et al., 1996; Svedäng and Wickström, 1997), it is not known whether these individuals if translocated to a river would migrate in a similar timeframe to resident river eel or require a period of adaptation to local conditions. Translocated individuals that do not migrate readily pose the risk of disrupting local food webs and impacting the resident eel population because growth, distribution and sex determination are all influenced by population density (Roncarati et al., 1997; Vollestad and Jonsson, 1988).

This study used acoustic telemetry to determine whether eel translocated from two disconnected reservoirs to a nearby river exhibited the same migratory behaviour as eel resident within the recipient river. The four main objectives were to compare: 1) size and development phase (silvering); 2) migratory readiness (time taken to commence migration post release); 3) migration rate through the lower freshwater catchment (time taken to reach the estuary after commencement of migration), and 4) migration rate through the estuary (time taken to reach the sea after entering the estuary).

2. Methods

In a telemetry study conducted from 1 October 2014 to 27 February 2015, adult eel (n = 80) were captured from two reservoirs, transported, implanted with PIT and acoustic tags, and released into the lower River Stour, UK, at a location 9.5 km upstream of the tidal limit (51°58′9.65″N, 0°58′18.31″E) (Fig. 1). Movements of translocated individuals were compared to those of a tagged control group of actively migrating adult eel (n = 30) that were captured from the lower River Stour and released in the same location.

2.1. Study sites

Alton Water (51°58′51.64″N, 1° 8′4.22″E) and Hanningfield Reservoir (51°39′27.60″N, 0°30′10.99″E) are 1.64 and 3.62 km^2 reservoirs constructed 31 and 62 years ago, respectively, by the damming of second order streams (Fig. 1). Pumped supplies from nearby rivers are the principal water inputs and the likely route of historic eel ingress, although occasional ascent of the spillways or stocking events may have occurred. Due to the design of the spillways and the infrastructure conveying compensation flows, coupled with the highly infrequent nature of dam spill, there is no feasible route by which adult eel could egress unassisted from either reservoir to reach the watercourses downstream.

The lower river Stour is typically 10–15 m wide and has a mean daily flow of 2.99 ± 3.99 m^3s^{-1} (± S.D.) (1962–2015) (UK National River Flow Archive). The study reach encompassed two former water mills, Dedham and Flatford, where the main channel flows via either penstock sluices or a lock (Dedham) or an Archimedes screw turbine and associated fish pass or lock (Flatford). Approximately 2 km

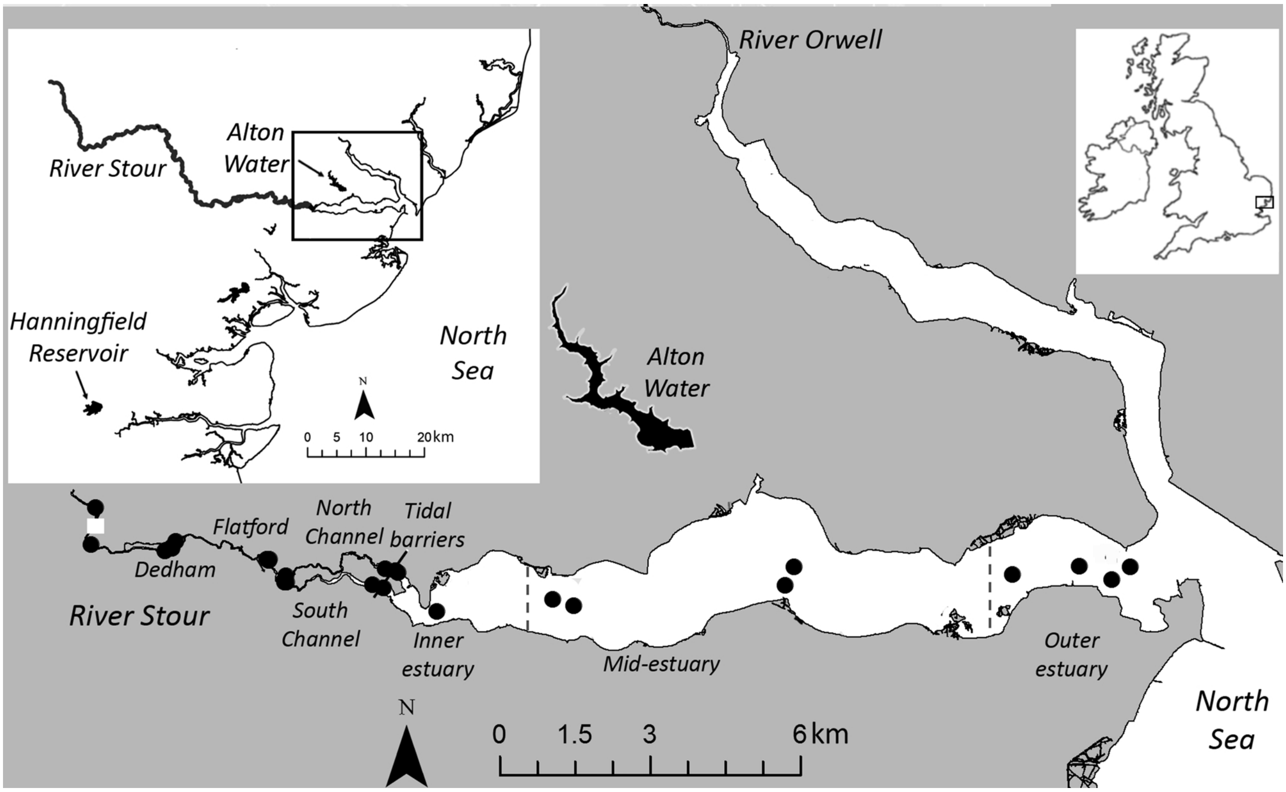

Fig. 1. Locations of the two reservoirs from which eel were translocated and detailed map of the lower River Stour and its estuary indicating the positions of intertidal structures. Fixed acoustic receivers (black circles) were used to track the movements of downstream migrating adult eel from the release site (white square), through a 9.5 km freshwater reach and out through the inner, mid and outer sections of the estuary.

upstream of the tidal limit, the main channel bifurcates to form the North and South Channels (Fig. 1). Water that spills over a broadcrest weir flows into South Channel which terminates in a tidal barrage that provides flood protection by regulating the height of tidal ingress through a combination of undershot lifting gates and top-hung tidal flaps. North Channel terminates in an automatically controlled bottom-hinged tilting gate and a top-hinged tide gate on the downstream (estuary) side. Water is abstracted 185 m upstream of this tilting gate through Brantham intake (3.2 m wide with a trash screen) at a maximum pumping rate of 0.64 m^3s^{-1} (for a detailed description of the study site see Piper et al., 2013, 2018).

Eel movements were monitored using a linear array of 25 fixed acoustic receivers (VEMCO, model VR2W, Nova Scotia, Canada) (Fig. 1). Water temperature (°C) at Flatford was recorded every 15 min (OTT Orpheus Mini, Sheffield, UK) and ranged from 4.9 to 10.2 °C during this study. River discharge (m^3 s^{-1}) recorded at Langham flow gauging station, 3.5 km upstream of the study reach, was obtained from the Environment Agency at a resolution of 15 min and ranged from 1.06 to 19.7 m^3s^{-1} with a median daily flow of 3.95 m^3s^{-1} (IQR: 2.90–5.81 m^3s^{-1}). Gauged tide height (m) at Harwich (51°57′6.78″N, 1° 17′21.96″E) was obtained from The National Oceanography Centre at 15 min resolution. The daily proportion of the moon illuminated was downloaded from the US Naval Observatory (http://aa.usno.navy.mil/data/docs/MoonFraction.php). Weather data: air temperature (°C); air pressure at sea level (hPa); windspeed (kn); wind direction, and cloud cover (oktas) at 1 h resolution were obtained from the UK Meteorological Office for the nearest weather station at Wattisham (52°7′29.23″N, 0° 56′20.84″E).

2.2. Fish capture and tagging

Eel were captured from Alton Water and Hanningfield Reservoir, and from the River Stour in a 2 km reach extending upstream from the release site, using fyke nets deployed by boat and checked each day. Netting occurred at Alton Water on 49 nights using a total of 943 ‘units of effort’, defined as one net (cod end) per night, and at Hanningfield Reservoir on three nights using 126 units of effort.

Captured eel were visually assessed for migratory stage and signs of external damage and disease. Those showing visible indication of silvering (i.e. enlarged eye and/or pectoral fin) and in apparently good condition were transferred to perforated holding barrels at the capture location and held (maximum eight days) until transportation to the tagging and release location in aerated tanks (600 L). Other captured individuals were either retained for health screening (see below) or released at the origin. Tagging and release of eel into the River Stour occurred from 8 October to 21 December 2014 in nine batches of 5 to 20 individuals, dependent on capture rates at the three locations and the need to minimise tag collision (i.e. missed detections) caused by excessive numbers of tagged fish within the same area. Whenever possible, batches of river and reservoir eel were tagged and released at the same time (Table 1).

Prior to tagging, eel were anaesthetised (Benzocaine 0.2 g L^{-1}), weighed (g), and measured (total body length, pectoral fin length and horizontal and vertical eye diameter, mm). Migratory stage was quantified using the Ocular Index (Pankhurst, 1982), and Fin Index (Durif et al., 2005). Individuals were placed upside down in a half pipe cradle and an incision (≤ 15 mm length) made approximately 50 mm anterior to the ventral opening. An acoustic tag (VEMCO model V9–2 L, tag interval 15–25 s, 29 mm × 9 mm, 4.7 g in air or V7–2 L, tag interval 15–25 s, 20 × 7 mm, 1.6 g in air, dependent on eel size) was inserted through the opening into the peritoneal cavity and the incision closed with two sutures (Resolon™, Advanced Medical Solutions, UK). A Passive Integrated Transponder (PIT) tag (23 × 4 mm, HDX, 0.6 g in air, Texas Instruments) was inserted at the same time to aid the identification of individuals if recaptured during river netting. The duration of surgical procedures was always less than 3.5 min. After tagging, eel

Table 1
Release dates of eel translocated from two reservoirs (Alton Water and Hanningfield Reservoir) and a control group captured from the River Stour that were tagged and released into the lower River Stour during the period 8 October–21 December 2014.

Date	Eel capture location	No. eel
8 Oct 2014	Alton water	10
22 Nov 2014	Hanningfield Reservoir	10
26 Nov 2014	Hanningfield Reservoir	10
	Alton Water	10
8 Dec 2014	River Stour	5
10 Dec 2014	River Stour	10
11 Dec 2014	River Stour	4
	Hanningfield Reservoir	10
12 Dec 2014	River Stour	11
13 Dec 2014	Hanningfield Reservoir	20
21 Dec 2014	Hanningfield Reservoir	10
	Total	110

were transferred into a perforated holding barrel for 8–12 h to allow post-operative recovery and acclimation before release. No mortality occurred during tagging or recovery. Releases took place after sunset whereby the lid of the holding barrel was removed and individuals left volitionally. Fish tagging was carried out in compliance with UK Home Office regulations.

In addition to individuals captured for tagging, eel samples from both reservoirs underwent mandatory Environment Agency health screening to gain the necessary consents to move fish between catchments. Otolith analysis was also conducted on 10 eel from Hanningfield reservoir to determine age at capture.

2.3. Data analysis

Data collation and statistical analyses were carried out in R v3.4.4 (R Core Team, 2018) using packages: MASS; dplyr v0.7.4; VTrack v1.21; survival v2.4, and agricolae v1.8. Standard error is denoted by S.E. and interquartile range by IQR throughout.

Eel length, mass and total residence time in the estuary were compared among capture locations using Kruskal-Wallis test with Bonferroni adjusted post-hoc comparisons because the assumptions of normal distribution or homogeneity of variances across groups were not met (Levene's test).

Cox proportional hazard regression was used to model covariate effects on the rate (i.e. time to an event) of: 1) *commencement of migration* after release; 2) *migration into the estuary* after migration commenced, and 3) *migration into the North Sea* after entering the estuary. Rate of *commencement of migration* was determined from the first detection at Dedham sluice, the first cross-channel structure located 2.4 km downstream from the release point. Individuals that were detected by the array after release but did not reach Dedham sluice during the study period were included as censored observations. Candidate models included the fixed covariates: eel capture location (Hanningfield Reservoir, Alton Water or River Stour), eel length, ocular index, and fin index; and the time-varying covariates: total river discharge; water temperature; lunar illumination; cloud cover, and air pressure, all at time of first detection at Dedham (or if non-migratory, at time of last detection in the array). Rate of *migration into the estuary* was calculated from the first detection at Dedham Sluice to the first detection in the inner estuary (Fig. 1). To account for variation in individual trajectories whereby some individuals settled in an area for an extended period or moved back upstream, the dataset was divided into 'movement phases'. An individual was deemed to have stopped migrating if it moved upstream, or was continuously detected at one receiver for > 2 h, or was not detected by any receiver for > 2 h. The 2 h threshold was informed by interval analysis with 99.7% of detection intervals falling below it. Many fish exhibited multiple movement phases before reaching the estuary, so phases were numbered consecutively and used to stratify the regression models to avoid pseudoreplication (Nyqvist et al., 2017). Each movement phase had the potential to culminate in arrival in the estuary and was either assigned the outcome of 1 (fish reached the estuary) or 0 (fish did not reach the estuary). Candidate models included the fixed covariates: eel capture location (Hanningfield Reservoir, Alton Water or River Stour), eel length, time taken to commence migration, ocular index and fin index; and the time-varying covariates: total river discharge, water temperature, lunar illumination, cloud cover, air pressure and abstraction rate at Brantham ($m^3 s^{-1}$), all at the start of the movement phase. Overall migration speed within each movement phase was calculated from the shortest possible swim distance between start and end detection points divided by phase duration. Rate of *migration into the North Sea* was determined from the last detection in the outer estuary (Fig. 1). Individuals that were last detected in the inner or mid estuary were included as censored observations. The dataset was divided into 'movement phases' separated by periods of > 9 h of non-movement (i.e. consistently detected at the same receiver) or non-detection. This 9 h cut off was derived from interval analysis and the minimum time it would take for an eel to pass through the entire estuary based on average speed in the freshwater reach. Candidate models were stratified by movement phase number and included the fixed covariates: eel capture location (Hanningfield Reservoir, Alton Water or River Stour), eel length, time to reach estuary after commencement of migration (h), ocular index and fin index; and the time-varying covariates: total river discharge, tide height, air temperature, lunar illumination, cloud cover, air pressure, windspeed, and wind direction, all at the start of the movement phase. For all models, the assumption of proportional hazard was tested for each covariate and for the model as a whole (Nyqvist et al., 2017). The Akaike information criterion (AIC) was used to arrive at the best model (lowest AIC) and identify other 'good' models within 2 AIC units from the best model and a minimum of 2 AIC units lower than the null model (Burnham and Anderson, 1998). Due to correlation between ocular and fin indices ($r = 0.34$), they were not allowed to co-occur in the same model unless with interaction terms.

3. Results

Eel translocated from the two reservoirs were significantly longer than those captured and tagged from the river ($H = 63.6$, $p = < 0.001$, Kruskal Wallis), but did not differ from each other (Table 1). Eel mass differed among all the capture sites ($H = 31.2$, $p = < 0.001$), with the heaviest individuals from Alton Water, followed by Hanningfield Reservoir (Table 2). European eel with ocular index ≥ 6.5 and fin index ≥ 4.3 (females only) are considered to be at the migratory silver stage (Durif et al., 2005; Pankhurst, 1982). The ocular index of 58 % and 69

Table 2
Morphometric summary of adult eel translocated from two reservoirs (Alton Water and Hanningfield Reservoir) and a control group captured from the River Stour that were tagged and released into the lower River Stour during the period 8 October–21 December 2014.

Metric	Eel capture location		
mean ± S.D. (or median)	Alton Water	Hanningfield Reservoir	River Stour
(range)	*(n = 20)*	*(n = 60)*	*(n = 30)*
Total length (mm)	937 ± 57 (832–1032)	942 ± 58 (732–1047)	633 ± 89 (511–884)
Mass (g)	1767 ± 330 (1040–2376)	1565 ± 261 (1151–2101)	529 (median) (268–1498)
Ocular Index	7.1 ± 2.3 (4.1–13.0)	7.9 ± 2.3 (4.7–16.8)	6.1 ± 1.2 (3.5–8.5)
Fin index	4.9 ± 0.6 (3.8–5.9)	5.2 (median) (4.1–7.4)	4.7 ± 0.5 (3.6–5.7)

Table 3

Good models identified using cox proportional hazard survival regression for covariate effects on the rate of: 1) commencement of migration; 2) migration into the estuary, and 3) migration into the North Sea. Models were compared using Akaike Information Criterion (AIC). ΔAIC_{null} is the difference in AIC between the model and the null model. ΔAIC_{min} is the difference in AIC between the model and the best model.

Event rate modelled	AIC_{null}	AIC with covariates	Delta AIC_{null}	Delta AIC_{min}	Variable	Coefficient	S.E.	*p*-value
1) Commencement of migration	681.66	667.60	−14.06	0 (best model, no other good models)	Eel capture location (ref level: River Stour)	0.81 (Hanningfield)	0.35	0.021
						0.79 (Alton Water)	0.27	0.004
					Ocular Index	0.09	0.05	0.062
	700.09	686.66	−13.43	0.63	Eel capture location (ref level: River Stour))	0.93 (Hanningfield)	0.26	< 0.001
						0.91 (Alton Water)	0.34	0.008
2) Migration into the estuary (stratified by movement phase)	492.65	460.34	−32.31	0 (best model, no other good models)	River discharge	0.06	0.02	0.012
					Proportion of moon illuminated	−1.75	0.73	0.004
					Water temperature	0.23	0.07	0.001
					Eel capture location (ref level: River Stour)	−0.66 (Hanningfield)	0.29	0.025
						−1.35 (Alton Water)	0.47	0.023
3) Migration into the North Sea (stratified by movement phase)	545.45				No good model			

% of tagged individuals from Alton Water and Hanningfield Reservoir equalled or exceeded the 6.5 threshold, respectively, compared to 41 % of the river eel. The fin index threshold was equalled or exceeded by 79 % and 97 % of eel from Alton Water and Hanningfield Reservoir, respectively, compared to 72 % of individuals from the river (Table 2). The age of eel from Hanningfield Reservoir ranged from 13 to 20 years (median = 17; IQR = 15–19) and total length from 808 to 950 mm (median = 895; IQR = 853–941).

Of the 110 tagged eel released, 99 commenced downstream migration, 90 % of the river eel and 90 % of the reservoir eel. Movements occurred mainly (83 %) during the hours of darkness (1600–0800). All eel, both migratory and non-migratory, were detected at least once by the array after release, but six migratory individuals passed the receiver upstream of Dedham sluices without detection (confirmed by subsequent detection downstream) and so were not included in the modelled dataset. Capture location had the strongest effect on the time taken to commence migration, with eel from both reservoirs migrating more readily than those originating from the river. The rate also increased with ocular index; eel that had a higher index migrated sooner after release (Table 3).

Ninety-seven of the 99 eel that migrated downstream reached the estuary, taking between 1.68 and 244.80 h (0.07–10.2 days) (median = 9.82 h; IQR = 3.87–104.03 h) from their commencement of migration. Two individuals appeared to be entrained at Brantham water intake in North Channel. One eel reached the mid-estuary without being detected in the inner estuary and so was excluded from the modelled dataset. Eel exhibited between 1 and 5 movement phases during migration with 73 % of individuals reaching the estuary within one or two phases. Median overall speed during active downstream migration was $0.32\,m\,s^{-1}$ ($1.15\,km\ h^{-1}$) (IQR = $0.10–0.45\,m\,s^{-1}$). The highest migration rates were associated with increased river discharge and water temperature, and the darker phases of the moon (Table 3). Eel capture location also had an effect with eel originating from the two reservoirs exhibiting slightly lower migration rates than those from the river (Table 3).

Ninety six of the 97 eel that entered the estuary were last detected in the outer estuary, and so were presumed to have successfully migrated into the North Sea. The remaining individual was last detected in the mid-estuary 11 h after arrival. Residence time in the estuary ranged from 4.94 to 1982 h (0.21–82.6 days) (median = 33.48 h; IQR = 15.53–121.66 h) and was higher among eel originating from Alton Water (median = 401.7 h) than from Hanningfield reservoir (median = 23.5 h) or the River Stour (median = 33.4 h) (H = 11.54, p = 0.003, df = 2, Kruskal-Wallis). To explore whether this effect may be a consequence of the early release (> 6 weeks) of one batch of eel from Alton Water compared to eel from other locations, these early individuals (n = 10) were removed from dataset. However, examination of the later-released eel (i.e. after 22 November) revealed a similar pattern with longer residence times associated with Alton Water relative to Hanningfield (H = 7.20, $p = 0.03$, df = 2, Kruskal-Wallis). Eel originating from the River Stour did not vary from either group (Fig. 2).

During their residence in the estuary, eel undertook between 1 and 7 separate movement phases interspersed with periods of > 9 h of assumed non-movement. In the cox regression models, the rate of successful migration to the North Sea during these movement phases was independent of the tested covariates (Table 3). The absence of a significant effect from capture location indicates that active migration behaviour was similar among eel from the three sources. The longer overall residence of eel from Alton Water was, therefore, a consequence of long periods of inactivity within the estuary.

4. Discussion

Determining whether trap and transported eel undertake successful seaward migrations is key to evaluating the efficacy of this management option. The majority (88 %) of eel translocated from two disconnected

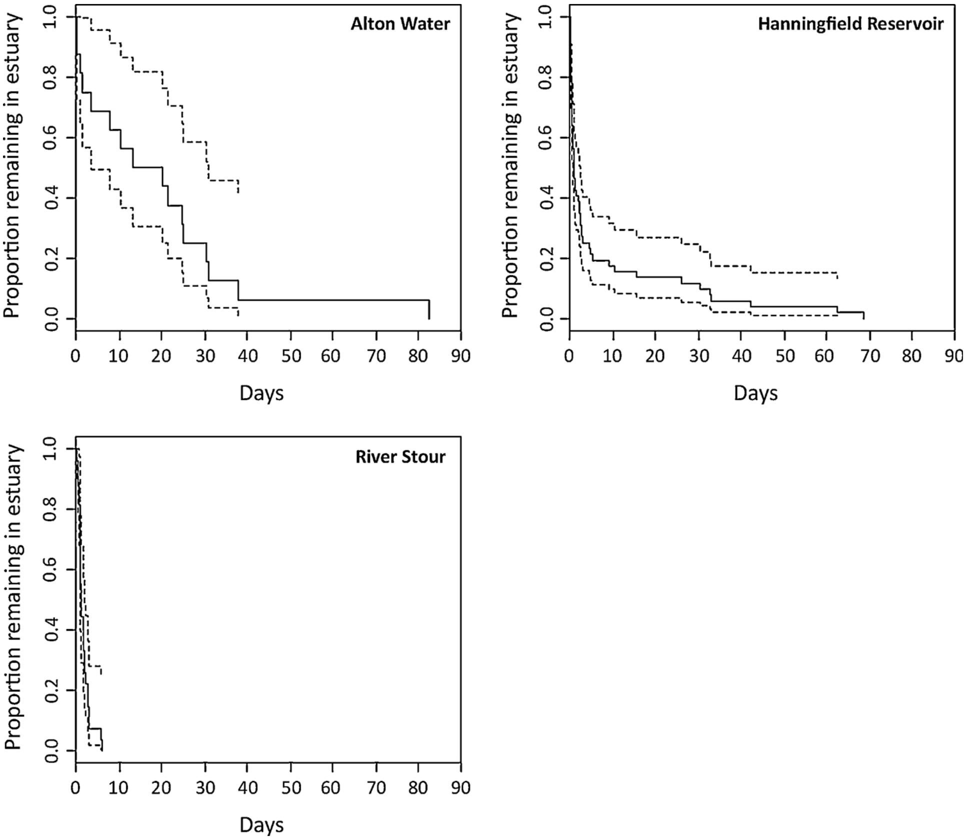

Fig. 2. Estimated Kaplan-Meier curves (solid line) and 0.95 confidence intervals (dashed lines) showing total estuary residence time (days) before successfully reaching the North Sea of tagged eel (n = 96) translocated from two reservoirs (Alton Water and Hanningfield reservoir) and a control group from the River Stour.

reservoirs migrated downriver and reached the sea within 86 days of release, and these individuals exhibited broadly similar migration behaviour to eel from the recipient river. Further, no apparent damage or mortality were incurred during capture, holding or transport activities and there was no indication that T&T impaired survival or fitness during migration through the freshwater and estuarine reaches. Findings suggest that T&T could be used to enable the substantial numbers of eel currently held within landlocked populations to undertake seaward migration and potentially contribute to the oceanic spawning stock, either now or in the future.

Tagged eel that originated from the reservoirs were larger and at a more advanced stage of silvering than those from the river, yet the overall proportion of T&T and river eel that migrated was the same. Size and age at maturation vary greatly among female eel, with the female life-history strategy apparently more variable and potentially environmentally dependent than the male's (Durif et al., 2009; Oliveira, 1999). If, as postulated by Svedäng et al. (1996), females minimise generation time by maturing and migrating as soon as possible, eel resident in the River Stour may be expected to embark on their spawning migration before reaching the size and age equivalent to eel detained within the reservoirs. Unable to migrate, eel from Hanningfield reservoir had an average age of 17 years, double the mean age of silvering metamorphosis of *A. anguilla* females sampled across Europe and North Africa (Vollestad, 1992). The more developed silvering characteristics (higher ocular index) of reservoir eel coincided with a shorter interval between release and the commencement of migration compared to river eel. The driver of this difference in silvering stage is unclear but may reflect the greater age of reservoir eel or environmental variation. To reduce potential impacts on the ecology of the receiving river by artificially delivering a large biomass of eel to a point location, T&T programmes should aim to maximise the probability that translocated individuals migrate without extended delay. Migratory readiness should, therefore, be a key consideration during selection of individuals for translocation post-capture. Findings suggest that ocular index is a stronger predictor of migratory readiness than fin index. All of the T&T eel that migrated had an ocular index exceeding 4.1, which is comparable to migratory *A. anguilla* individuals in other studies (e.g. ≥4.6 Calles et al., 2010; ≥3.7 Dębowski et al., 2016)

Despite their larger size, T&T eel descended the freshwater reach slightly slower than river-resident eel, yet the overall proportion that escaped to the estuary was similar. Environmental factors, irrespective of eel origin, were also strong determinants of migration rate in the freshwater catchment. Increased discharge and darker phases of the moon were associated with faster migration and are both widely reported as important cues for downstream migration in European eel (Bultel et al., 2014; Vollestad et al., 1986) and other anguillids (e.g. Crook et al., 2014 for short-finned eel *Anguilla australis*). Locomotor capability in teleost fishes is, to varying degrees, phenotypically plastic (Davison, 1997; Nelson et al., 2015), therefore slower freshwater migration among translocated eel may reflect a lack of exposure to river flow, resulting in inferior swimming performance due to lower fitness. Further, adult eel align with streamlines during downstream migration, adopting an advective behaviour (Piper et al., 2015), and an inexperience of river flow patterns among eel from lentic waterbodies may render them less adept at exploiting advantageous hydrodynamics to expedite their transit downstream. The difference may also reflect some physiological impairment associated with the transport process. Fish that undergo T&T are at risk of elevated and cumulative stress due to handling and transport in tanks at high densities for what may be extended durations (Maule et al., 1988). In the current study, eel were held at their capture location for up to 8 days before tagging and journey times between the capture and tagging/release sites ranged from 25 to 50 min. While not desirable, holding fish may be necessary because in a full-scale T&T programme it may not be economically feasible to transport and release what may be just a few individuals captured each day. Fish may need to be accumulated over several days and released in batches. In a study of European eel migration through Alta Fjord, Norway, 81 % of individuals retained for up to four months commenced migration after release (Davidsen et al., 2011). Measurement of stress level among the transported eel was not conducted in the current or previous T&T studies (e.g. Béguer-Pon et al., 2018; Stanley, 2014). Visual observations made during tagging and the telemetry data provided no indication of delayed mortality or heightened predation risk due to capture, holding or transport within the T&T process, but this aspect warrants further investigation.

Having reached the estuary, there was substantial variation in residence time among individuals. Most (75 %) moved out towards the North Sea within five days, but 16% resided for 20 days or longer. None of the environmental factors investigated were predictors of migration rate through the estuary. A study of short-finned eel found many migrating individuals resided in the estuary for an unexpectedly long period, with a median residency of 77 days, and that eventual movement to sea was associated with a waning moon (Crook et al., 2014). In a relatively high discharge catchment such as the Loire River, France, the majority (83 %) of tagged European eel left the estuary during a single flood event, but some individuals remained for up to three months (Bultel et al., 2014). The Stour estuary extends over 15 km so is relatively long given the modest size of the freshwater catchment, which may explain the absence of a relationship between river discharge and eel migration rate in the estuary. Aarestrup et al. (2010) similarly found that discharge had no effect on eel migration in the outer section of Randers Fjord, Denmark. Where tidal forces exceed the effect of discharge, estuarine movements are likely to be strongly linked to tidal currents with eels shown to employ selective tidal stream transport, migrating downstream with the ebbing tide to maximise the distance moved for the energy expended (Verhelst et al., 2018). Only one eel that reached the estuary in the current study failed to egress to the North Sea, which contrasts with other studies that report high losses in the early marine phase of adult migration, principally due to fishing (Aarestrup et al., 2008, 2010).

5. Conclusions

Findings indicate that T&T of silvering adult eel from landlocked lentic waterbodies to nearby catchments represents a feasible method to enhance local spawner escapement, with likely minimal impacts on the ecology of the receiving river. Where T&T schemes are in operation, they are often considered to be a temporary measure until more permanent safe passage solutions can be implemented. Due to the high costs and variable efficacies of screening, behavioural guidance technologies, fishways and ‘fish friendly’ turbine and pump technologies, water managers may reason that T&T will enable them to more effectively meet their obligations to enhance the escapement of eel, at least in the short term (Lagenfelt and Westerberg, 2008; van der Meer, 2012). In the longer term, facilitating the safe ingress of eel into disconnected waterbodies, either through the restoration of upstream migration routes or assisted migration, could be used to increase the availability of eel habitat for the growing (yellow) lifestage. Given the recent and severe decline in European eel, the exact causes of which remain unclear, such waters may even have merit as ‘eel banks’ to maintain a baseline standing stock available for T&T in the future when the prospects for oceanic spawners and their progeny will, hopefully, be more assured. However, it is not currently understood how delayed migration and the associated multiple cycles of silvering and reversion may affect eel reproductive fitness and likelihood of successful spawning.

The design, implementation, monitoring and regulation of any effective T&T scheme requires substantial time and financial investment (McCarthy et al., 2014). Our results highlighted the potentially high capture effort that may be required, and therefore the importance of quantifying eel abundance and population structure in the source waterbody. Future work should be directed towards optimising the efficiency of eel T&T. Direct translocation from landlocked lentic waterbodies to the marine environment could present the optimum way to expedite seaward escapement and minimise river impacts such as water intakes, barriers, fishing and predation. Silver and yellow eel have been shown to acclimate well to rapid transfer between fresh and saline waters in terms of osmoregulation (Rankin, 2009), but its potential effect on eel behaviour and spawning viability requires further investigation.

CRediT authorship contribution statement

Adam T. Piper: Conceptualization, Funding acquisition, Methodology, Investigation, Formal analysis, Writing - original draft. **Paula J. Rosewarne:** Investigation, Data curation, Formal analysis, Writing - original draft. **Rosalind M. Wright:** Conceptualization, Funding acquisition, Resources. **Paul S. Kemp:** Supervision, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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