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Energetically efficient behaviour may be common in biology, but it is not universal: a test of selective tidal stream transport in a poor swimmer

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ABSTRACT: Selective tidal stream transport (STST) is a common migration strategy for a wide range of aquatic animals, facilitating energetically efficient transport, especially of species considered poor swimmers. We tested whether this mechanism applies during the upstream migration of a poor swimmer, the European river lamprey *Lampetra fluviatilis*, in a macrotidal estuary. Lamprey ($n = 59$) were acoustically tagged and tracked in a 40 km section of the River Ouse estuary (NE England) in autumn 2015. Against expectations, lamprey did not use STST and migrated upstream during flood, ebb and slack tide periods. Lamprey also migrated during both day and night in most of the study area, probably due to the high turbidity. The global migration speed (all individuals, over the entire track per individual) was (mean ± SD) 0.15 ± 0.07 m s^{-1}. The migration speed varied significantly between tidal periods (0.38 ± 0.04 m s^{-1} during flooding tides, 0.12 ± 0.01 m s^{-1} during ebbing tides and 0.28 ± 0.01 m s^{-1} during slacks). It was also higher in areas not affected by tides during periods of high freshwater discharge (0.23 ± 0.08 m s^{-1}) than in affected areas (0.17 ± 0.14 m s^{-1}). If the energetic advantages of STST are not employed in macrotidal environments, it is likely that the fitness costs of that behaviour exceed potential energy savings, for example due to increased duration of exposure to predation. In conclusion, STST is evidently not universal in relatively poor swimmers; its use can vary between species and may vary under different conditions.

KEY WORDS: Energy efficiency · Selective tidal stream transport · Fish migration · Telemetry · Estuary · Anadromous · River lamprey · *Lampetra fluviatilis*

INTRODUCTION

Energetic efficiency and optimality theory has played a strong role in the field of behavioural ecology, including in studies of migratory behaviour (Arnold 1988). Migration is a common strategy for a wide variety of animal taxa (Alerstam et al. 2003, Dingle & Drake 2007), and migratory species evolve traits, including behavioural changes, that allow them to perform more efficient displacements by reducing rates of energy expenditure (Weber 2009, Shepard et al. 2013, Bennett & Burau 2015, Lennox et al. 2016). Hence, it is common for migratory species to take advantage of wind or water currents to migrate (Åkesson & Hedenström 2007, Chapman et al. 2011, Benjamins et al. 2015). In fact, the use of currents allows even species with low swimming or flight performances to migrate long distances, sometimes thousands of kilometres (Alerstam et al. 2003, Gill et al. 2009).

When currents are cyclic in time, animals may exploit this cycle. Thus, in estuarine and coastal areas, migratory species can use selective tidal stream transport (STST) to move by taking advan-

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tage of tidal currents (Queiroga et al. 1997, Forward & Tankersley 2001, Gibson 2003, Islam et al. 2007, Trancart et al. 2014). Species using STST move into strong currents on the selected tide (flood or ebb tide for upstream and downstream movement, respectively) and avoid the opposite tide, usually taking refuge on the bottom or the channel edges (Olmi 1994, Forward & Tankersley 2001, Trancart et al. 2012, Bennett & Burau 2015). STST is particularly relevant in species or life stages with poor swimming performance, due to their limited capacity to migrate against the current, but has also been widely described in strong swimmers, potentially due to energy savings (Forward & Tankersley 2001, Gibson 2003). The energy saving using STST in comparison with a continuous migration was estimated for flatfishes to be 20–90% (Weihs 1978, Metcalfe et al. 1990).

STST has been described for a variety of taxa and life stages, from larvae to adults and from invertebrates to fish (Forward & Tankersley 2001), including a wide range of diadromous fish species (Aprahamian 1988, Moore et al. 1995, 1998a,b, Aprahamian et al. 1998, Forward & Tankersley 2001, Beaulaton & Castelnaud 2005, Edeline et al. 2007, Béguer-Pon et al. 2014, 2016, Trancart et al. 2014, Bennett & Burau 2015, Fukuda et al. 2016). Lampreys, exhibiting modified anguilliform locomotion, show relatively poor swimming performance (Moser et al. 2015) and are negatively buoyant like flatfishes. In addition, as for several other anadromous species, lampreys do not feed during their spawning migration and completely rely on stored energy reserves (Moser et al. 2015). Consequently, lampreys are expected to use STST to migrate in macrotidal areas. Although anadromous lampreys are economically, socially and ecologically important (Close et al. 2002, Foulds & Lucas 2014, Araújo et al. 2016) and many species are threatened (Maitland et al. 2015), information on their migratory behaviour in estuaries is scarce. However, information on migratory behaviour of diadromous species in estuarine areas is fundamental for the proper management and conservation of these threatened species and the fisheries they support (Aprahamian et al. 1998, Martin et al. 2009, Bennett & Burau 2015, Nachón et al. 2016).

The aims of this study were to (1) test the hypothesis that upstream-migrating lampreys exhibit STST during estuarine migration and (2) determine the effects of environmental factors such as freshwater discharge, water temperature and day–night transitions on estuarine lamprey migration.

MATERIALS AND METHODS

Site description

The study was carried out in autumn 2015 in the River Ouse estuary, northeast England (Fig. 1), which combines with the River Trent to form the Humber estuary (mean flow 250 m^3 s^{-1}). The Ouse and Humber estuary exhibits strong vertical mixing due to its rapid tidal currents (Uncles et al. 2006). This system does not (unlike some estuaries such as the Mississippi, USA, or Rhone, France) have a salt wedge that travels upstream on the flood tide, while the freshwater continues to flow downstream over the top of it. Vertically it is essentially a single water body without stratification, although frictional energy losses make flows slower near the bed than in the middle/surface of the water column. The typical tidal range for the Humber is 3.5–7.0 m (neap–spring) and for the lower Ouse is 1.5–3.5 m (neap–spring) (Uncles et al. 2006). These generate high

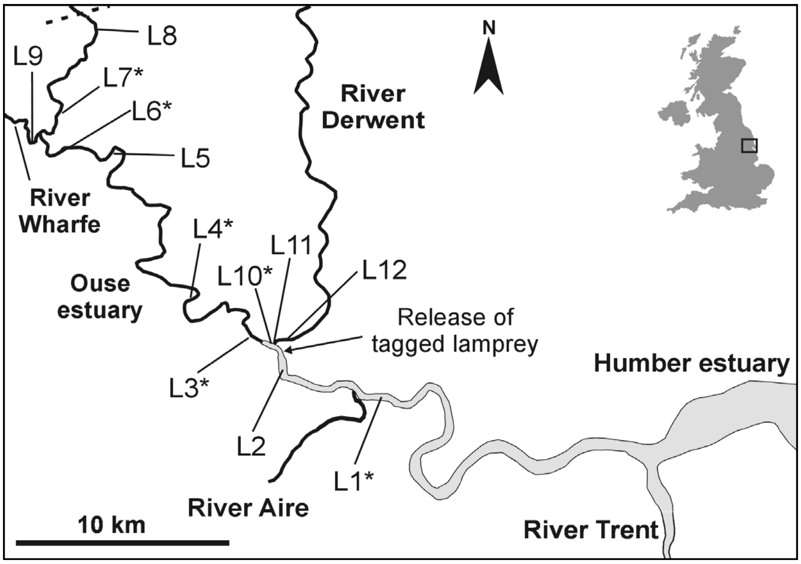

Fig. 1. Study area showing the acoustic logging locations in the Ouse estuary (L1–L8), the River Wharfe (L9) and the River Derwent (L10–L12). Dashed section on River Ouse denotes tidal limit at Naburn weir. Inset, the study area within Britain. River lamprey *Lampetra fluviatilis* were captured between L7 and L8. *Location with 2 acoustic receivers; absence of asterisk indicates a single acoustic receiver

water velocities upstream during flooding tides, and downstream during ebbing tides, which, on the Ouse, are asymmetrical in duration. Peak speeds exceed 1.5 and 1 m s^{-1} during flooding and ebbing spring tides, respectively (>1 and >0.6 m s^{-1} for flooding and ebbing tides on neaps) in the lower Ouse (Uncles et al. 2006).

Experimental design, lamprey capture and tagging

Lamprey movement in relation to the tidal cycle was recorded from acoustically tagged lamprey using a series of acoustic receivers, spread along the study reach (Fig. 1), with a mixture of lamprey released at the start of the flooding and ebbing tides. Lamprey were captured from the upper Ouse estuary using unbaited 2-funnel eel pots (Masters et al. 2006), since the fast tidal currents in the lower Ouse and Humber make capture of lamprey there extremely difficult. The location of capture (between localities L7 and L8; see Fig. 1) is a tidal area (showing current reversals, M.C.L. pers. obs.) with normal tidal amplitude of 1–2.5 m, lost only temporarily when exceptionally strong river discharge occurs (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m584p161_supp.pdf).

Lamprey for tagging were anaesthetised using a buffered 0.1 g l^{-1} solution of tricaine methanesulphonate (MS-222). Total body length (±1 mm) and weight (±1 g) were obtained for each individual. In total, 59 individuals were tagged by implanting a coded 69 kHz acoustic transmitter (Model LP-7.3, 18 mm long × 7.3 mm diameter, 1.9 g in air, 10–30 s code interval nominal repeat, 30 d minimum tag life; Thelma Biotel) into the body cavity. Lamprey were also tagged with a 32 × 3.65 mm passive integrated transponder (PIT) tag (HDX, Texas Instruments model RI-TRP-RRHP, 134.2 kHz, weight 0.8 g in air). The PIT tag was for another investigation (Silva et al. 2017) and therefore PIT data were not analysed in this study. A mid-ventral incision closed with 3 separate sutures (coated Vicryl, 4/0) was used for tagging under a UK Home Office Licence following the Animal Scientific Procedures Act (1986). Only individuals with a total length ≥380 mm were tagged. The overall average length and mass of all tagged lamprey were (mean ± SD) 400 ± 15.2 mm (range: 380–444 mm) and 104 ± 15.8 g (range: 87–155 g), respectively (Table S1). Tag burden was 2.6 ± 0.33% (range: 1.7–3.1%) (Table S1). Fish were allowed to fully recover (held for a minimum of ca. 1 h) in aerated water before release.

Acoustic tracking

To track the movement of the acoustic tagged lamprey, a set of 18 omnidirectional acoustic receivers (Vemco VR2) were deployed in 12 locations in the tidal Ouse and 2 of its tributaries, the Rivers Derwent and Wharfe (Table S2, Fig. 1). The total distance covered in the Ouse estuary was 40 km (Table S2). The loggers were operational from 26 October 2015 to 22 January 2016. Several tests were carried out at different flow and tide conditions to determine the range of detection of the loggers (detection radius was ca. 80–100 m).

Acoustic tagged lamprey were released in the tidal River Ouse 480 m upstream of location L2 (Fig. 1). Releases of these individuals were spread through the study period (1 to 8 lamprey released per day on 13 different days between 24 November and 18 December 2015). They were also split between tides, with an average pattern of release of 1.5 individuals at the start of the ebbing tide and 1 at the start of the flooding tide (Table S1).

Environmental data and data analysis

The efficiency of the acoustic loggers was determined *in situ* by comparing lamprey detected at each receiver, against that expected based upon known routes. For example, tagged lamprey reaching the most upstream receiver were expected to be detected at all the loggers located between that receiver and the release point.

One lamprey was never detected by any logger (ID 340, Table S1). Another lamprey (ID 379) was only detected at L2 (4 single detections at this site) and L6 (1 single detection) but was not detected at any of the 7 loggers set between these 2 locations. The tags send a signal every ~30 s, and lamprey take at least several minutes to pass the range of detection (ca. 160–200 m; radius of 80–100 m) of each logger, normally generating much more than 1 to 4 detections. Therefore, the detection pattern for this tag did not correspond to lamprey behaviour and the lamprey was considered likely to have been predated. Consequently, both tags were removed from the analyses of logger efficiency and lamprey migration (speed, movement vs. diel or tidal cycle, etc.). Lamprey migrating to the River Derwent (n = 16) were also removed from the analyses. Thus, the final sample for analysing the migratory tidal behaviour was 41 individuals (21 released at flooding and 20 at ebbing tides; Tables S1 & S3).

Environment Agency records at water level recording stations (values every 15 min) were obtained for locations L10 (~L3), L4, L6, L8 and L9 and for Ouse discharge at Skelton (17 km upstream of L8). Flows were related to the percentage of annual exceedance (Q_x) by using an annual flow duration curve based on historic discharge data (1973–2014) (http://nrfa.ceh.ac.uk/data/search). Water temperatures were measured at 15 min intervals using an automatic logger (Tinytag, TG-4100) at the lamprey release point (Fig. 1).

For all analyses, the first detection of each lamprey at each logger was used. The direction of movement (upstream or downstream) was obtained by identifying the location of the previous detection. For each detection, the time of day (also categorised as day, night and twilight) and the tide (flooding, ebbing and slack periods) were recorded. Astronomical twilight and sunrise and sunset were used to define the day, twilight and night periods for the near locality of York (obtained from www.dateandtime.info). Water levels at different locations were analysed and plotted to determine the tidal cycle and range (Fig. 2). The peaks and troughs of water level were used to identify the high and low tides. Slack water intervals, characterised by slow velocity periods around the

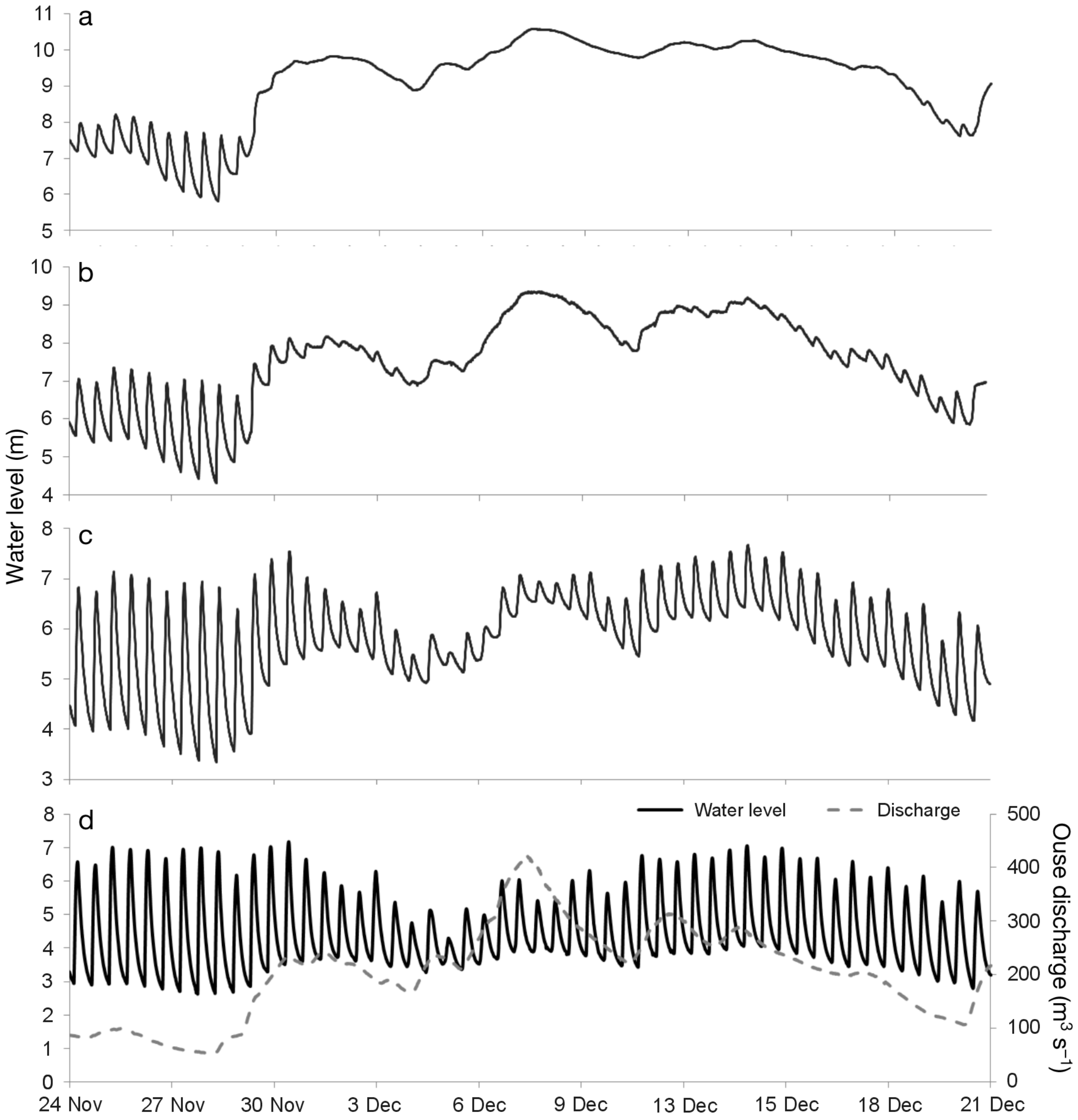

Fig. 2. River Ouse discharge at Skelton and Ouse water levels at acoustic logging locations (a) L8, (b) L6, (c) L4 and (d) L3 during the study period

time at which the tide turns, were determined based on the detailed description of water level and flow velocity fluctuations in the Ouse made by Uncles et al. (2006) and on our own water level data and observations. Thus, the slack periods covered from high tide to 1 h after high tide and from 1.5 h before low tide to 0.5 h after.

Due to the high discharge conditions during much of the study period, the tidal effect in logging locations L6–L9 was absent or negligible after 30 November 2016 (Fig. 2). In contrast, L4 and the section located downstream were clearly tidal through the study period (Fig. 2). L5 was considered to be in an intermediate situation. Downstream movements of lamprey were scarce (n = 10 displacements) as were detections of lamprey at locations downstream of the release site (1 lamprey at L1 and 9 at L2). Therefore, movements in the section between the release point and L4 were selected to analyse the tidal effect on lamprey migration. Due to the small number of downstream movement events, downstream movements were not used for data analysis.

Under the selective tidal migration hypothesis, ca. 100% of lamprey movements detected at flooding tides would be expected (Forward & Tankersley 2001), with lamprey avoiding the ebbing tide by taking refuge on the bottom or the channel edges during the slack periods (Forward & Tankersley 2001). On the other hand, if there is no selection and lamprey keep moving during the ebb and the flood tides, as well as during both slack water periods, the proportion of detections in each tidal stage will depend on its relative duration and the average lamprey speed (speeding up migration on flooding tides and delaying it at ebbing tides) as follows:

$$S_{i\ (F,\ E\ \mathrm{or}\ S)} = D_i \,/\, t_i \tag{1}$$

$$D_T = D_F + D_E + D_S \tag{2}$$

$$D_i\ (\%) = 100\ (D_i \,/\, D_T) \tag{3}$$

where S_i is the average lamprey migration speed at each tide stage (F: flooding; E: ebbing; S: slack), D_i is the distance moved per tide stage (T: entire tide), t_i is the time covered by each tide stage and D_i (%) is the percentage of lamprey displacement per tidal cycle performed at each tide stage. The flooding tide comprised 18.5% of the tidal cycle, the ebbing tide 57.3% and the slack water periods 24.2% in the selected section of the tidal Ouse during the study period. Our data show that average lamprey speed in the tidal Ouse was 0.38 m s^{-1} during flooding tides, 0.12 m s^{-1} during ebbing tides and 0.28 m s^{-1} during slack water periods. With these values and under a continuous migration scenario, 33% of the migration would be performed during the ebbing tide, 34% during the flooding tide and 32% during slacks. This would be reflected in a similar proportion of lamprey detections in the acoustic loggers.

Global lamprey speed was obtained in the same way but using time and distance between release and the first detection at the most upstream logger. Interlogger lamprey speed was calculated by dividing the time between detections at consecutive loggers by the distance between those loggers. The speed at different stages of the tidal cycle (flooding, ebbing or slacks) was obtained from displacements performed in a single ebbing or flooding tide in the section affected by tides (from the release point to L4).

Chi-squared tests were used to analyse if the percentage of lamprey detections was affected by the diel and tidal cycles. Spearman and Pearson correlations, Student's *t*, Kruskal-Wallis *H*- and Mann-Whitney *U*-tests (with Bonferroni corrections; Bland & Altman 1995) were carried out to determine which factors had a significant effect on lamprey speed. The distribution of detections during the day and tide cycles were represented in rose histograms.

RESULTS

Tidal and diel cycles

The tidal cycle was completed in an average (± SD) of 12.4 ± 0.5 h at L3 and 12.4 ± 0.8 h at L4 during the period of study in which movement of tagged lamprey was recorded (24 November to 21 December 2015). The flooding and ebbing tides comprised an average of 2.3 ± 0.5 h at L3 and 2.3 ± 0.8 h at L4 (19%) and 7.1 ± 0.6 h at L3 and 7.1 ± 0.9 h at L4 (57%) per tide, respectively. The slack water periods comprised 3 h per tide (24%), 1 h of high water slack period (8%) and 2 h of low water slack period (16%). The tidal range was 2.8 ± 0.8 m at L3 and 1.6 ± 0.9 m at L4. The diel cycle was 12.0 ± 0.17 h of night (50%), 7.7 ± 0.24 h of day (32%) and 2.2 ± 0.03 h each twilight (4.4 h both together; 18%). River Ouse discharge was (mean ± SE) 204.8 (Q_3) ± 86.0 m^3 s^{-1} (range: 54.0–421.2 m^3 s^{-1} [Q_{31}–$Q_{0.1}$]) (Fig. 2). Thus, the study was carried out under high flow conditions. The water temperature was 6.8 ± 1.2°C (range: 4.6–9.5°C) in the tidal Ouse.

Detection efficiency of acoustic loggers for fish-borne tags was (mean ± SE) 97 ± 1.8%. From the 41

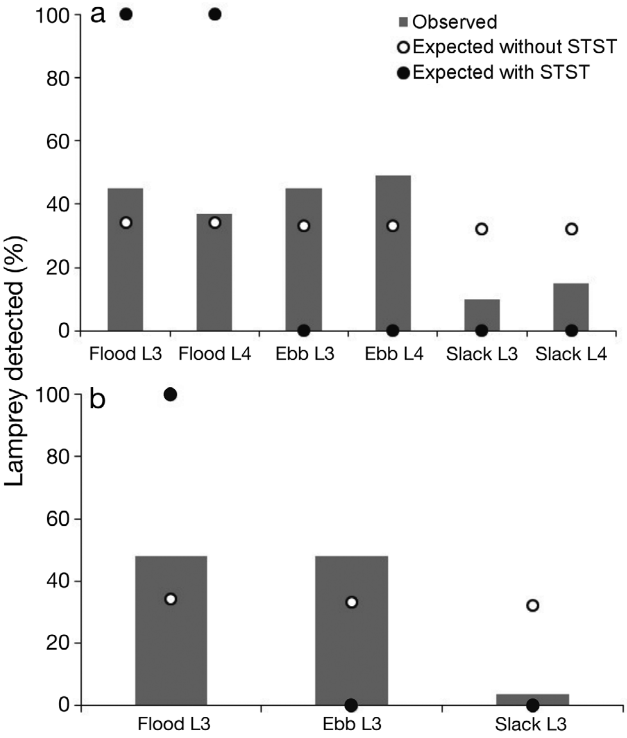

Fig. 3. Percentage of river lamprey *Lampetra fluviatilis* first detected on flooding tides, ebbing tides and at slack tide periods, in localities L3 and L4, and percentage expected with and without using selective tidal stream transport (STST), (a) using all lamprey movements (n = 40 at L3; n = 41 at L4); (b) using lamprey movements between acoustic loggers within a single tide period (n = 13 at L3)

lamprey migrating through the tidal Ouse, a total of 245 interlogger movements were detected, 235 (96%) in an upstream direction and 10 (4%) in a downstream direction.

Distribution of migration detections in relation to tidal and diel cycles

A total of 40 and 41 lamprey were detected at L3 and L4, respectively (Table S3, Figs. S2 & S3), and were used to analyse the lamprey migration in relation to the tides. The percentage of lamprey detected moving at each tide period was significantly different from that expected if lamprey were using STST (χ^2 = 818.265, df = 2, $p < 0.001$ at L3; χ^2 = 1028.014, df = 2, $p < 0.001$ at L4), as lamprey were also migrating at ebbing tides (Fig. 3). In addition, it was not within the expected values for a non-selective tidal continuous migration (χ^2 = 9.123, df = 2, p = 0.010 at L3; χ^2 = 6.964, df = 2, p = 0.031 at L4) due to the low number of detections recorded at slack periods (Fig. 3). Nonetheless, detections at flooding and ebbing tides were within the expected values for a non-selective tidal migration (χ^2 = 0.008, df = 1, p = 0.929 at L3 and χ^2 = 0.872, df = 1, p = 0.351 at L4; Fig. 3). The same results were recorded when using a more conservative approach (using only interlogger movements within a single ebb, flood or slack). That analysis also showed that the percentage of lamprey detected moving at each tide period was significantly different from that expected if lamprey were using STST (χ^2 = 560.878, df = 2, $p < 0.001$; Fig. 3). It also showed a different pattern from that expected for a non-selective tidal continuous migration (χ^2 = 9.165, df = 2, p = 0.010) due to the low number of detections recorded at slack periods (Fig. 3) but with detections at flooding and ebbing tides within the expected values for a non-selective tidal migration (χ^2 = 0.006, df = 1, p = 0.937; Fig. 3). When dividing the tidal cycle in 6 equal intervals (2.06 h), the pattern of detection differed from that expected

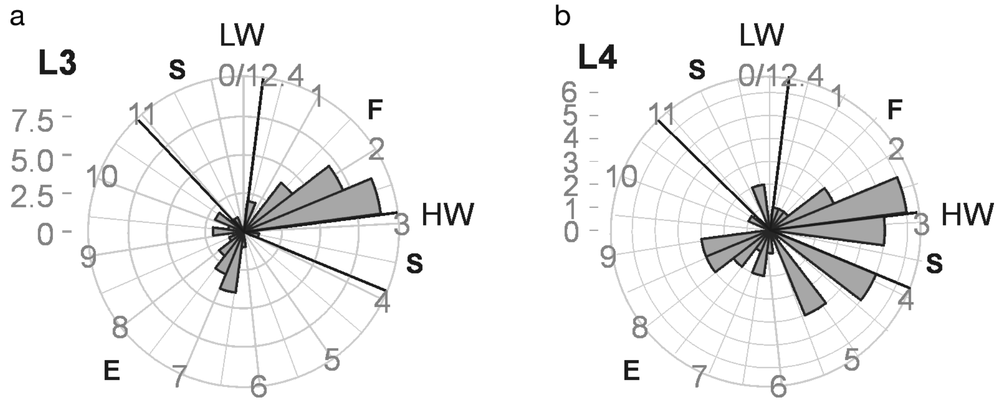

Fig. 4. Rose diagrams showing distribution of the first detection of each river lamprey *Lampetra fluviatilis* at locations (a) L3 (n = 40) and (b) L4 (n = 41) through the tidal cycle (12.4 h) (20 lamprey released at ebbing and 21 at flooding tides). Tidal stages delimited by black lines. S: slack; F: flooding tide; E: ebbing tide; HW: high water; LW: low water. Radial sectors: hours since low water; concentric ring scale: frequency of first detections in tide state sectors

for equal probabilities per interval at L3 (n = 40; χ^2 = 32.000, df = 5, p < 0.001) but not at L4 (n = 41; χ^2 = 9.780, df = 5, p = 0.082; Fig. 4). We detected 27 lamprey at the same tide of release at L3 (1 at slacks and 13 at ebbing and 13 at flooding tides) but none at L4.

In relation to the diel cycle, 29.4 % (n = 69) of the upstream movements were detected during the day, 56.6 % (n = 133) at night and 14 % (n = 33) during twilight. The distribution did not differ from expected (based on day, night and twilight duration) at L3 (n = 40; χ^2 = 1.735, df = 2, p = 0.420), L4 (n = 41; χ^2 = 2.025, df = 2, p = 0.363), L5 (n = 40; χ^2 = 2.272, df = 2, p = 0.321), L6 (n = 40; χ^2 = 5.878, df = 2, p = 0.053) and L8 (n = 35; χ^2 = 0.221, df = 2, p = 0.896) (Fig. 5, and see Figs. S2–S5 in the Supplement). It differed significantly only at L7 (n = 35; χ^2 = 13.173, df = 2, p = 0.001), with more lamprey detected at night and fewer during the day than expected. The distribution did not differ from expected at any location when using 4 h intervals with the same probability of lamprey detection: L3 (n = 40; χ^2 = 11.000, df = 5, p = 0.051), L4 (n = 41; χ^2 = 3.049, df = 5, p = 0.692), L5 (n = 40; χ^2 = 4.400, df = 5, p = 0.493), L6 (n = 40; χ^2 = 6.500, df = 5, p = 0.261), L7 (n = 35; χ^2 = 9.743, df = 5, p = 0.083) and L8 (n = 35; χ^2 = 4.257, df = 5, p = 0.513).

Migration speed

From the 41 lamprey detected migrating through the Ouse estuary, 35 (85.4 %) were last detected at the most upstream logger (L8; 32.9 km upstream from the release point), 1 at L7 (2.4 %; 27.5 km upstream from the release point) and 5 at L6 (12.2 %; 24.3 km upstream). Lamprey arriving to the most upstream location took a mean (± SD) of 102 ± 124 h (range: 30–586 h) to do so from release. This corresponds to a global average speed of 0.15 ± 0.07 m s^{-1} (range: 0.02–0.30 m s^{-1}) and 0.36 ± 0.18 body lengths (BL) s^{-1} (range: 0.04–0.75 BL s^{-1}).

The average (± SD) interlogger speed for upstream movements (n = 235) was 0.20 ± 0.11 m s^{-1} (range: 0.002–0.58 m s^{-1}), which corresponds to an average of 0.51 ± 0.26 BL s^{-1} (range: 0.005–1.33 BL s^{-1}). Interlogger speed was correlated with the water temperature (r_S: +0.200, p < 0.01), and differed between sections of the study area (Kruskal-Wallis test, H = 22.15, df = 5, p = 0.001), with higher and less variable values in the reaches with negligible tidal influence over the majority of the study period (L6–L8; Fig. 6). Interlogger speed was 0.23 ± 0.08 m s^{-1} (range: 0.06–0.48 m s^{-1}) or 0.57 ± 0.21 BL s^{-1} (range: 0.14–1.23 BL

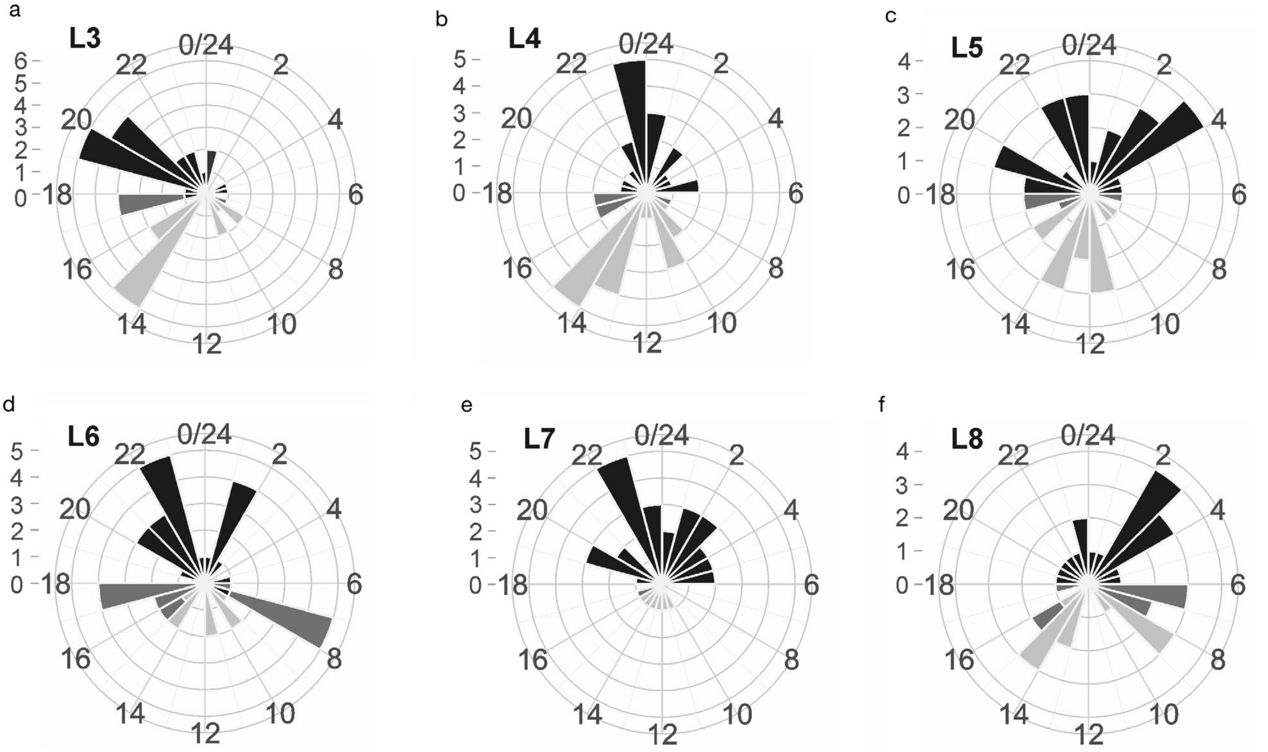

Fig. 5. Rose diagrams showing diel distribution (black: night; dark grey: twilight; light grey: day) of the first detection of each river lamprey *Lampetra fluviatilis* at locations (a) L3, (b) L4, (c) L5, (d) L6, (e) L7 and (f) L8. Radial sectors: time of day; concentric ring scale: frequency of first detections in time-of-day sectors

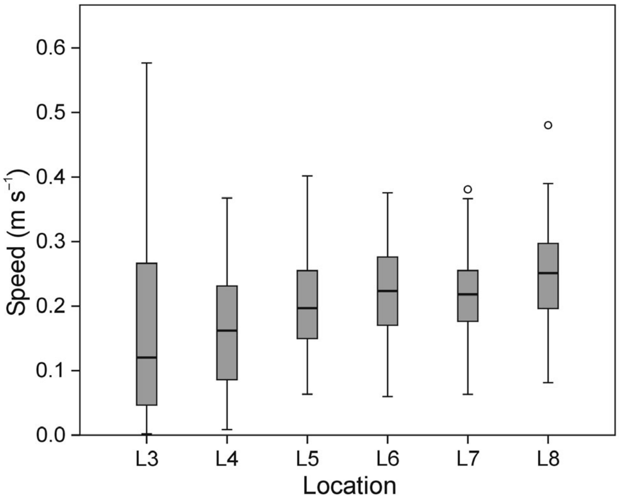

Fig. 6. River lamprey *Lampetra fluviatilis* speed between acoustic logging locations situated in the Ouse estuary. Locations in the graph correspond to the upstream location of each movement; n = 40 at location L3, 41 at L4, 40 at L5, 40 at L6 and 35 at L6, L7 and L8. Box plots show median, lower and upper quartiles, maximum and minimum values and outliers

s $^{-1}$) in areas mostly not affected by tides, due to high discharges, and 0.17 ± 0.14 m s^{-1} (range: 0.002–0.58 m s^{-1}) or 0.42 ± 0.33 BL s^{-1} (range: 0.005–1.33 BL s^{-1}) in permanently tidal areas.

In areas upstream of the release point and strongly affected by tides over the whole study period (L3, L4) there was a significant difference in lamprey speed between tidal periods (Kruskal-Wallis test, $H = 18.519$, df = 2, $p < 0.001$), namely between ebbing and flooding tides ($t(15) = 6.609$, $p < 0.001$). Lamprey speed was (mean ± SD) 0.12 ± 0.01 m s^{-1} (range: 0.04–0.19 m s^{-1}) during the ebbing tide, 0.38 ± 0.04 m s^{-1} (range: 0.17–0.58 m s^{-1}) during the flooding tide and 0.28 ± 0.01 m s^{-1} (range: 0.26–0.29 m s^{-1}) during slacks. Therefore, lamprey speed increased 69% on average during the flooding tide and 22% during the water slack and decreased 47% during the ebbing tide, in comparison with average speed observed in the section not affected by tides. In the area affected by tides, individual total length and weight were significantly positively correlated with lamprey speed (Pearson's correlation coefficient = 0.428; $p < 0.05$ for total length; 0.395, $p < 0.05$ for weight).

In the section little affected by tides over most of the study period (from L6 to L8) lamprey speed varied significantly between diel cycle components (Kruskal-Wallis test, $H = 8.328$, df = 2, $p < 0.05$). Significant differences were obtained between day (mean ± SD: 0.19 ± 0.07 m s^{-1}) and night (0.24 ± 0.07 m s^{-1}) (Mann-Whitney *U*-test, $U = 480$, $p < 0.01$) but not between twilight (0.21 ± 0.11 m s^{-1}) and day or night (Mann-Whitney *U*-test, $p > 0.05$). For that section little affected by tides, due to high river discharge, the water temperature (r_S: 0.360, $p < 0.001$) and the river discharge (r_S: −0.239, $p < 0.05$) had a significant impact on lamprey speed. Lamprey speed was significantly different between individuals in this section least affected by tides (Kruskal-Wallis test, $H = 92.904$, df = 40, $p < 0.001$). In contrast, inter-individual differences were not significant in the tide-affected section (Kruskal-Wallis test, $H = 47.930$, df = 40, p = 0.182) due to the high variance of lamprey speed caused by tides (Fig. 7).

DISCUSSION

Energetic efficiency, cost–benefit tradeoffs and STST

Although STST is considered the most energetically efficient behavioural mechanism by which to migrate in strongly tidal environments, and is a common migration strategy for a wide range of animal groups, including diadromous species (Forward & Tankersley 2001, Gibson 2003), evidently it is not universal. STST has been described as highly favourable for species considered poor swimmers (Forward & Tankersley 2001). However, the results of our study show that the river lamprey, a poor swimmer and an obligate migrator which spawns in freshwater, did not exhibit STST in the Ouse estuary under the environmental conditions studied. Those conditions in the lower Ouse are typical of its upstream migration through that part of the estuary (Masters et al. 2006, Foulds & Lucas 2014).

Much of the historical literature on decision-making by animals emphasises energetic benefits and costs (Arnold 1988), and this is also evident for migration and implicit within the STST hypothesis. The main factors considered to be maximized by natural selection in animal migration evolution are reductions in the energetic cost of migration, reductions in mortality (usually related to predation), reductions in time to reach the destination and gains with regard to foraging (Scheiffarth et al. 2002, Brönmark et al. 2008, Alerstam 2011, Bennett & Burau 2015). The foraging gain is not relevant for the spawning migration of lampreys, as they do not feed during that period. In contrast, estuaries tend to be high risk areas in terms of predation (Dieperink et al. 2001, Lochet et al. 2009). Although the use of STST could provide a small energy saving, it increases the time of residence in the

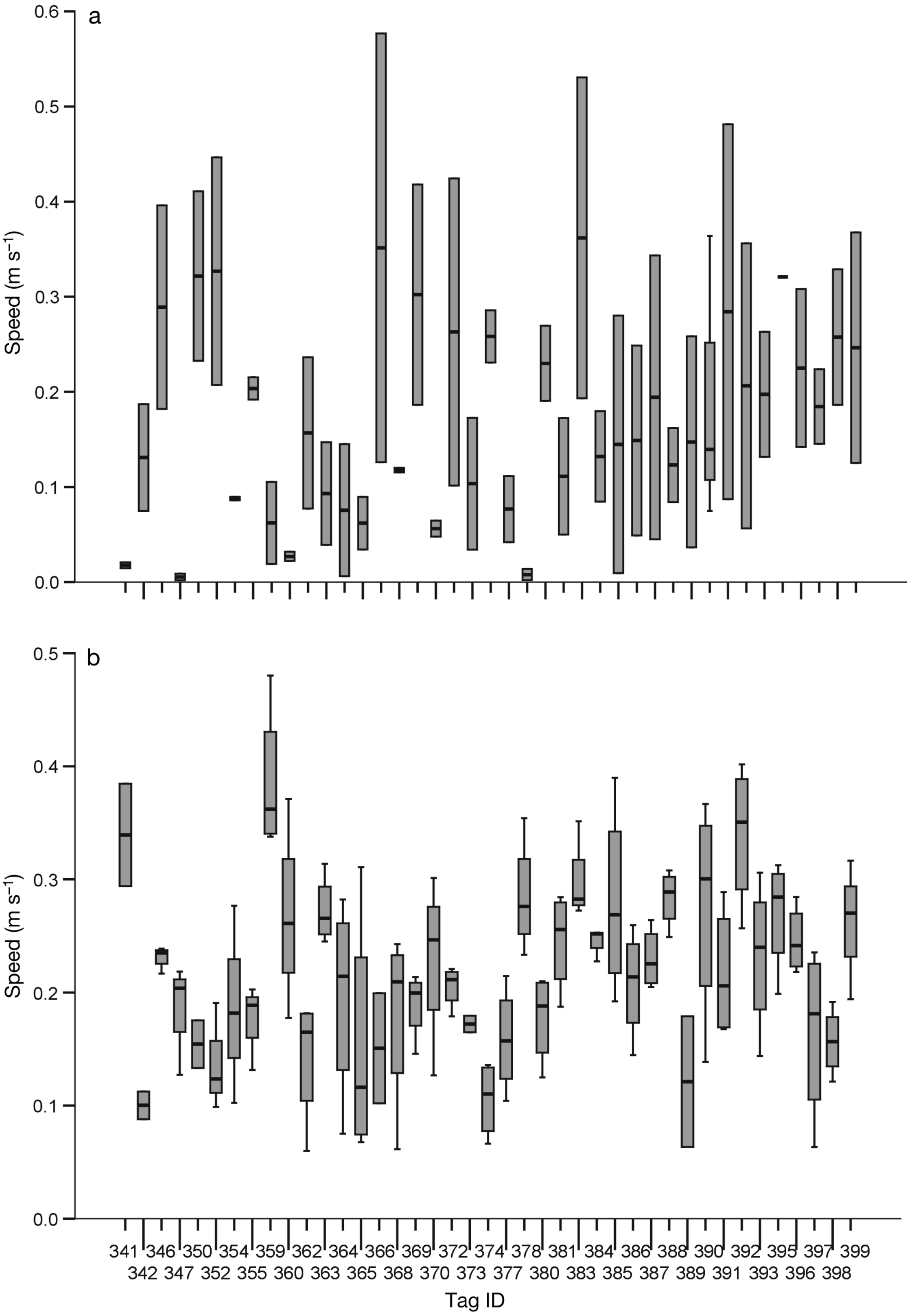

Fig. 7. River lamprey *Lampetra fluviatilis* speed between acoustic logging locations situated in the study area that were (a) strongly affected (locations L3–L4) and (b) least affected by tides (L5–L8) due to the high discharge through much of the study period. Box plots show median, lower and upper quartiles, and maximum and minimum values

open estuary and may therefore increase the risk of predation (Lochet et al. 2009, Martin et al. 2009). During the adult river lamprey migration season, great cormorants *Phalacrocorax carbo*, sawbill ducks (*Mergus* spp.), seals (*Phoca vitulina, Halichoerus grypus*) and harbour porpoise *Phocoena phocoena*, which predate adult lamprey, are all abundant in the Humber-Ouse estuary (M. Lucas unpublished data). Besides predation, lamprey fisheries (as for river lamprey in the upper Ouse estuary) are another source of mortality in estuaries (Hardisty 2006, Masters et al. 2006, Araújo et al. 2016), which might also select for migration strategies of less residence time in the estuary. Nonetheless, in the Ouse the current fishery has only been active for about 2 decades, having previously operated in the late 19th and early 20th centuries.

Faster migration in the estuary would leave more time for freshwater migration that may allow lampreys to reach spawning areas earlier or reach more remote spots with higher quantity and/or quality of habitat and less competition. This may be affected by the distance to the spawning areas and the existence of obstacles that delay the migration and require extra energy expenditure (Lucas et al. 2009, Moser et al. 2015, Lennox et al. 2016). STST is also expected to be more beneficial for upstream migrants in estuaries or estuary sections where a relatively high proportion of the tidal cycle comprises the flood phase. In the Ouse estuary, the tidal cycle period is dominated by the ebbing tide so the time window for upstream migrants under STST would be very limited (only 19% of the time comprises the flooding tide, although flooding tide velocities are higher than during the ebb). Current velocities (dependent on discharge, tidal range, estuary topography) may also affect STST selection.

Migrant lamprey attach themselves to available surfaces to stop and rest during the spawning migration using their mouth as a sucker (Moser et al. 2015). Similar to other estuaries, the Ouse-Humber estuary bed is highly dominated by fine sediments (Freestone et al. 1987). As a result, the availability of places to attach to and rest (i.e. stones) is very limited or non-existent. This might make it more energetically expensive to stop the migration during the ebbing tide and may increase the risk of predation (due to the lack of refuges), reducing the potential advantage of STST.

Weihs (1978) and Metcalfe et al. (1990) also suggested that when currents are markedly slower than the animal's swimming capabilities, continuous migration is expected to be more efficient than STST (although tidally assisted transport has been observed for many species of marine megafauna). Although lampreys are poor swimmers, they commonly use slow current areas in freshwater to allow or facilitate migration while reducing the energy expenditure both in open areas (Holbrook et al. 2015) as well as when seeking to pass obstacles (Keefer et al. 2011, Kemp et al. 2011, Reid & Goodman 2016, Tummers et al. 2016, Silva et al. 2017). Based on the high water velocities that can be reached in the Ouse–Humber estuary (Freestone et al. 1987, Uncles et al. 2006) and the poor sustained swimming performance of river lamprey (Tummers et al. 2016), the observed migration during the ebbing tide is also expected to be carried out close to the shores and/or the estuary bed, where the flow is slower due to frictional energy losses (Uncles et al. 2006). Recent developments in acoustic telemetry, allowing a fine-scale 3D track of individuals (as in Holbrook et al. 2015) may provide an excellent tool to shed more light on this issue. The lower frequency than expected of lamprey migration recorded during slack flow periods in this study may indicate that the reversal in flow direction causes a delay in migration while lamprey adjust their behaviour to respond to this change. Studies with 3D tracking technology may also provide a suitable tool to better investigate changes in behaviour in these transitional periods.

The time of lamprey release may have partially influenced the pattern of lamprey detections recorded at L3 due to the proximity of this location to the release point. Thus, although lamprey took an average (± SD) of 18.5 ± 56.4 h (range: 0.5–326.8 h) from release to this location, 27 individuals out of 40 were recorded within the same tide of release. Nonetheless, this was not the case in more upstream locations. Thus, at L4 no lamprey were detected on the tide phase of that at release, and they took an average of 68.3 ± 117.3 h from release to this location (Table S3). The moment of release also did not affect the period of migration, as each lamprey was detected moving during a variety of daytime periods (Table S3).

Our study illustrates a strong contradiction to STST predictions, but in some other studies, its occurrence may be condition dependent. Although the use of STST for different life stages of the European plaice *Pleuronectes platessa* in coastal areas is well documented and widely accepted (Forward & Tankersley 2001, Gibson 2003), populations from the northern North Sea do not use STST, probably because the tidal currents in that area are too weak to be useful for either guidance or for saving energy (Hunter et al. 2004). Other studies showed that anguillid eels or salmonid smolts changed from using STST in the estuary to a more continuous migration when reaching coastal areas (Moore et al. 1995, 1998b, Hedger et al. 2008, Martin et al. 2009, Lefèvre et al. 2013, Béguer-Pon et al. 2014). Diadromous species have also been observed, sometimes as a complementary behaviour to STST, migrating upstream and downstream with the tides or against tides, increasing the residence time in the estuary (Moser et al. 1991, Moser & Ross 1994, Almeida 1996, Aprahamian et al. 1998, Hatin et al. 2002, Martin et al. 2009). However, this was considered a behaviour to allow adaptation to the change from fresh to salt water, to feed or to reduce their vulnerability to predators while in the estuary, instead of being a migration strategy (Stasko 1975, Quinn et al. 1989, Moser et al. 1991, Moser & Ross 1994).

The capture location (L7–L8) lost a tidal effect after 30 November (Fig. S1) due to extraordinarily high freshwater flows. The lack of tidal variation in this location might influence the decision of lamprey to not use STST and exhibit a more continuous migration when released downstream in a highly tidal area. However, for lamprey captured under tidal conditions (up to 30 November, n = 14, Table S1), most individuals (n = 8, 57%) were tracked migrating during ebbing tides, evidencing that the absence of STST in the main period of study was not a response to capture in an area with temporarily reduced tidal conditions. In addition, river lamprey migration during ebbing tides was also recorded at L5 under strong tidal conditions in a previous study (M. Lucas unpubl. data) for 1 of 2 acoustic tagged lamprey captured and released between L2 and L3 (strong tidal area), further supporting the previous statement.

Diel behaviour and environmental effects

Lamprey migration in freshwater has been described as highly nocturnal (Almeida et al. 2000, Moser et al. 2015), a common strategy of fish to reduce predation (Lucas & Baras 2001, Gibson 2003). However, our results showed that river lamprey migrated both during night and day in most of the study area. The Humber system, including the Ouse estuary, is one of the most turbid estuaries in the British Isles (Uncles et al. 2006). High turbidity has previously been suggested to provide dark underwater conditions and an obscured visual field, that reduce the risk of predation and allow fish migration during the day (Abou-Seedo & Potter 1979, Gregory & Levings 1998, Payne et al. 2013, Bultel et al. 2014, Fukuda et al. 2016, Reid & Goodman 2016, Silva et al. 2017). Almeida et al. (2000) described highly nocturnal behaviour of migrating adult sea lamprey *Petromyzon marinus* tracked in the freshwater section of the River Mondego, Portugal. Nonetheless, in the estuary these authors recorded a large degree of activity of *P. marinus* during the morning (1 h after sunrise to 11:59 h), as much as at night (Almeida et al. 2000).

As in this study, other research has shown that migration speed of diadromous species can be higher during the night than during the day (Martin et al. 2009, Lefèvre et al. 2013). This may be a result of the common strategy of reducing movement during the day to reduce predation risk from day-active species, as explained before. The global speed recorded in this study for river lamprey is within the values previously reported for lampreys (Moser et al. 2015), although lamprey speed recorded in flood tides was above those values. Lamprey speed increased at higher temperatures (well within the range of thermal tolerance) and for larger fish sizes as is widely reported in the fish migration literature (Lucas & Baras 2001). Nonetheless, besides the significant effect of individual factors identified in this study, such as lamprey size, results also suggest that individual temperament or motivation are a natural contributor to the variation of migration rate of lampreys, as described by Moser et al. (2013) for the Pacific lamprey *Entosphenus tridentatus*.

CONCLUSIONS

This study shows that although STST is a common strategy among aquatic biota, it is not universal, as river lamprey did not use STST in the River Ouse estuary. Therefore, the potential benefits from a more continuous migration (lower mortality, earlier arrival to spawning areas, more time available for freshwater migration, etc.) are likely to be of higher fitness benefit than the energetic saving obtained by using STST. Thus, the use of STST will differ between species and may even vary for the same species under different conditions. Lamprey also migrated during the whole diel cycle and not only at night (as usually observed — a strategy to reduce predation risk), probably due to the high turbidity in the estuary. Further studies in a wider range of conditions, such as during low river discharge, or with other tidal conditions and/or predators, and by fine-scale tracking of fish behaviour or the use of accelerometer tags (Cooke et al. 2012), could better determine the degree to which lamprey contradict the STST model under all circumstances, or whether there is plasticity according to local conditions.

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