



Fish passage solution: European eel kinematics and behaviour in shear layer turbulent flows

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ARTICLE INFO

Keywords:

Anguilla
Elver
Upstream
Migration

ABSTRACT

High velocity barriers pose a risk to upstream migrating European eels (*Anguilla anguilla*, Linnaeus) as the flow can be too fast for them to swim against. These barriers delay or even prevent migration, potentially exacerbating population declines of this critically endangered species. Eel tiles are an emerging solution for this application, already successfully deployed to increase passage at gravity barriers. Here, eel tiles mounted to the bed of an open channel recirculating flume were assessed in terms of eel passage, behaviour and kinematics relative to movement in the absence of the tiles. The tiles effectively increased passage and allowed the eels to rest without the need to swim back downstream. The tiles also reduced the amount of energy needed to travel upstream. For the first time eel swimming was examined in a flow with multiple shear layers and turbulent structures of varying lengthscale. Swimming kinematics were analysed for complex turbulent flows and revealed a new swimming gait in the shear layer beside the tile. By allowing the eels to continuously move upstream, the tiles potentially decrease predation and infection risk at resting hotspots. Overall, the tiles were effective in helping eels pass upstream in an experimental flume.

1. Introduction

The European eel (*Anguilla anguilla*, Linnaeus) has been in a population decline since before the 1980s, leading to the species being classified as critically endangered by the IUCN in 2013 (Jacoby and Gollock, 2015; Pike et al., 2020). This catadromous fish that begins its life in the Sargasso Sea (Wright et al., 2022; Miller et al., 2019) is transported by oceanic currents to the coastlines of Europe (Pike et al., 2020; Anderson, 2022). Recruitment of this fish is around 1–5% of pre-1980 levels (ICES, 2020) and this decline has occurred throughout the eel's geographical range. There are multiple causes for this decline. Ocean currents in the Atlantic are shifting as a result of global warming, altering the path larval eels (leptocephali) take to reach fresh water (Baltazar-Soares et al., 2014). When eels arrive in estuaries, they face polluted waters and chemical barriers as well as fishing pressures and infections, including from *Anguillicola crassus*, a common parasite that affects the swim bladder (Kirk, 2003; Righton et al., 2021; Teunen et al., 2021) and impacts eel swimming behaviour (Newbold et al., 2015). Other threats to the upstream migration are the significant number of physical barriers

due to anthropogenic alterations to rivers that make upstream journeys difficult or even impossible (Warren and Pardew, 1998; Piper et al., 2017; Belletti et al., 2020; Halvorsen et al., 2020).

River barriers fragment, disconnect, and reduce habitat availability, this affects many diadromous species but also river resident fish (Belletti et al., 2020; Fuller et al., 2015; Jones et al., 2019; van Puijenbroek et al., 2019). Of these potential 5 million physical barriers in Europe, 1.3% are sluices and tidal gates, 9.8% are dams, 30.5% are weirs, and 17.6% are culverts (Belletti et al., 2020). Each of these obstacles offers a unique challenge for eels in upstream and downstream migration, particularly when passing through hydropower barriers. Fish passes are now commonly implemented at most hydraulic structures. Culverts and river flumes are not gravity barriers but they are velocity barriers (unless they have an overhang), often constricting the flow into a narrow section and typically they have smooth walls; both aspects lead to increases in flow velocity without offering any refugia (Jones et al., 2021; Warren and Pardew, 1998). The high velocities can be too fast for juvenile eels to navigate and the lack of resting opportunities exacerbates energy expenditure by requiring the fish to swim in fast flows over long

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<https://doi.org/10.1016/j.ecoleng.2024.107254>

Received 2 February 2024; Received in revised form 28 March 2024; Accepted 14 April 2024

Available online 24 April 2024

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distances. Fish that attempt these crossings can be exhausted as a consequence of the fast flows and seek to rest immediately upstream of the structure if successful, or immediately downstream if unsuccessful. If many fish are all using the same areas to rest this can create predation hotspots (Jepsen et al., 2010; Wright et al., 2015). Unfortunately, fish that are successful in swimming upstream are soon likely to encounter other barriers and the cumulative effects of navigating multiple barriers can lead to a reduction in the available habitat and exhaustion of the fish.

Eel tiles are a potential solution to velocity barriers. Each tile, made from high density *co*-polymer, is 0.505 m wide and 0.505 m long with a 25 mm base and 50 mm high cylindrical conical protrusions of two densities to accommodate different eel sizes (Fig. 1). The tiles were originally designed to be used on the downstream faces of weirs and similar inclined structures where they might facilitate elvers to pass upstream by climbing (Jellyman et al., 2017; Watz et al., 2019). Elvers can climb upwards using the substrate provided by the protrusions in the tiles. Tiles used in this manner will have flow going through the protrusions, which in normal operating conditions will not exceed the height of the protrusions. These tiles have been tested against other commonly used substrates, such as bristle passes at various inclinations, and in all trials they improved eel passage (Jellyman et al., 2017; Watz et al., 2019). The tiles are sturdy, cheap relative to other passage solutions, and are quick and easy to install, making them an ideal solution for not only streambed inclines but also velocity barriers to potentially create flow conditions more suitable for eels, as well as providing resting areas. (See Table 1.)

The flow over and around eel tiles has been investigated with the use of particle image velocimetry for a wide range of flow conditions, covering diverse flow velocities and flow depths (Sonnino Sorisio et al., 2021). The analysis revealed that the tiles are effective in decreasing flow velocities both within the protrusions and around them without severely affecting the flow carrying capacity of the channel. Two main shear layers are present: a vertical shear layer forms between the tiles and the flow above them and a horizontal shear layer generated in the

Table 1

The flow conditions used for the experiment. Bulk velocity (U) was kept constant while flow depth (H) was varied by adjusting the flume's weir at the downstream end and changing the flowrate (Q). The flow Reynolds number (Re) was calculated based on the hydraulic radius of flow cross-section. The height of the tiles (h) and the flow depth (H) were used to calculate the relative submergence (H/h).

Treatment	Tile Presence	U [ms^{-1}]	H [mm]	Q [Ls^{-1}]	Submergence (H/h) [-]	Flow Re [-]
T56	Tiles	0.35	56	17.50	0.77	1.79×10^4
T75	Tiles	0.35	75	26.25	1.00	2.33×10^4
T129	Tiles	0.35	129	45.15	1.72	3.71×10^4
T155	Tiles	0.35	155	54.25	2.07	4.31×10^4
C56	Control	0.35	56	17.50	0.77	1.79×10^4
C75	Control	0.35	75	26.25	1.00	2.33×10^4
C129	Control	0.35	129	45.15	1.72	3.71×10^4
C155	Control	0.35	155	54.25	2.07	4.31×10^4

lateral region adjacent to the tiles and the 'free stream' flow towards the centre of the channel. Where the areas of slower flow meet the faster flow in the rest of the channel, a mixing layer exists with elevated levels of Reynolds shear stress that create a Kelvin-Helmholtz instability that generates large scale fluctuations that can potentially destabilise swimming fish, which is undesirable for efficient passage (Sonnino Sorisio et al., 2021). This phenomenon occurs in both the vertical (τ_{uv}) and horizontal planes (τ_{uv}); in the vertical the size of the turbulence is limited by the flow depth as the relative submergence of the tiles (ratio of flow depth to protrusion height) was kept below or equal to 2.07 in the flume experiments (Sonnino Sorisio et al., 2021). The vertical

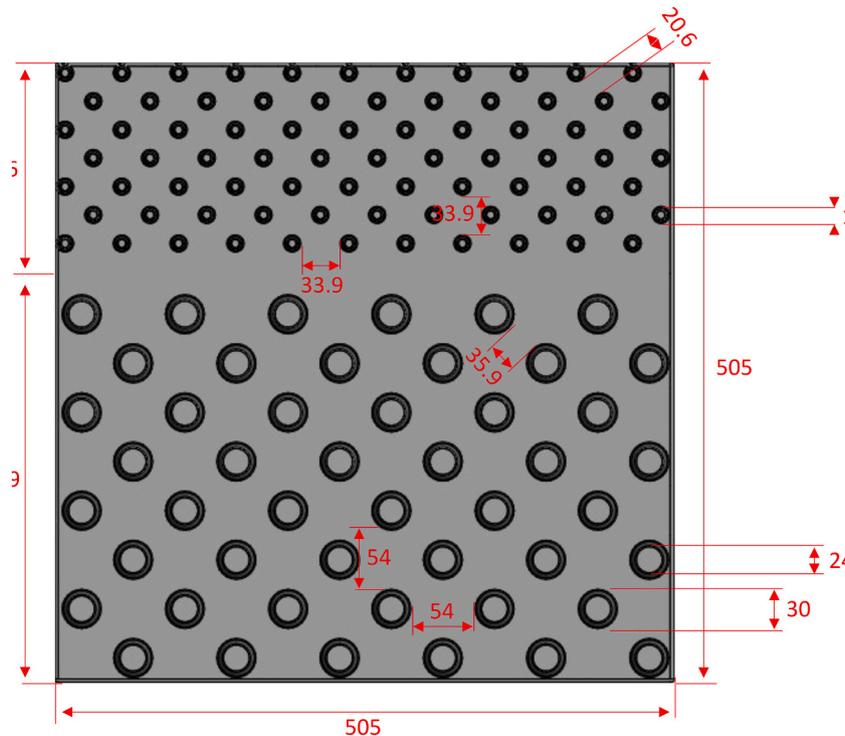


Fig. 1. Top view of a dual density eel tile. In the diagram, the small protrusion section of the tile is at the top and the large protrusion section at the bottom. The tiles are made from a high-density *co*-polymer and have a 25 mm tall base and 50 mm tall protrusions. Units are in millimetres, after (Sonnino Sorisio et al., 2021).

shedding penetrates into the protrusions but velocities in the protrusion sublayer stay low. In the horizontal plane, the turbulent length scale is not bounded by the size of the channel and is of the scale of the spanwise extension of the protrusions and is strongest immediately above the tiles (Sonnino Sorisio et al., 2021).

Understanding the flow interaction between a tiled region, the free stream flow, and the eel's behaviour, including how they adapt to the conditions, is important when evaluating passage solutions. Eels primarily swim during hours of darkness and near the bottom of channels (Harrison et al., 2014; Cresci, 2020) and the way they swim has been observed and often defined as undulatory or anguilliform (Müller et al., 2001; Tytell, 2004a; Tytell, 2004b; Tytell and Lauder, 2004; Lauder and Tytell, 2005). The swimming amplitude envelope of eels is similar to that of other fish with different morphologies, it is symmetrical about the centerline, with a small head amplitude which increases along the body, reaching the maximum at the caudal fin (Lauder, 1995; Gillis, 1998; Tytell, 2004b; Tytell, 2004a; Videler, 2019). Eels do not typically make significant usage of their pectoral fins during swimming. However, the number of wavelengths formed by their body is typically higher than fish with a lower body length to height/width ratio as they are comparatively more slender than other species and therefore less 'rigid' (Borazjani and Sotiropoulos, 2009; Gillis, 1998; Tytell, 2004a). This makes them efficient swimmers but they lack the high swimming speeds of more powerful fish like salmonids (Clough et al., 2004; Clough and Turnpenny, 2001; McCleave, 1980; Van Den Thillart et al., 2004). Generally, head amplitude will remain small at sustained and constant swimming speeds, and increases during acceleration and at burst velocities (Tytell, 2004a). Strouhal number has been used to compare tail velocity and swimming velocity (Triantafyllou et al., 2000). The Strouhal number for eels is generally constant at a value of 0.32, thought to be an efficient swimming mode (Triantafyllou et al., 2000; Read et al., 2003), but this value increases at lower swimming speeds (Tytell, 2004a). However, these observations have been made for eels swimming in stationary water or in an uniformly distributed velocity field, and much less is known about their swimming kinematics in turbulent flow and how they respond to different turbulent structures and shear layer flow. Their crawling gait has been investigated, and on sand, eels were found to adopt a gait with a much more uniform amplitude along the body, with a large amplitude from the head to the caudal fin (Gillis, 1998).

This study evaluates eel tiles as a potential passage solution for eels at velocity barriers. To do this, eels were exposed to flow conditions of increasing flow depth (and therefore tile submergence) and we evaluated their behaviour, kinematics and energetics. These were compared with the hydrodynamic data for these tiles (Sonnino Sorisio et al., 2021) to find how the eels react to different types of shear layer flow. Finally, passage statistics were analysed to determine how tiles impact passage of European eels.

2. Methods

2.1. Fish origin and maintenance

European eels (*Anguilla anguilla*, Linnaeus, $N = 29$) were caught by electrofishing from the Ely Bridge on the Ely River (51.483802, -3.231746) on 29/07/2022 by Natural Resources Wales. The river temperature was 17 °C. The eels were transported (approximately 20 min from the time they were taken from the river) to the School on Engineering at Cardiff University in water containing Stress coat™ and oxygenated via a battery powered air pump. In all instances where the eels were transferred from one body of water to another, they were acclimated to the temperature of the water they were being moved into at a rate of 1 °C per 30 min. The eels were between the elver and yellow life stages and ranged in total length from 129 mm to 274 mm with an average length of 174 mm.

Eels were housed in a large (diameter = 1.3 m, water depth = 0.35 m,

volume = 460 L) circular black tank with water dechlorinated with Tetra Aquasafe. A water cooler (D-D Aquarium Solution, DC 750) maintained the temperature at 17 ± 1 °C. After being cooled the water passed through a water filter (Aquamanta, EFX 600 External Canister Filter) and returned to the tank. Both hoses bringing water in and out of the tank were covered in mesh to prevent the eels swimming into them and the hose returning the water to the tank (flowrate <0.75 L/s) was angled to create a small amount of flow. The water quality was monitored every other day with a water quality test kit to ensure ammonia, nitrite and pH were within safe limits (ammonia 0–0.2 mg/L; nitrite 0–0.25 mg/L; and pH 7–8). A 12:12 h light:dark cycle with lights on at 06:00 a.m. was maintained throughout the experiment and the eels were fed thawed bloodworm once a day. Plastic tubes, ceramic pots and rocks were added to the tank as enrichment and refugia for the eels. The tank was covered in a plexiglass sheet to prevent the eels from escaping. Experiments began after a five day acclimation period, on the 03/08/2022. On completion of the experiments, the eels were health checked, measured, weighed and transported back to their exact site of collection to be released on the 10/08/2022. No eel was damaged or displayed symptoms of ill health during the experiment and all were returned to their site of collection.

A recirculating open channel flume was used to conduct experiments where eels were exposed to tiles. The flume was 10 m long, 1.2 m wide and 0.3 m tall with a fixed bedslope of 1/1000. The bed of the flume was plastic and the walls were glass. The working section was 7 m long, and was bounded by flow straighteners. Eel tiles measuring 505 mm length by 505 mm width by 75 mm tall shown in Fig. 1 produced by Berry and Escott Ltd. (Berry and Escott, 2023) were sourced by the Environment Agency. The tiles were mounted in the flume with the small protrusions near the flume wall. A third flow straightener was used to separate a 0.8 m long section at the downstream end of the working section in which no eel tiles were mounted and which was used to acclimate the eels to the flow conditions as shown in Fig. 2. The flume was filled with water dechlorinated with Prime Dechlorinator and kept at 17 ± 2 °C with a D-D Aquarium Solution, DC 2200 cooler. The treatments chosen for this experiment had a fixed bulk velocity while varying flow depth, this resulted in the shallowest condition having the tiles exceed the water depth (emergent) and other conditions fully submerging the tiles (submerged).

All experiments were conducted between the hours 19:00 to 03:00 in darkness, a Testo 540 lightmeter measured between 0 and 4 Lx throughout the working area. During the experiment, one eel was tested at a time and the same eel was allowed to recover for at least 24 h before being tested again. All eels were tested in all conditions and were fed after flume trials.

Before the eels were exposed to flow conditions of the flume, they were allowed to acclimate in flume water for 60 min. The eels were introduced into the acclimation section of the flume and exposed to the flow conditions for 15 min (Meister, 2020). At the end of the 15 acclimation minutes, the eel was moved into the working section of the flume with a net. The eel was allowed to swim freely throughout the working area for 5 min during which the experimental data were recorded. The eel was removed from the flume either after impinging on the downstream flow straightener for 60 s (after which the back of the flow straightener was gently tapped to verify the impingement), when the eel stayed upstream for 120 s and did not re-enter the working section with the tiles or when 5 min had expired.

A Baumer VLXT-50 M.I high speed camera recorded the eels swimming at 80 frames per second in the fourth tile and fifth tiles from the downstream end of the working area. This camera was manually triggered whenever an eel entered the field of view. The tiles in question were painted white to increase the contrast between the eel and the background. Different colours have been shown to affect fish behaviour (Sonnino Sorisio et al., 2023) so behavioural data was analysed to validate the use of the white tiles for a kinematic analysis representative of the tiles in their normal colour. The analysis revealed no differences.

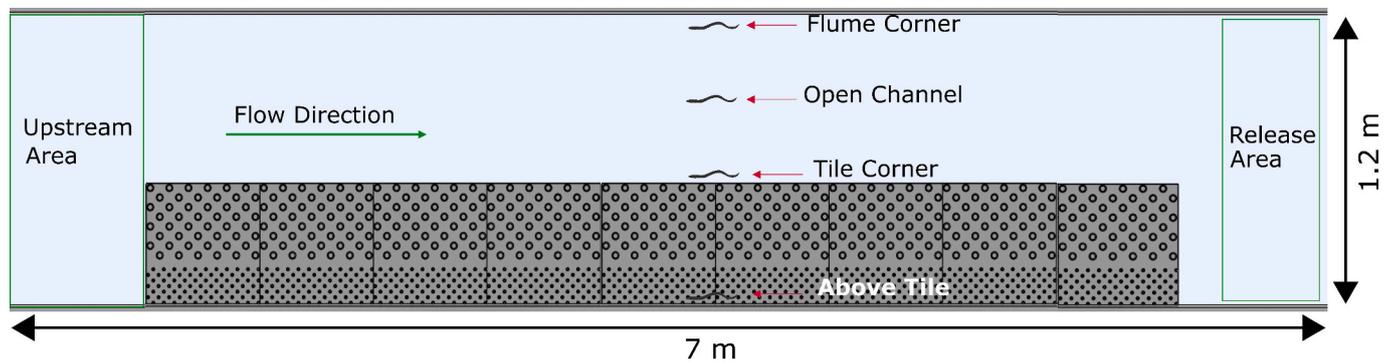


Fig. 2. Diagram of the layout of the working section of the flume including the four main areas where the eels swam. Nine tiles were attached to the flume bed with the small protrusions nearest to the wall, the fish were released downstream of the tiles and allowed to swim upstream. In the control treatments no tiles were present. The flume used was 10 m long, 1.2 m wide and 0.3 m tall.

2.2. Behavioural analyses

To monitor the behaviour of the eels, three Swann Swpro-735cam cameras were set up to cover the entire working area (shown in Fig. 2), these cameras recorded in infra-red due to the absence of light. Behaviour was quantified with JWatcher (Blumstein et al., 2000; Blumstein and Daniel, 2007). Using the videos of the entire working section, the behaviours recorded quantified whether the eel was swimming forward, backwards, holding station, crawling, or resting. The position where each of these behaviours occurred was also tracked by indicating the streamwise position of the nearest tile (or equivalent streamwise position within the channel) and whether the eel was with the small or large protrusions, above them, immediately to the side of the tile, in the open channel, or in the corner formed by the flume wall and the bed. In addition to these behaviours, the number of passage attempts was scored based on how many times the eels started making progress from the downstream area from the tiles, impingement was recorded with the criteria specified above, and successful passage was recorded as the eels having swam past all nine tiles and reached the upstream area.

2.3. Kinematic analysis

High speed videos were converted to avi files using a custom Matlab (The MathWorks Inc, 2022) script. Tracking for kinematic analysis was performed with the free software Kinovea (Charmant, 2022), this allowed for semi-automatic tracking of points on the eel's body with manual inputs or corrections. To do this, a coordinate system was set and calibrated for each video, then a tracker was added for each point on the eel's body that was to be tracked. For all clips of the eels swimming in the field of view of the high-speed camera, the head and tail were tracked and for 12% of clips (spread evenly over different areas), the entire body was tracked with 13 points on average. From the coordinates of each point on every frame, kinematics parameters were extracted. Amplitude was evaluated by calculating the maximum range of movement from the centreline of each tracked point, head amplitude and tail amplitude were evaluated for every clip. Tailbeat frequency (Hz) was also calculated in all cases as one full cycle of tail movement. The swimming velocity was calculated by adding the swimming speed of the fish evaluated from the tracking data to the flow velocity at the location of the swimming fish. All parameters with units, including metres, were normalised by body length (BL) to make a comparison with fish of different sizes. Stride length was calculated by dividing the normalised overall swimming speed by the tailbeat frequency (i.e. one "stride"), tailspeed was calculated by multiplying tailbeat frequency by tail amplitude. For full body kinematics data, a centreline was calculated from the tracked points along the body and successive centrelines for each frame for the duration of approximately one tailbeat were levelled

at the head to form a diagram of the amplitude envelope of the whole body.

For the energetic analysis, full body tracking was used. The tracked points were imported into Matlab where a polynomial spline was applied to the centreline of the body for each frame to best fit the shape of the body of the eel. The curvature of the centreline was then computed and the difference in curvature between each successive frame was found. Following the method from Harvey et al. (2022), the moment of area of the muscle cross section from 15 sections along the body of the eel (measured with Fusion 360), the rate of change of curvature was the multiplied by the moment of area and integrated along the length of the eel, excluding the head and caudal fin. This calculation yields a comparative measure of the energy used by the eel while swimming but does not provide measurements of energy usage in Joules. These data were then analysed in RStudio (R Core Team, 2022) and modelled with tailbeat frequency, the relationship was found to be very significant ($p < 1E-11$) and the R squared value was 0.79 for the model. Because of the close relationship between the two variables, the energy expenditure was estimated from the tailbeat frequency data, thus using all available clips of swimming eels to evaluate comparative energy usage by using tailbeat frequency as a proxy. The energy expenditure for the crawling gait could not be analysed by the same method since the act of pushing against a solid surface may involve different muscles compared to when moving freely within a fluid.

Comparisons of kinematics were made to hydrodynamic data defined as: Reynolds Shear Stress in the horizontal and vertical respectively, $-\rho u'v'$ and $-\rho u'w'$, and turbulent intensity, $\frac{u'_{rms}}{U}$. Where u' is the fluctuation in the streamwise velocity, U is bulk velocity, ρ is density, v' is the fluctuation in the horizontal cross channel velocity, w' is the fluctuation in the vertical velocity, and rms stands for 'root mean square'.

2.4. Statistical analyses

All statistical analyses were performed in RStudio R version 4.2.2 (R Core Team, 2022). The packages nlme (Carey and Wang, 2001) and lme4 (Bates et al., 2015) were used for generalised linear mixed models (GLMM) and MASS package (Venables and Ripley, 2002) was used for generalised linear models (GLM). GLMMs were used wherever it was necessary to consider the pseudoreplication caused by using the same eels for each treatment. Null GLMM models were run to determine the magnitude of the effect of the random variable on each model and if the effect was considered small (R squared value below 0.01) then GLMs were also run and the model with the best residuals plots and AIC was selected. To compare the passage of the eels between treatments with and without tiles, length, and flow depth a binomial GLMM was used. A poisson GLMM was used to compare the number of passes between treatments, with length, and with flow depth. Negative binomial GLMMs were used to compare the number of attempts of upstream passage per

fish between treatments, fish length, and flow depth. For the passage time variable, a gaussian GLM (identity link) was used. To analyse the time spent by eels in different areas of the flume, a combination of gaussian, inverse gaussian and Gamma GLMs were used with identity links in all cases. The amount of time spent crawling, and time spent in the flume corner was compared between treatments with a gaussian GLM with an identity link whereas for the time swimming in, and above the tiles, an inverse gaussian GLMs with $1/\mu^2$ links were utilized. For the total time spent in the tiles, a Gamma GLM with identity link was used. Gamma GLMs with identity links were also used to compare time spent in each area of the flume within treatments. For the kinematic analysis, generalised additive models were trialed but rejected on the basis that their performance was similar or inferior to that of GLMs for the same variables. Gamma GLMs with identity links were used for tailbeat frequency with normalised velocity, and all turbulence parameters, whereas a gaussian GLM was used for amplitude, head amplitude, amplitude ratio, amplitude and location, tail speed and Strouhal number, tailbeat frequency and Strouhal number, length, stride length and location, normalised points of contact and protrusion type, fish length, and direction. The confidence interval used throughout the study was 95%.

3. Results

3.1. Passage and behaviour

The tiles increased overall upstream passage of the eels (GLMM, $p = 0.02$) by 16% overall (from 74 to 87) and up to 32% for the shallowest condition (from 17 to 25), in which the tiles were emergent (T56). Total fish length did not significantly impact the probability of an eel passing (GLMM, $p = 0.11$) and neither flow depth, passage not increasing or decreasing steadily with depth (GLMM, $p = 0.24$). The number of attempts to pass was not associated with eel length (GLMM, $p = 0.86$) and there was no difference for any of the flow conditions between number of attempts with and without tiles ($p > 0.07$). Fig. 3 shows that the passage time was significantly higher with the tiles than in the control (GLMM, $p < 0.0001$) and between corresponding treatments (GLMM, $p < 0.014$) but not with fish length (GLMM, $p = 0.77$). In the presence of tiles, all eels made some progress upstream, even though not all passed upstream whereas in the control conditions, a quarter of the eels were impinged on the downstream flow straighteners compared to no impingements for treatments with tiles.

The time spent in the open channel section of the flume was much higher in the control treatments, as shown in Fig. 3 (GLM, $p < 0.0001$) but not significant in relation to fish length or flow depth (GLM, $p > 0.18$). Across all individual treatments, the time in the open channel was higher for control treatments (GLM, $p < 0.031$). Similarly, the time spent in the flume corner was higher in the control conditions (GLM, $p = 0.001$), but only treatments C129 and C75 were significantly higher than T129 and T75 (GLM, $p < 0.035$). Within the tiled treatments, there was no significant difference in time spent crawling in the large protrusions (LP) between treatments (GLM, $p > 0.05$). There was also no correlation between the eel size and which protrusion type they spent more time on as usage was uniform across eel sizes. Fish in treatment T155 (the treatment with the highest relative submergence) spent significantly more time crawling in the small protrusions (SP) than any other treatment (GLM, $p < 0.02$) but there was no difference between other treatments. There was also no difference in time spent swimming in the protrusions (GLM, $p > 0.46$), possibly due to the low number of occurrences of this behaviour. Similarly, there was no difference between T129 and T155 in time spent swimming above the protrusions, a comparison to other treatments cannot be made because the flow depth was too shallow and there was no layer of flow above the tiles. The total time spent in the tiles was significantly higher (GLM, $p < 0.02$) for T155 than other treatments (among which there were no differences). Interestingly, the time spent crawling increased with flow depth and protrusion submergence (GLM, $p = 0.0005$), most prominent with the T155 treatment. There was no difference however, with regard to time spent in the tile corner (GLM, $p > 0.49$), eels exhibited similar usage of this space across the tiled treatments. The eels spent significantly more time resting downstream in the control treatments (GLM, $p = 0.025$) and fish were significantly less likely to pass the more they rested downstream (GLM, $p = 0.022$).

Within all treatments with the tiles, most time was spent within or around the tiles and significantly more than the open channel and flume corner (GLM, $p < 0.05$). However, for the control experiment for the shallowest condition (C56), there was no differences in time spent between sides of the flume but more time was spent at rest and in the corners than in the open channel (GLM, $p < 0.02$). The same was true of C75 and C129 but in C155 significantly more time was spent at rest than anywhere else (GLM, $p < 0.018$).

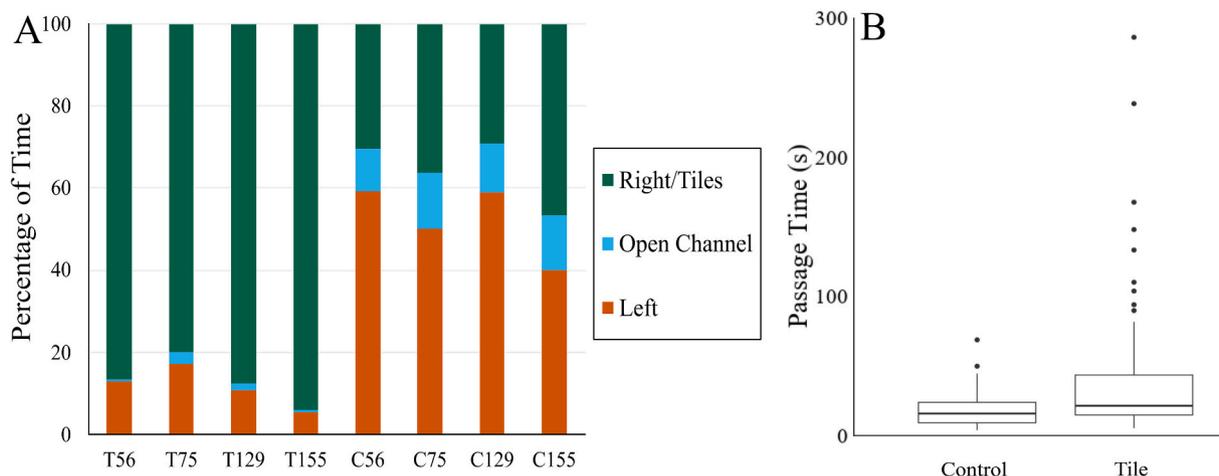


Fig. 3. Eel behavioural plots. A) Proportion of time spent on right hand side (where tiles are present in treatments denoted with T and absent in treatments denoted with C), left hand side and in the open channel region. Right and left refer to the side of the flume looking downstream and comprise of the corner formed between wall and bed and the 150 mm adjacent to that. B) Boxplot of the time eels took to pass upstream in the control conditions compared to when the tiles were present, the control data includes all control treatments and the tile data includes all tile treatments. The boxes show interquartile range, the whiskers 95% interval levels and the dots represent the outliers.

3.2. Kinematics

The tailbeat frequency of swimming fish increased linearly with normalised swimming speed (GLM, $p < 0.0001$). The relationship between tailbeat frequency and swimming speed of the eels was area specific (as shown in Fig. 4B), in the above tile area, eels had the lowest swimming speeds but also the steepest increase in tailbeat frequency with speed whereas eels within the open channel area consistently utilized fewer tailbeats per body length per second. In the tile corner and flume corner areas, eel kinematics showed a similar relationship of tailbeat frequency and swimming speed as seen in Fig. 4B. Fig. 4D shows the amplitude of the caudal fin is linearly correlated with head amplitude (GLM, $p < 0.0001$), with an increased head amplitude at higher caudal amplitudes and swimming speeds. Caudal amplitude, was also linked with an increase in swimming speed (GLM, $p = 0.047$). The overall amplitude ratio (the ratio of head amplitude to tail amplitude)

however, had a strong correlation with swimming speed (GLM, $p = 0.0001$). The caudal amplitude did not significantly vary between areas of the flume, showing that this may be partially decoupled from swimming speed and turbulence. While tailspeed increased with increasing Strouhal number (GLM, $p < 0.0001$), the tailbeat frequency decreased, this may be due to an increase in amplitude that caused an increase in tailspeed but not tailbeat frequency. The average Strouhal number was 0.49, but this varied by location, as the equation involves swimming speed directly; it was at a maximum where the swimming speed was at a minimum which was above the tile (GLM, $p < 0.0001$). This however, implies that tailbeat frequency did not decrease at the same rate as swimming velocity in this area, something that is also evident in Fig. 4B. Stride length variation by area further confirms this, the lowest value being in the above tile area and the highest in the open channel. The eel's stride length necessarily increased with local streamwise flow velocity, showing that the eels were using more a powerful gait in high

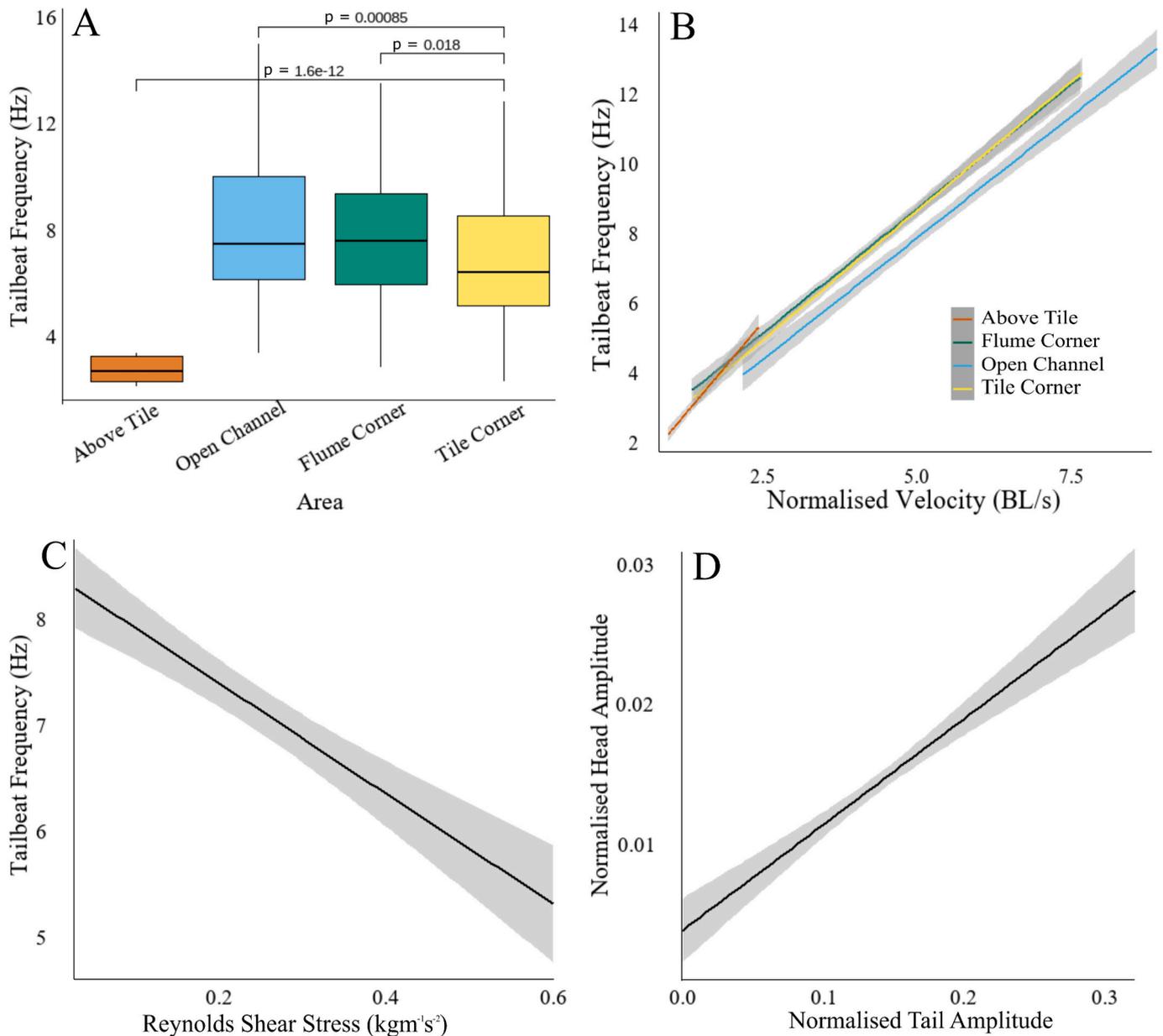


Fig. 4. Kinematics parameters from the eel swimming data. A) Tailbeat frequency in different areas of the flume with p values to show significance between areas; B) Linear regressions with 95% confidence intervals for the relationship between tailbeat frequency and normalised swimming speed for different areas which includes ground speed and flow velocity; C) Regression plot of the relationship between tailbeat frequency and Reynolds shear stress in the horizontal plane (τ_{uv}); and D) Relationship between head and tail amplitudes.

velocity areas.

An analysis of turbulent parameters of the flow combined with kinematics data revealed that the horizontal Reynolds shear stress (RSS, τ_{uw}) had a significant effect on tailbeat frequency (GLM, $p = 0.003$) while vertical RSS (τ_{uv}) and horizontal and vertical turbulent intensity (TI) had non-significant effects. Tailbeat frequency decreased with increasing horizontal RSS (τ_{uw}). Notably, the normalised swimming speed of the eels negatively correlated with fish length as did the normalised caudal amplitude.

Crawling kinematics were highly varied in both amplitude envelopes, crawling speed, and all other pre-established kinematics parameters. Some distinctions and observations were made however, the number of points of contact between the eel and the tiles was normalised by eel length and was found to increase with flow depth (GLM, $p < 0.05$). The points of contact also increased in the small protrusions (GLM, $p < 0.0001$) but did not significantly differ on the direction of motion of the eel.

By associating the energy expenditure to the tailbeat frequency in the manner outlined in the methods, the tailbeat frequency can be used as a proxy for energy usage for this data. Tailbeat frequency analysis by area shows that above the tiles the fish expended the least amount of energy, followed by the tile corner, then the flume corner and finally the open channel, where expenditure reached a maximum (GLM, $p < 0.018$). The crawling energetics cannot be calculated in the same manner but if the methods were used the expenditure would be much lower than any swimming gait due to the relatively slow movements when crawling. All analyses agree however that the slower swimming permitted by the flow attenuation of the tiles reduced energy expenditure.

The swimming gait is best visualised by the amplitude envelope of the eels seen in Fig. 5. Fig. 5A shows a typical gait for open channel swimming, the eel is swimming with a high velocity compared to other

areas and the amplitude is therefore large throughout the body and especially at the head, increasing steadily throughout the length of the body. The profile of the gait is also symmetrical against an imaginary centreline. In Fig. 5B, the swimming gait in the tile corner is characterised by a much smaller head amplitude which steadily increases towards the caudal fin where it reaches a maximum. The reduced head amplitude is to be expected due to the reduced swimming speed of the eel in this area. The profile of the gait, however, is asymmetrical and shows how the eel is maintaining the head towards the left (which in this case is near the edge of the tiles). The skewed alignment of the head and the rest of the body while oscillations are made asymmetrically into the open channel, suggests that the eels are attempting to maintain the majority of their body within the lower velocity zone near the tiles for as much of the time as possible. The eel in Fig. 5B is benefitting from the low velocity from the tile while not swimming within the protrusions. In contrast to A and B, Fig. 5C shows a more complex gait. The head amplitude remains small and the amplitude stays small along more of the body compared to A and B, due to the comparatively low swimming velocity. The amplitude does not increase steadily from head to tail nor is it symmetrical, although the maximum amplitude is at the caudal fin. Not all examples for swimming above the tile exhibited the same peaks and troughs as in the envelopes shown here but the eels had very similar gaits, suggesting the gait was unstable but exhibited the same typical features.

4. Discussion

Overall, the eel tiles increased fish passage, but that was not the only benefit they provided to the eels. While an increase in passage is the primary objective of the tiles, the eels used the tiles and increased passage even at a velocity where most eels were still able to pass upstream

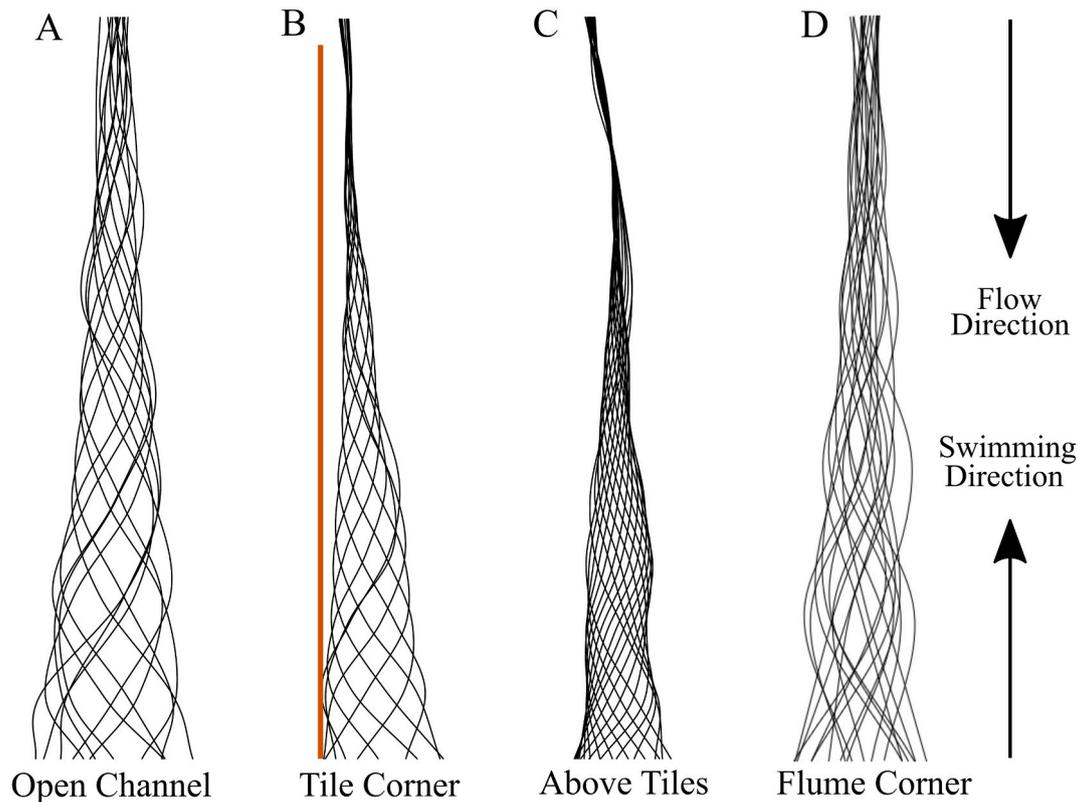


Fig. 5. Eel amplitude envelopes for different areas of the flume. The head of the eel is at the top and the caudal fin at the bottom of the diagram. Each line represents the centreline of an eel for one frame (12.5 ms) and each envelope consists of many centrelines so that the full swimming gait of the eel may be visualised. A) Eel is swimming in the centre of the open channel; B) Eel is swimming along the edge of the tile shown by the orange line; C) Eel is swimming above the tiles with the flume wall to its left; D) Eel is swimming near the bed and the wall of the flume, this is similar to A but with reduced amplitude because of the lower swimming speed.

without tiles and the hydrodynamic data from the tiles suggests that even at higher flow velocities the tiles produce favourable conditions so the increase in passage is expected to be even greater at higher flow velocities since the tiles also allow the eels to rest and crawl. Despite not all eels passing upstream with the tiles, they were always able to progress onto the tiles and move upstream. Real world passage is likely to be even higher than the present results suggest as the tiles (and the small protrusions especially) were used for resting, which would allow even small eels with poor swimming performance to pass upstream over an appropriate length of time. The current study was constrained by time and the eels may not have had long enough to pass upstream (as implied by the higher passage time shown in Fig. 3), but given more time and the ability to rest in the tiles more eels could potentially pass upstream, and even be able to pass long culverts. The tiles give the eels the ability to rest at any point in their navigation upstream and therefore not lose any progress that has been made. In the absence of the tiles, an exhausted eel would be swept back downstream and therefore be unlikely to pass upstream for as long as the velocity remains high. Even eels that are successful in passing upstream without the tiles may be more exhausted leading to resting immediately upstream of the tiles. These behaviours have the potential to cause resting hotspots up and downstream of the tiles, creating potential predation hotspots driven by 'density-dependent predation' which could exacerbate the passage issues of the velocity barrier (Jepsen et al., 2010; Wright et al., 2015). A gathering of many eels in one place is also likely to deplete resources faster and to increase the transfer of directly transmitted parasites (de Leaniz, 2008). Tiles can therefore be useful for any length of velocity barriers by allowing continuous progression upstream. The passage time was significantly higher with the tiles but this should not be considered a downside as the difference in passage time is in the order of seconds and minutes which is unlikely to impact an upstream migration and conversely, the added resting time can allow the eel to pass upstream more easily and with less effort. Baffle type passes used for similar applications do not always feature resting spots (Solomon and Beach, 2004), but some bristle passes do employ the use of resting pools to allow elvers to rest between sections (Solomon and Beach, 2004).

Behaviourally, the eels showed a strong preference for the tiles (Fig. 3) when they were present and not only spent more time within them than in the flume corner, but the time swimming in the open channel was reduced. The current study did not evaluate attraction to the tiles as the tiles occupied 42% of the channel width and were therefore easily found by the eels. This study reinforces the idea that in a box culvert or flume the eels will spend most of the time swimming near the bank as in the control conditions this is overwhelmingly where they swam, therefore suggesting that this would be the best place to mount tiles as eels are likely to be present here.

The kinematic analysis revealed further benefits that the tiles offer. The swimming speeds of the eels were slower when they swam in the vicinity of the tiles (and above them in particular), reducing the need for the eels to swim in bursts. The crawling speed was an order of magnitude lower than any swimming, which is also encouraging in terms of reducing energy expenditure and the crawling kinematics were widely diverse. Crawling showed a level of similarity with terrestrial locomotion in terms of the amplitude being similar along the body (Gillis, 1998). The relationship between tailbeat frequency and swimming speed was dependent on the area in which the fish were swimming however, in all cases the swimming speed correlated very closely with the tailbeat frequency (Gillis, 1998; Tytell, 2004b; Tack et al., 2021) but it appears that eels swimming in the open channel area needed significantly fewer tailbeats to achieve the same speed compared to those moving in the flume corner and tile corner. Although this may suggest more efficient swimming in the open channel and potential disturbances from the turbulence elsewhere, which according to the relative swimming speeds in each area agrees with the findings of cost of transport being reduced at higher speeds (Tack et al., 2021). The effect of the reduced cost of transport, however, seems to be outweighed by the

energetic benefits of slower flow velocities as Fig. 4A shows that the proxy for energy was still lower near the tiles. The comparative energy expenditure of eels was highest in the open channel (in the control conditions) due to their higher swimming speeds, and lowest in the above tile and tile corner areas (Fig. 4A). The tiles reduced the energy expenditure of the eel while in motion as well as providing habitat for resting. The most energy efficient mode of locomotion however, is likely to be crawling due to the slow movements and very low flow velocities within the tiles. The crawling energetics, however, could not be calculated so the comparative energy expenditure is unknown. The tiles not only provide apparent energy savings for the eels by allowing them to move upstream with locomotion methods that reduce energy expenditure, but by allowing the eels to rest, should they need to, they do not need to go downstream to rest so any progress they make is conserved. It should be noted that the method used to calculate comparative energy expenditure is an indirect method of doing so and the data presented here are therefore only useful in the context of this laboratory study.

Eel swimming speeds and tailbeat frequencies were not different among the flume corner and the tile corner but the tile corner indicated a lower energy usage. A mechanism for this reduction of energy consumption in the tile corner may be found in the analysis of the amplitude envelope of the eels in different areas. The open channel swimming gait show good agreement with the findings of previous studies concerned with eel kinematics, especially when examining higher swimming speeds (Gillis, 1998; Tytell, 2004b; Lauder and Tytell, 2005; Tack et al., 2021) but previous studies generally have been concerned with swimming in more simplified velocity field or tank (no flow) conditions and not in a high complexity flow of turbulence and shear layers as studied here. In the tile corner, the eels consistently swam asymmetrically by keeping the majority of their body close to the tiles for most of the time. This meant that the eels were exposed to lower flow velocities with most of their body, which is likely to reduce drag. This is the first time this behaviour has been studied and offers new insight into eel swimming strategy. This behaviour was not seen in the flume corner and this may be due to the smoother change in velocity, whilst in the tile corner there is a mixing layer driving the slow flow of the tiles and the fast flow of the open channel, making this transition more abrupt and easier to sense and exploit by the eels. This finding is unlikely to be the only way eels adapt their gait but is the first step in beginning to understand the plasticity of their gait in complex flows and shear layers which are more representative of flow conditions in nature. The above tile amplitude envelope however, shows a complex gait that defies easy characterisation. The above tile gait is irregular and this may be explained by the turbulence in that area being at its highest and therefore interfering with the swimming stability of the fish. This, however, did not seem to negatively impact passage or to cause any major destabilization or 'spill' as defined in previous studies (Tritico and Cotel, 2010; Muhawenimana et al., 2019). This is not surprising since the turbulence shed by the tiles is not coherent enough, or the correct length scale to destabilise these eels (Muhawenimana et al., 2019; Tritico and Cotel, 2010; Sonnino Sorisio et al., 2021). The kinematics data linked lower tailbeat frequencies with elevated turbulence parameters and specifically with Reynolds shear stress in the horizontal plane (τ_{uv}) but the effects of velocity and turbulence on tailbeat frequency cannot be disentangled as the highest levels of turbulence were present in the lower velocity areas. The relationships between other kinematic parameters were also found to match the literature, such as swimming speed increasing with amplitude (Tytell, 2004b; Tack et al., 2021) and tailspeed (Tytell, 2004b). Strouhal number decreased at higher swimming speeds and the average values matched the peak values found by previous work (Tytell, 2004a). The tiles increased passage while reducing energy expenditure, allowing eels to rest within the tile protrusions, and not significantly affecting the hydrodynamics in the rest of the channel. For these reasons they appear as a good solution for eel passage at high velocity barriers that does not require high swimming speeds at any point, to be confirmed by further field trials. Tiles are a proven technology for

gravity barriers (Vowles et al., 2017) so should such a barrier be present at the downstream end of a culvert, where typically there can be a 'step', the tiles can be employed without the use of two different solutions for the gravity and high velocity barriers. While the tiles are cost-effective for both purchase and retrofitting, it is crucial to exercise caution during installation to ensure that no gaps are left between them. These gaps could potentially provide a passage for eels to swim beneath the tiles, encouraging them to establish residency within the tiles, rather than facilitate their upstream movement.

5. Conclusion

Eel tiles have been evaluated as a passage solution for eels and the findings show that an increase in passage is produced by adding the tiles to a high velocity barrier. The tiles bring the additional benefits of allowing the eels to rest and preserve any upstream progress and enabling them to crawl, swim in reduced flow velocity or swim normally. They also allow the eels to expend less energy in their upstream passage, something that is useful considering the multitude of barriers eels encounter in their migration. The kinematics of eels were analysed for the first time in flows with hydrodynamic complexity (e.g. multiple shear layers and turbulent structures of varying lengthscale) and revealed new mechanisms of drag reduction through asymmetric swimming gaits exploiting a shear flow layer. Overall, the tiles have the potential to be a suitable solution for upstream passage of eels at high velocity barriers and have potential to work for other species of fish while not modifying the flow in the rest of the channel for fish species which may not require the tiles.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoleng.2024.107254>.

CRedit authorship contribution statement

Guglielmo Sonnino Sorisio: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Catherine A.M.E. Wilson:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Andy Don:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Jo Cable:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Guglielmo Sonnino Sorisio reports financial support was provided by Natural Environment Research Council. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data is freely available at: DOI: 10.17632/72g8znvhcc.1

Acknowledgements

This study was funded by the Natural Environment Research Council (NERC) funded FRESH Centre for Doctoral Training (CDT) grant NE/R011524/1. We thank Paul Greest, Andrew Gott and Natural Resources Wales for providing the eels and the Environment Agency for providing the eel tiles and advice. We also thank Paul Leech for technical support, Dr. Petr Denissenko for advice on the energetic analysis, and Dr. Numair Masud, Charlotte Robison-Smith, and Laura Hayes for statistical support. All work was approved by Cardiff University Animal Ethics

Committee and linked to UK Home Office PP8167141.

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