

Evaluation of eel tile hydrodynamics and passage of a non-target shoaling species, the three spined stickleback (*Gasterosteus aculeatus*)

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ABSTRACT

Culverts are high velocity barriers that pose a challenge for fish navigation. The high velocities generated within culverts have the potential to halt migrations and fragment habitats. Passage solutions for small, river resident, freshwater fish are scarce and eel tiles present a possible multi-species solution. In this study, moulded tiles designed to promote eel passage were mounted in a recirculating open channel flume, we quantified the associated hydrodynamics and assessed whether a sentinel species, the three spined stickleback (*Gasterosteus aculeatus*) could navigate fixed flow conditions in the presence and absence of tiles, either alone or in shoals of three fish. The tiles produced a large reduction in streamwise velocity within them as well as around them and did so consistently for all flow conditions. The vertical and horizontal Reynolds shear stresses produced by the tiles was similar to canopy flow turbulence but the turbulent structures were not as discrete. The hydrodynamics of the tiles appear appropriate for fish passage due to the induced slow flow and moderate turbulence. The tiles significantly decreased impingement on the downstream flow straightener and exhaustion. Shoaling significantly increased passage, but in harsher local velocity conditions fish in shoals did not maintain cohesion. The tiles benefitted the fish by providing lower flow velocities but produced turbulence that in some cases destabilised the swimming fish. Despite this the tiles improved the swimming ability of minor species in areas where they would have otherwise become quickly exhausted.

1. Introduction

The rivers of Europe are among the world's most fragmented. Anthropogenic barriers are ubiquitous in many freshwater systems and are present in headwater streams to large rivers (Jones et al., 2019; Belletti et al., 2020). The number of barriers is unknown but estimates range from 1.2 to 3.7 million barriers in Europe alone, 61 % of which are unreported (Belletti et al., 2020). Many of these unreported barriers are small installations with little to no head drop in the river but they still pose a threat to diadromous and potamodromous fish and general habitat connectivity. Of the estimated total number of barriers, 17.6 % are culverts (Belletti et al., 2020). These can cause discontinuity in habitats and impair the ability of fish to swim upstream by constricting the flow, creating high velocity flows due to their smooth uniform boundaries (Warren and Pardew, 1998; Gibson et al., 2005; Bouska and Paukert, 2010; Erkinaro et al., 2017; Rodgers et al., 2017; Shiau et al., 2020), and cause a reduction in fish passage especially for smaller

bodied fish (Jones et al., 2021). Fish pass designs that are often implemented at barriers are designed for migratory fish, such as salmonids, some of the most powerful freshwater swimmers (Clough and Turnpenny, 2001; Clough et al., 2004; Kemp and O'Hanley, 2010) because of the migratory needs or status of endangerment.

Fish pass efficiencies vary widely (Kemp, 2016; Shaw et al., 2016), but little is known about the passage of "non-target species" such as the three spined stickleback (*Gasterosteus aculeatus*). These form an important component of aquatic food webs and therefore habitat fragmentation can cause detrimental pressure on these ecosystems. Smaller, resident riverine fish, especially those that are non-migratory and/or benthic, are typically less powerful swimmers and cannot reach the same swimming speeds as salmonids (Clough and Turnpenny, 2001; Blake et al., 2005; Tudorache et al., 2007). Such fish are impacted by all barrier types and this is a contributing factor in the decline of freshwater biodiversity (Fahrig, 2003). A move away from species focused passage designs is therefore necessary to help restore ecosystems; passes should

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be navigable by multiple fish species. The design and implementation of fish passage solutions that are effective across a range of fish morphologies, sizes and swimming characteristics is currently an under-researched area and a clear knowledge gap (Jones et al., 2020; Jones et al., 2021). Textured substrates are effective for smaller bodied fish traversing ramps (Franklin et al., 2021), and baffle designs can be adapted to match the passage needs of small fish (Magaju et al., 2021). Despite velocity barriers being a known hindrance to the migration of small fish, some existing solutions do potentially benefit these species (Knapp et al., 2019).

Three spined sticklebacks are present in water bodies throughout Europe and parts of North America. Typically between 30 and 50 mm in length when fully grown, they are usually found in ponds and streams, away from high velocity flow and in the shelter of vegetation. This species is marked as “least concern” in the IUCN Red List of Threatened Species but anthropogenic migration barriers have been found to drive genetic diversification and isolation in populations of these fish (Scharsack et al., 2012; NatureServe., 2019). This is compounded by an increase in migration between salt and freshwater habitats due to increased saltwater pollution (Scharsack et al., 2012). These sticklebacks are primarily labriform swimmers, their caudal fin only is engaged when swimming in bursts and when maneuvering, but most often is compressed (Blake et al., 2005). Populations of this species can have diverse life cycles, some live their whole lives in freshwaters and never migrate, others migrate between freshwater, brackish and saltwater. Migrating sticklebacks can attain higher swimming speeds than river-resident individuals, swimming as fast as 0.43 ms^{-1} whereas the non-migratory fish only reach 0.34 ms^{-1} (Tudorache et al., 2007). Sedentary populations of sticklebacks have been suggested as effective environmental sentinels for the UK, being a robust species found all over the country (Pottinger et al., 2002). Sticklebacks are a shoaling species (Barber and Ruxton, 2000; Mehliş et al., 2015), which benefits their social interactions, foraging, and defense from predators. Many studies have also shown the hydrodynamic advantage of shoaling and this should not be discounted when considering fish movement (Johansen et al., 2010). Fish adapt their shoaling behaviours to flow conditions (Mayer, 2010), with some fish species shoaling more consistently in the presence of flow (de Bie, 2017; de Bie et al., 2020). Some of the mechanisms behind the hydrodynamic benefits of shoaling are well understood (Daghooghi and Borazjani, 2015) but not for labriform species where the balance of hydrodynamic and social benefit of shoaling under flow conditions is a knowledge gap.

Eel tiles are a passage solution comprised of a base from which cylinders protrude, irrigated by relatively small flows passing through the protrusions. They have the potential to allow fish passage through high velocity barriers, thereby restoring connectivity. The tiles were originally designed as a surface-mounted climbing substrate to help juvenile eels climb past barriers like weirs (Vowles et al., 2017). They can also be effective in barriers such as culverts (Sonnino Sorisio et al., 2024). They are fixed to the bed of the river or structure and are usually fully submerged. They provide cover for fish and reduce the flow velocity within the protrusions as well as creating low velocity areas above and horizontally adjacent to them (Sonnino Sorisio et al., 2024). The Berry and Escott tiles (Berry and Escott Ltd., 2023) consist of dual density protrusions, which have the advantage of creating areas with different characteristics, potentially allowing fish to select to swim in the area best suited to their ability. In experimental trials with eels, the tiles successfully increased passage; turbulence above the tiles was only destabilising for the fish to a minor degree (Sonnino Sorisio et al., 2024). Eel tiles are a promising solution to fish passage due to their ease of installation and low cost relative to other fishways. They also have flexibility for a range of different installations, including lining sections or one side of the channel while keeping the remainder free. For field deployment, however, it is important to know if fish with different swimming styles, and swimming strengths can make similar use of the tiles or at least to check that they have no detrimental impact.

Eel tiles have rows of cylindrical protrusions which create hydrodynamic flow regimes that bear similarities with models of rigid vegetation present in freshwater streams (White and Nepf, 2008; Caroppi et al., 2018). The shedding and turbulent structures in submerged vegetation (defined as when the vegetation top is below the water surface) is often analysed as canopy flow; this type of flow occurs in nature in a multitude of scenarios, including air flow over trees or water flow over corals. The difference in bulk velocity between the layers of flow creates an instability, known as the Kelvin-Helmholtz (KH) instability, which was first used to understand how wind creates waves in the ocean (Brown and Roshko, 1974; Drazin, 2002; Kelvin, 1871). Batchelor (1967) provided a mathematical description of this phenomenon, wherein he also detailed some of the turbulent structures and fully formed eddies within the vortex sheet arising from the interaction between the two flow layers. In submerged vegetated flows, the KH vortices will reach the scale of the canopy height unless they are suppressed by low water depth (Ghisalberti, 2002). The spacing and density of the canopy can also influence the stem-scale size of the turbulence. If the distance between individual cylinders is smaller than their diameter, then the length scale of the vortices will be of the spacing and not the diameter (Tanino and Nepf, 2008). The density of the array also determines how the individual stem-scale vortex streets will interact, sparse arrays with relatively small diameter cylinders can produce distinctly identifiable vortex streets, whilst more densely packed arrays of larger diameter cylinders are more likely to produce wakes that interact with each other and form more homogeneous and less discrete turbulent flow; turbulence intensity increases with increasing density regardless of these effects (Tanino and Nepf, 2008). The density also impacts the average velocity within the canopy layer, with higher densities being associated with lower velocities (Rominger and Nepf, 2011). Stem scale turbulence is important in understanding sediment and nutrient transport in channels (White and Nepf, 2008; Lou et al., 2021) but for fish larger than the protrusion diameter, the stem scale turbulence may be too small to affect swimming (Muhawenimana et al., 2019).

Typically, eel tiles are mounted close to the bank of a stream or channel to favour their use by eels (and potentially other fish) as they exploit the favourable lower flow conditions of the banks and maximise cover. The interaction between the flow in the two adjacent areas of protrusions of different densities and diameter is not well understood. It is important to understand the flow within and around the tiles because fish appear to prefer certain flow regimes (Russon and Kemp, 2011; Fjeldstad et al., 2018). For these tiles to be an effective passage solution they need to produce a flow that can be easily used by eels, this would also enable their use as a guidance system to other passage facilities for migration barriers where different passage solutions are required but the entrance of which can be difficult to find for eels (Brown and Castro-Santos, 2009). Another important factor in assessing these tiles for use in fast flows is to evaluate the level of turbulence and the forms this takes to determine the suitability of the tiles as a swimming aid for fish. Certain types of turbulence, at a scale similar to the dimensions of the fish, and certain orientations can destabilise fish (Tritico and Cotel, 2010; Muhawenimana et al., 2019) so it would be beneficial to know if the turbulence produced by the tiles has the potential to impair fish swimming behaviour.

This study evaluated eel tiles as a potential passage solution for three spined sticklebacks as a model species for other small-bodied fishes. The presence of shoalmates was also investigated to determine whether shoaling impacted passage strategy and success. Individuals or shoals of non-migratory sticklebacks were placed in a laboratory flume with and without tiles to investigate the impact of shoaling in swimming conditions approaching the limit of their capabilities (Tudorache et al., 2007). To do this, the hydrodynamics of the tiles were first quantified. Eel tiles were mounted near the wall of a flume with either the small or large protrusion side adjacent to the wall, leaving more than half of the channel width uncovered.

2. Methods

2.1. Fish origin and maintenance

Three spined sticklebacks (*Gasterosteus aculeatus*, $n = 320$; hereafter referred to as sticklebacks) were caught with hand nets from the St Fagans ponds (Grid Reference: 51.48742630926287, -3.270094010847469), Cardiff, UK on the 22/03/2023. Water temperature on the day of collection was 12 °C. The fish, transported to Cardiff School of Engineering on the same day with Stress Coat (API Stress Coat +) added to their water, were slowly acclimated to the temperature and water chemistry of their holding tank. The fish were maintained in a circular (1.5 m in diameter) tank filled to a water depth of 0.3 m with a volume of 530 L. Tank water was dechlorinated with Tetra Aquasafe and maintained at 15 °C with a D–D Aquarium Solution, DC 750 cooler. The water was filtered by an Aquamanta, EFX 600 External Canister Filter and checked every day to ensure the water chemistry was suitable (Ammonia 0–0.2 mg/L; nitrite 0–0.25 mg/L; and pH 7–8). The fish were kept under a 12:12 h light:dark regime (lights on at 07:00 am) and enrichment was provided to the fish in the form of ceramic pots, rocks and tubes to provide refugia. The tank was subdivided into two sections by a plastic mesh that allowed water mixing but restricting the sticklebacks so that after the first day of experiments fish already tested in the flume would not be used again. The fish were allowed to acclimate to the holding tank for a minimum of 24 h before being used in the experiment and they were not fed for those initial 24 h. Starting from the second day of captivity, the fish were fed thawed bloodworm every morning before the experiments began. After the experiments, a subsample of the fish underwent an external health check that revealed no visible injuries, then returned to their place of origin, ensuring to re-acclimate to their habitat by introducing pond water to the container they were in before releasing them. Fish total length averaged 34.2 (± 0.5 , range 18–59) mm and was not significantly different between treatments (GLM, $p > 0.89$), detailed in Table 1. Shoalmates were size matched (± 2 mm).

2.2. Flume setup and flow conditions

The experiment was carried out in an indoor recirculating open channel flume with rectangular cross-section 1.2 m wide and 0.3 m deep. The length of the flume was 10 m. The flume had a fixed bedslope of 1/1000 and a weir at the downstream end to control the water surface profile. The bed of the flume was lined with plastic and the walls of the flume were made of glass. The flume water was dechlorinated (Prime Dechlorinator) and kept at 15 ± 2 °C by a cooler (D–D Aquarium Solution, DC 2200 cooler). Nine Berry and Escott dual density eel tiles were mounted to the plastic bed of the flume with the small protrusions section of the tile adjacent to the flume wall (Fig. 1). Each tile measured 505 mm by 505 mm (width and length) and 75 mm tall (h), with a 25

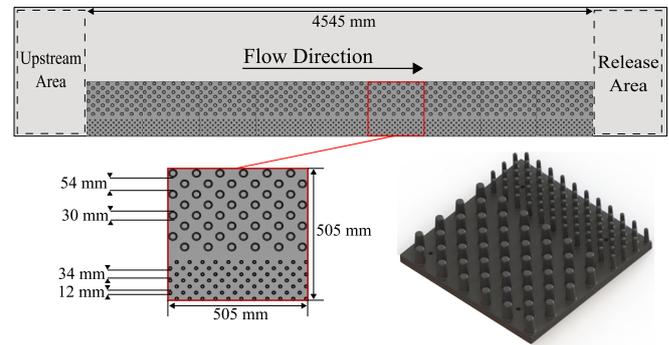


Fig. 1. Top view of the flume used for the experiment with the tiles mounted along one side in the SP orientation (small protrusions next to the flume wall) and top view of a magnified tile with dimensions of the protrusions and the spacing between them shown (bottom left). The protrusion spacing given in the diagram is equal in both streamwise and spanwise directions. The large protrusions have a diameter of 30 mm at the base and the small protrusions have a diameter of 12 mm at the base. An isometric view of the eel tile is shown on the bottom right (Berry and Escott, 2023).

mm thick base and 50 mm tall cylindrical protrusions. The total length of the tiled section was 4.55 m and the 8 m working section of the flume was bounded by flow straighteners up and downstream that also acted as screens to keep the fish within the area. Downstream of the tiles a 1 m long area was used as an acclimation zone for the sticklebacks before they were released at the start of the experiment and upstream of the tiles a portion of the flume was used to collect sticklebacks that swam upstream. The flow conditions were kept constant with a flow depth (H) of 0.155 m, a bulk velocity (U) of 0.35 ms^{-1} , a flowrate (Q) of 65 L s^{-1} , and a Reynolds number (Re) of 40,931 based on the hydraulic radius (measured along the flume at 1 m intervals with a vernier scale and PIV). These were chosen to represent challenging conditions for the sticklebacks (Blake et al., 2005; Tudorache et al., 2007) but still within their range of burst swimming capabilities. The relative submergence (H/h) of the tiles was 2.07 under these flow conditions.

2.3. Hydrodynamics of the tiles

Particle Image Velocimetry (PIV) was used to analyse the flow around the eel tiles using a high-speed camera (Baumer VLXT-50 M.I) with a Kowa LM8JC10M 8.5 cm lens. The camera was mounted above the flume for aerial view recordings and on the side of the flume for section view recordings. The images were sampled at a rate of 120 frames per second, the image size captured was 1952×950 pixels and 2048×1000 pixels for the aerial view and section view, respectively. Streampix single-camera software was used to log the images and establish the field of view. A Rigol 1032Z wave generator was used to

Table 1

Mean, minimum, and maximum fish total length per treatment and details of the treatments, average length did not vary significantly between treatments or between focal fish and shoalmates (GLM, $p > 0.89$). The focal fish is denoted as the fish for which all data were recorded and where shoalmates 1 and 2 are the other two fish making up the shoal of three fish for which no data is recorded beyond body measurements. In the case of the single fish treatments, the fish is also denoted as focal. The treatment codes refer to the flume setup (C = no tiles, T = tiles) and the number of fish in the flume (1 = one fish, 3 = shoal of three fish). For each treatment, 30 repeats were performed and all fish were only used once.

Treatment	Number of Fish	Tiles/Control	Fish	Mean mm	Minimum mm	Maximum mm
C1	1	Control	Focal	34	23	55
C3	3	Control	Focal	34	22	57
C3	3	Control	Shoalmate 1	35	20	59
C3	3	Control	Shoalmate 2	35	18	53
T1	1	Tiles	Focal	34	21	55
T3	3	Tiles	Focal	34	22	54
T3	3	Tiles	Shoalmate 1	34	25	52
T3	3	Tiles	Shoalmate 2	34	21	55

trigger the Polytec BVS – II Wotan Flash stroboscope operating at 15 % intensity and the high-speed camera (through a STEMMER IMAGING CVX Triggerbox). The Stroboscope emits the laser pulse through optics to produce a sheet of light 300 mm wide. The flow was seeded with AXALTA Talisman 30 White 110 particles at a density of 0.0632 g/L.

For all conditions in Table 2, uniform flow conditions were maintained. Flow depth was measured with a custom pointer gauge with a vernier scale (± 0.1 mm), flowrate was measured with a flowmeter (± 0.1 Ls⁻¹) and the bulk velocity was measured with PIV equipment detailed above.

PIV was recorded for the tiles in both aerial and section views (Fig. 2). In aerial view, the laser was placed horizontally on the side of the flume near the glass wall and the camera was positioned above. Starting from the layer of flow immediately above the tiles, the laser was moved upwards in 20 mm increments until the surface layer of flow was reached. As flow depth varied, the number of aerial views was not the same for all conditions. In the section view, the laser was mounted vertically above the flume and oriented so that the 300 mm long pulse was visible from the side of the flume where the camera was mounted. The laser was moved from near the glass wall across the flume width taking 11 readings (moved by 15–145 mm for each reading).

The images were analysed with PIVlab version 2.55 on MATLAB R2021b. Calibration was carried out using images of the flume with objects of known length at the correct distance from the camera for each position of the laser, variation of calibration values across the frame was checked to verify that particles at the extremities of the frame were not significantly more distant than particles at the centre of the frame. MATLAB scripts were written to use PIVlab outputs to calculate turbulent parameters not included in the PIVlab package. Reynolds Shear Stress ($RSS_{uv} = -\rho(u'v')$), and ($RSS_{uw} = -\rho(u'w')$) was calculated by determining the product temporal fluctuation of the two velocity components at each timestep before temporally averaging them over the sampling time and multiplying them by the density of water calculated at the flume temperature. The RSS was spatially averaged over the water column or across the flume width. Turbulent Intensity ($TI = \overline{u'_{rms}}/\overline{U}$) was calculated by finding the average root mean square of the fluctuations of each velocity component divided by the average of that component. Turbulent intensity was spatially averaged over the the water column or across the flume width. Turbulent Kinetic Energy ($TKE_{uw} = 0.5(\overline{u'^2} + 2\overline{w'^2})$) and ($TKE_{uv} = 0.5(\overline{u'^2} + 2\overline{v'^2})$) was determined by adding the squared velocity fluctuations for each component, multiplying by 0.5 and then temporally and spatially averaging. Since only

Table 2

Recirculating flume flow conditions tested in the current study varied in both flow depth and bulk velocity. Two series of flow condition were produced: 1 to 6 where the bulk velocity was varied and flow depth kept constant, and A to E where the velocity remained constant and flow depth varied (shaded rows). Condition 4/C is shared by the flow depth varying series and the bulk velocity varying series of conditions. The Reynolds number (Re_R) is based on hydraulic radius (R) and bulk velocity (U). H is the flow depth, h is the protrusion height and H/h is the relative submergence of the protrusions. Tile orientations are with the small protrusions next to the flume wall (SP: see Fig. 1) or the large protrusions next to the flume wall (LP).

Tile orientation	Test Name	Bulk Velocity, U (ms ⁻¹)	Flowrate, Q (Ls ⁻¹)	Re_R (-)	Water Depth, H (m)	H/h (-)
SP and LP	1	0.12	26	16,165	0.181	3.12
SP and LP	2	0.21	46	28,218	0.1805	3.11
SP and LP	3	0.29	64	38,773	0.180	3.10
SP and LP	A	0.35	54	35,280	0.129	2.08
SP and LP	B	0.35	65	40,931	0.155	2.60
SP and LP	4/C	0.35	76	46,608	0.181	3.12
SP and LP	D	0.35	88	51,962	0.208	3.66
SP and LP	E	0.35	98	55,630	0.2335	4.17
SP and LP	5	0.42	90	55,026	0.1805	3.11
SP and LP	6	0.46	99	60,901	0.1825	3.15

two velocity components were available for the TKE calculation, the vertical or cross-streamwise component was used twice as a substitute for the missing velocity in TKE.

To further visualise the flow field and the vortex structures around and within the tiles, flow visualization was conducted using dye injection. Dye (Cole-Palmer Fluorescent Red 00298–16) was placed into syringes and injected into the flow whilst a Nikon D5100 with a NIKKOR AF-S 10–24 lens was used to capture images and video of the flow from above the flume or from the side.

2.4. Experimental design

Four treatments were tested in this experiment (Table 1): a single fish with tiles (treatment T1), a single fish without the tiles (treatment C1), a shoal of 3 fish with the tiles (treatment T3) and a shoal of 3 fish (Currier et al., 2021) without the tiles (treatment C3). The codes for the treatments represent the presence of the tiles (T = tiles, C = control) and the number of fish in the flume (1 = single fish, 3 = shoal of 3 fish), a total of 30 repeats were performed for each treatment. Treatments C1 and C3 in this case served as controls. For all treatments the procedure was as follows. Before fish were released into the flume they were measured for total length, and visually checked for any abnormalities. Each fish or shoal was acclimated in flume water for a minimum of 1 h before the start of the experiment, the flowrate was then increased slowly from ~ 0 ms⁻¹ over 3 min to the experimental condition and the fish were allowed to acclimate for a further 2 min at the downstream end of the working section ahead of being released into the test section. The short acclimation time was necessary to avoid exhausting the sticklebacks before the test began. The fish or shoal was then released and allowed to swim freely in the test section for 10 min then removed from the flume and returned to the holding tank. The fish were only removed before 10 min had elapsed if they passed upstream or if they became impinged against the downstream flow straightener. Impingement was defined as the fish lying flat against the straightener for 60 s without successfully moving from this position. If the fish were unable to move even when the back of the straightener was tapped the fish was considered impinged. Gently tapping the back of the flow straightener was used as a method of scaring the fish into moving away and was selected rather than making physical contact with the fish itself to avoid any potential injuries to the fish. When impinged, the fish showed signs of distress such as fast gasping and when removed from the flume, they were not able to react to the net or resist being lifted out of the flume, further demonstrating their exhaustion. This definition of impingement was used due to the lack of a standardised measure for this metric. In the event of impingement, the fish was removed and the experiment terminated before the full 10 min. The impinged fish was then checked visually for any external injury, measured and placed back in the holding tank. The experiments were carried out in the hours of daylight (between 09:00 and 17:00) with blinds used to block out natural light and artificial light used throughout to eliminate light intensity as a variable factor. Sticklebacks can demonstrate both diurnal and nocturnal behaviours but in this experiment all data were collected during day time with constant light intensity (552 Lx on average).

2.5. Data recording

JWatcher (Blumstein et al., 2000; Blumstein and Daniel, 2007) was used to record fish behaviour live by direct observation by two observers. Behaviour and modifiers were defined such that the fish could be tracked by logging the position of the fish within the flume by defining five main areas: within the small protrusions, within the large protrusions, on the side of the tile (at the interface with the free stream region, 100 mm wide), above the tile and in the open channel region. Modifiers from 1 to 9 were applied to these areas to indicate which tile a behaviour was associated with. A different set of keys was specified for the same behaviour listed above corresponding to number of fish in a

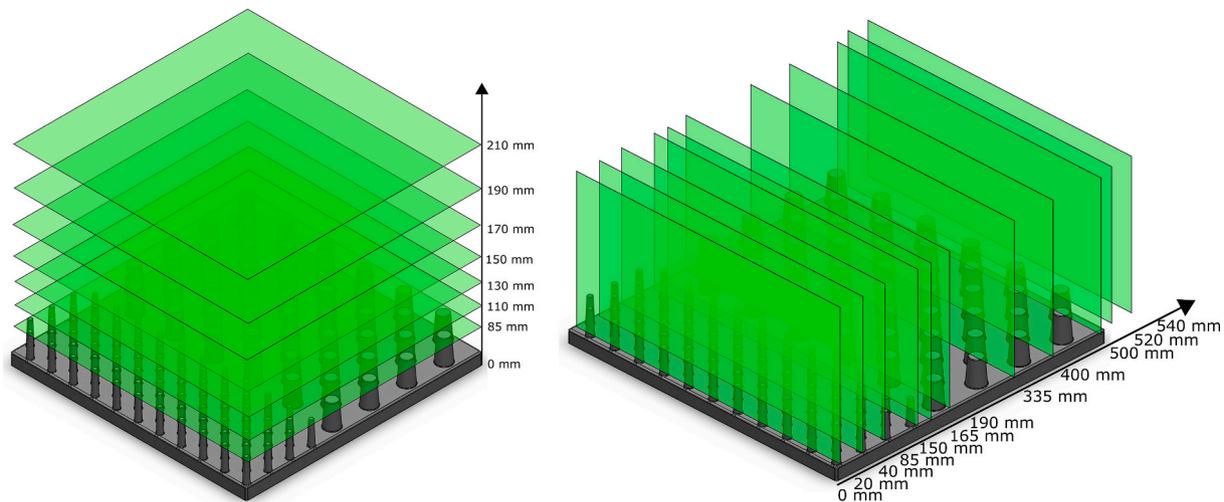


Fig. 2. Schematic outlining locations of PIV measurements in and above the tile protrusions. For PIV recordings, the flume was set to one of the pre-established conditions (Table 1), a minimum of 120 s was given for the flow to reach a steady state condition after which the room lights were turned off so recordings could be made in the dark. The Rigol wave generator was then triggered and the flow was recorded for 10 s. This length of time was chosen in accordance with a sensitivity analysis of the time averaged streamwise velocity profiles and root mean square fluctuations of the streamwise velocities that was conducted by examining different lengths of time. This analysis confirmed that for a sampling rate of 120 Hz in all tested flow conditions, 10 s was sufficient to obtain a stable profile.

shoal. Other behaviours that were logged were successful passage upstream, resting, impingement and spills. The fish was deemed to be resting if it was stationary and positioned facing the flow and clearly in control of its position whereas if the fish lay flat against the flow straightener despite efforts to move it was recorded as impinged. A ‘spill’ was defined as a temporary destabilisation and loss of control by a fish while swimming (Tritico and Cotel, 2010). To accurately record fish movements, two people observed and monitored the fish to ensure the robustness of the behaviour scoring, the same two observers conducted all the trials. In the case of the shoals, a randomly selected focal fish was chosen before the fish were released after acclimation and only the behaviour of this fish was monitored in terms of position of the fish within the flume and number of shoalmates when it was shoaling (which included the focal fish). Fish were considered to be shoaling when within a maximum of five fish lengths of each other (Tien et al., 2004). In treatments with three fish, only the focal fish was recorded and all metrics associated with these treatments only apply to this fish.

2.6. Data analysis

The data were analysed in RStudio version 4.2.2 (R Core Team, 2022). The data were first inspected with histograms and a Shapiro-Wilk test to examine the distribution of the data. Generalised linear models (GLMs) were used to fit the data using the MASS package (Venables and Ripley, 2002). Different models were considered based on the data distribution, the residual distributions and AIC values were then inspected and the best model chosen. An Inverse Gaussian GLM with $1/\mu^2$ link was used for total length comparisons across treatments and shoalmates, maximum progress (furthest upstream position reached by the fish) and length, time to pass with treatment and length, time shoaling with treatment, and time above with treatment. For time in a shoal of two fish and treatment, and time in a shoal of three fish and treatment an Inverse Gaussian GLM with identity link was used. A Binomial GLM with probit link was used to model the pass against treatment data, while a Negative Binomial GLM was used to analyse spill against treatment (log link), to compare the spill count with passes (log link), to model number of spills and total length (sqrt link), and the spills by area (log link). Gaussian GLMs were used in the case of total length and passes (sqrt link), time on the tile side with total length and treatment (identity link), and proportion of time spent in each area in treatments T1 and T3 (identity link). A Gamma GLM was used to model

the maximum progress with treatment (identity link), time resting with treatment (identity link), time in the small and large protrusions with treatment and total length (inverse link), time in the open channel section with treatment and total length (inverse link), and time spent alone with treatment (identity link). A Zero Inflation model (ZINB) with a logit link was used for total time impinged against treatment and length using the pscl package (Zeileis et al., 2008). When modelling total time, a transformation of $+0.001$ was used to avoid zero values. The confidence interval used in all cases was $p = 0.05$.

2.7. Animal ethics

All work was approved by the Cardiff University Animal Ethics Committee and conducted under UK Home Office licence PP8167141, and permission to collect fish was obtained from St Fagans National Museum of History.

3. Results

3.1. Hydrodynamics

The hydrodynamics of the channel without tiles was first analysed to provide a baseline for all other conditions. This bare channel was denominated the control condition and the hydrodynamics within this revealed a steady flow characterised by no identifiable turbulent structures and constant flow velocity (Fig. 3). With the eel tiles in place, the vertical profiles of the streamwise velocity (u) revealed that velocity was reduced both within and above the tiles compared to the control condition by a maximum of 95 %. Within the tiles the velocity increased near the top of the tiles where the reduction was 20–40 % and in the mixing layer above the tiles until it equalled or surpassed the velocity in the control condition in the upper parts of the water column as illustrated in Fig. 3 for both SP (small protrusions next to the wall) and LP (large protrusions next to the wall) configurations (maximum velocity increase was 12 % at the top of the water column for the shallowest condition). The vertical profiles of the vertical velocity (w) show that there was comparatively low velocity in the control condition compared to the increased levels in conditions with tiles. Nevertheless, the magnitude of the vertical velocities with the tiles was moderate (less than 0.05 ms^{-1}), reaching a maximum in the mixing layer. The horizontal velocity profiles over the tiles also exhibited a reduction of

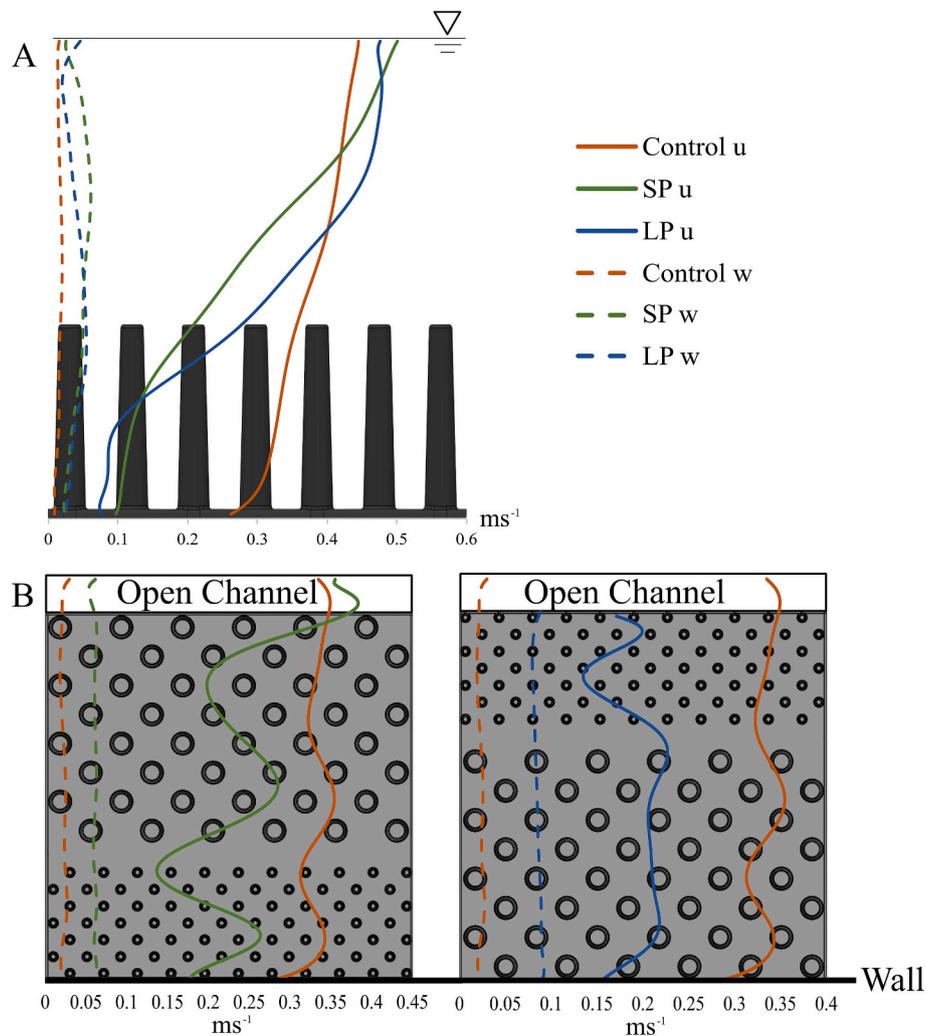


Fig. 3. Exemplar plots showing temporally and spatially averaged streamwise velocity (u) profiles from a side view (plot A) and an aerial view (plots B). The data shown is from treatment 4/C and measurements were taken 85 mm from the wall for A and 85 mm from the bed for B. All velocities are in ms^{-1} . In plot A the dashed lines represent the vertical velocity (w) and in plot B represent the cross-streamwise velocity (v). In B, the plot to the left shows velocity profiles for the tiles mounted in the SP configuration whereas the plot to the right shows the tile in the LP configuration.

streamwise velocity with the presence of the tiles. With the tiles mounted in SP (small protrusions next to wall), the streamwise velocity is low at the wall and increases for a short distance from the wall (as may be expected) before dropping to a minimum of 0.13 ms^{-1} near the intersection of the two protrusion areas. Over the less porous large protrusions, the velocity increases again and an even more pronounced increase is present where the tile meets the open channel flow. When the large protrusions were mounted near the wall (LP), the velocity was lower across the top of the tiles compared to the SP, but the same small peak is present at a short distance from the wall. The velocity further decreases over the small protrusions, only becoming higher near the open channel. The cross-streamwise velocity (v) in both SP and LP was higher than control but markedly higher in LP compared to SP.

The relative velocity reductions of SP and LP configurations compared to the control were calculated to visualise the proportion of velocity being attenuated by the tiles throughout the water column for each flow condition in Fig. 3, where values larger than zero indicate a reduction in velocity compared to control whilst a negative value shows an increase. Fig. 4A compares the relative reduction for all treatments in the SP configuration (small protrusion adjacent to the wall) for the spatially-averaged profile with increasing bulk velocity and constant flow depth, the envelope of all plotted lines is narrow, particularly in the upper portion of the plot. On average, the crossover point above the tiles

where the velocity starts to be attenuated instead of being accelerated is around $z/H = 0.72$ (or 72 %) of the way up the water column below which there is a steep increase in attenuation until it reaches a maximum of up to 95 % in the near-bed region. Overall, the attenuation (shown by relative velocity reduction) is similar across these test conditions. In Fig. 4B, the same is shown for the series of flow conditions varying in flow depth where bulk velocity remained constant. Interestingly, the crossover point of the y axis, separating the attenuation region from the acceleration region, remains approximately the same independent of flow depth, the attenuation is similar across treatments with the exception of the region below the protrusion top where generally there is an increased attenuation for higher flow depths. Fig. 4D shows the same data as in Fig. 4B for the large protrusion configuration (LP), the trend is similar to small protrusion configuration (SP; Fig. 4B) and the y intercept is the same for each flow depth regardless of the configuration. The shallower flow conditions ($H = 129 \text{ mm}$; $H = 155 \text{ mm}$) appear to be less effective in attenuating flow in the lower 50 mm of the water column but a flow velocity reduction of over 50 % is still present in all cases in this region. Fig. 4C showing the relative reduction of increasing bulk velocities in the LP configuration highlights a tight grouping of all the plotted lines and is similar to the SP configuration (Fig. 4A) except for being less effective at attenuating velocity in the canopy layer of the flow, where for the LP configuration the attenuation remains constant

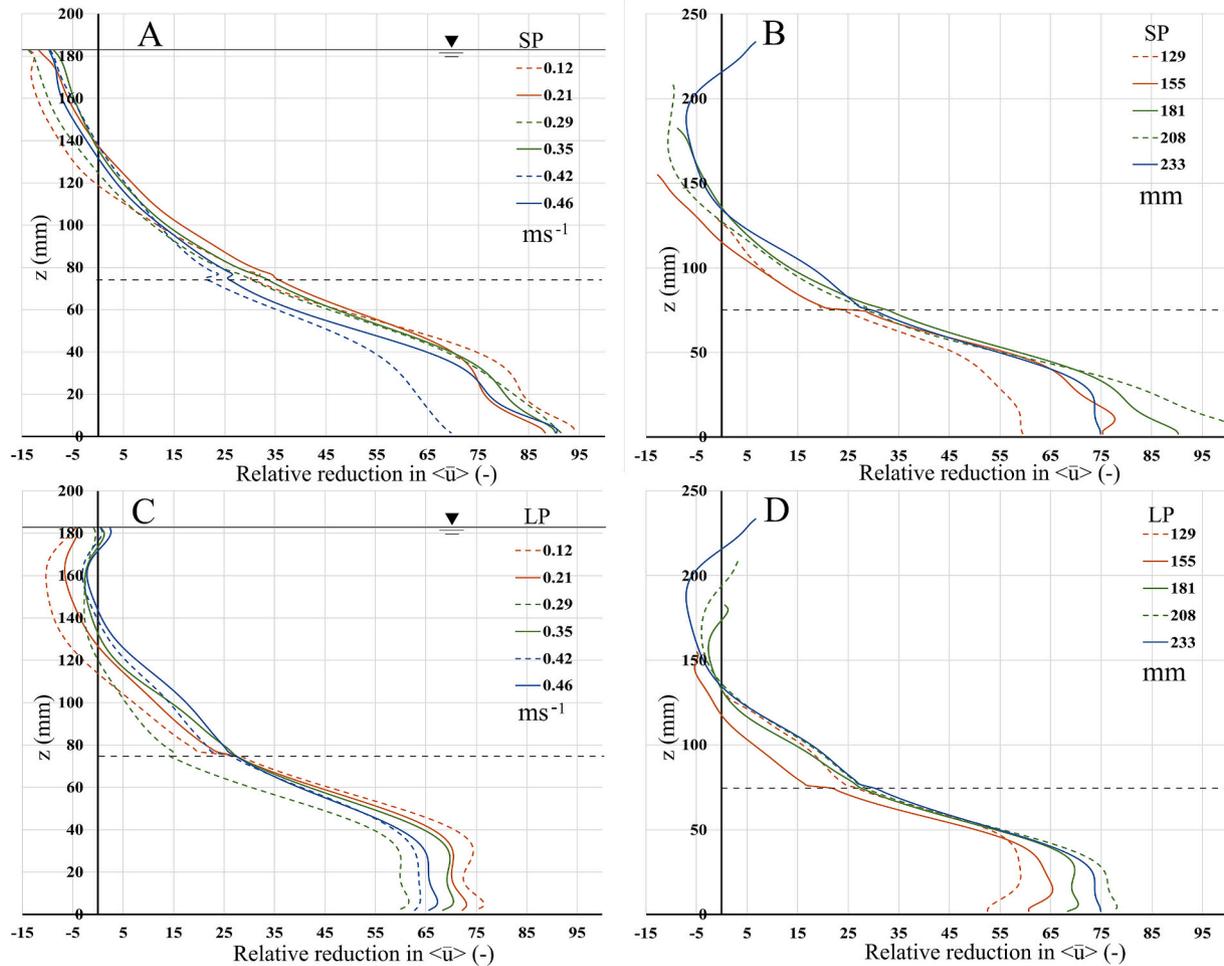


Fig. 4. Vertical profiles of percentage relative reduction in spatially-averaged streamwise velocity. A and C show the velocity reduction for increasing bulk velocity treatments ($H = 180$ mm) whereas B and D show the velocity reduction for treatments with increasing flow depth ($U = 0.35$ ms⁻¹). Each line is the average percentage velocity reduction across the tile, A and B show the results for the tiles mounted in configuration SP (small protrusions adjacent to flume wall) and C and D for configuration LP (large protrusions adjacent to flume wall). The horizontal dotted line indicates the tops of the protrusions.

for the lower 50 mm of the water column. The SP configuration appears to be more effective at slowing the flow in the canopy layer of the flow whereas the LP configuration is marginally more effective in the region immediately above the protrusion tops but overall the velocity reduction created by the tiles is significant and has the potential for fish to exploit these lower velocities for passage.

In the vertical plane, the vertical Reynolds shear stress (RSS, $-\rho u w$) peaks just below the top of the canopy layer, in the shear layer created by two adjacent flow regions moving at different velocities. Reynolds shear stress decreases steadily from the peak towards both the water surface and bed. As would be expected for control conditions, the profile remains low throughout the water column (maximum values of -0.3 kgm⁻¹ s⁻²) and increases for increasing flow velocities as Reynolds number increases. The vertical Reynolds shear stress for the SP and LP configurations also increases with velocity to a maximum of -2.8 kgm⁻¹ s⁻², being close to control conditions at a bulk velocity of 0.2 ms⁻¹ but steadily increases with increasing bulk velocity. The SP configuration has higher peak values of vertical Reynolds shear stress than the LP configuration (by around 5 %) but the profile remains unchanged throughout the different test cases, suggesting that the protrusion size and density affects turbulent momentum magnitude while, as would be expected, protrusion height determines the peak of the vertical RSS curve. The horizontal Reynolds shear stress data ($-\rho u v$) is less clear; there is a peak in both SP and LP configurations where the tiles meet the open channel, confirming the presence of a shear layer which is

around 50 % of the magnitude of the vertical RSS. Above the protrusions, in SP configuration there are two major peaks, one above the small protrusion section and one above the large, however at the intersection between the two protrusion densities, there is no peak in either SP or LP configuration due to the differential in zonal velocities not being large enough. The overall magnitude of horizontal Reynolds shear stress is smaller than in the vertical for both configurations.

The vertical turbulent intensity (TI) remains always low in the control conditions, while in the tests with tiles it increases in magnitude with increasing bulk velocity and peaks just below the level of the protrusion tops (similar to the vertical Reynolds shear stress) reaching a minimum at the bed, as shown by Fig. 5. In the horizontal plane, the turbulent intensity also increases with bulk velocity but is relatively constant over the width of the tile.

Following the trend of the Reynolds shear stress and turbulent intensity profiles, the turbulent kinetic energy (TKE) reaches a maximum in the vertical shear layer and a minimum in the canopy layer. Examining the vertical and horizontal planes (XZ and XY respectively), the increase of magnitude of TKE with bulk velocity is pronounced compared to the increases seen in other metrics. In the horizontal plane, the TKE profile increases with distance from the wall for the higher velocity conditions.

These results show the primary shear layers created by the tiles; most notably, where the fast-moving flow above and beside the tile meets the slow moving flow within the tiles. The velocity differential between the

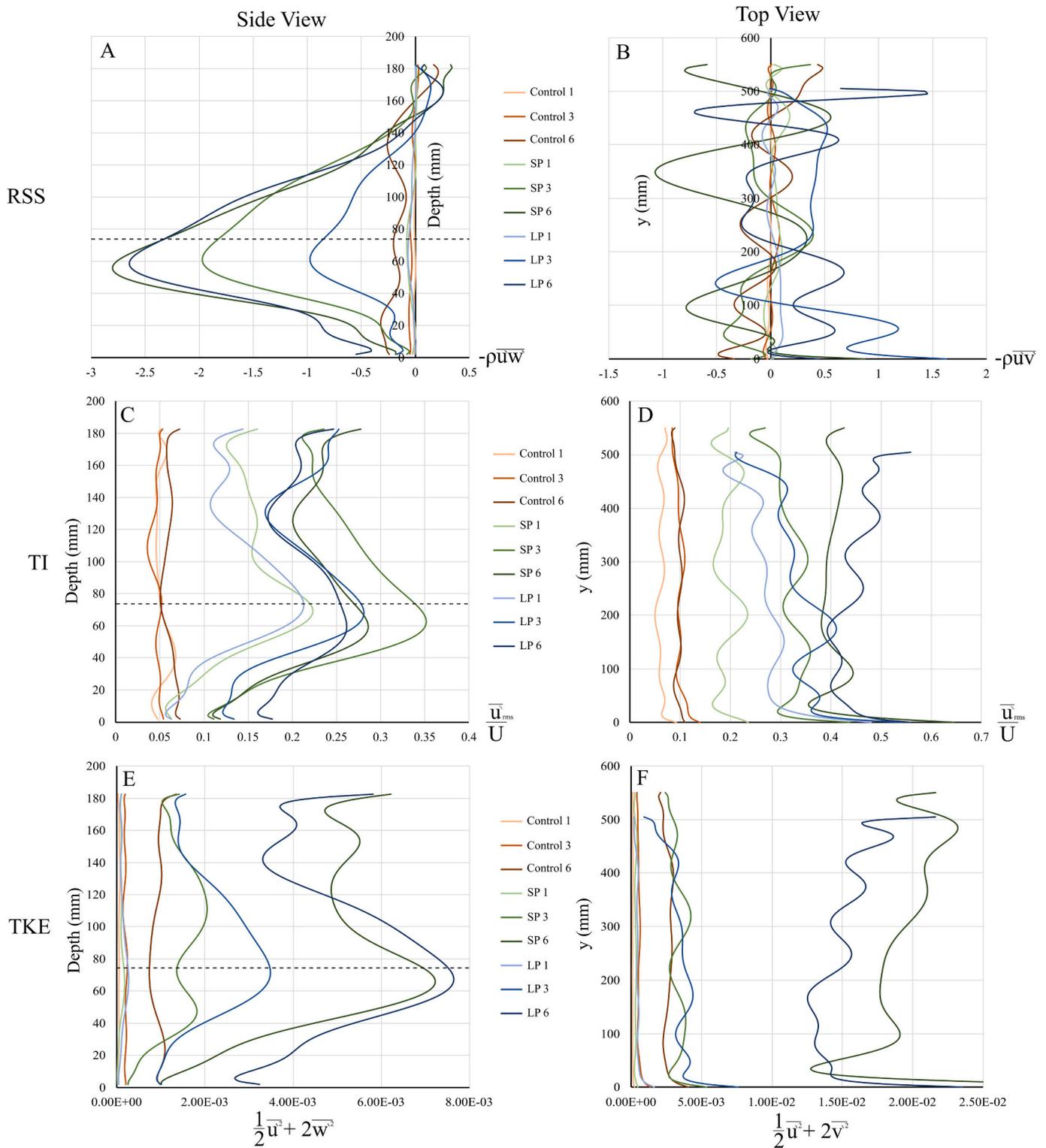


Fig. 5. Plots showing three turbulence parameters of the flow from a side view and a aerial view (where $y = 0$ is the flume wall). A and B show data for vertical and horizontal Reynolds shear stress (RSS - $\rho u w$, $\rho u v$), C and D show turbulent intensity (TI), and E and F show turbulent kinetic energy (TKE). Only three tests per tile configuration (control, SP, and LP) are displayed, tests 1, 3, and 6; this approach was taken to show the overall trend without overcrowding the plot. Each flume condition is represented by a colour, getting darker with increasing bulk velocity of the test. The data for the plots was in all cases taken at 85 mm from the wall for the side view and 85 mm from the bed for the aerial view (10 mm above the top of the tiles). Horizontal dotted lines represent the tops of the protrusions.

large and small protrusions is not sufficiently large to generate a shear layer in this location, favouring the use of the tile by fish.

3.2. Passage and swimming performance

Overall, passage within the experimental time was increased by shoaling more than it was by the presence of tiles although both shoaling and tiles produced more passes. The number of successful upstream

passes was 26.7 % more in T3 compared to C1, a significantly higher pass rate (GLM, $p = 0.02$) with 40 % of fish passing compared to 13.3 %. Treatment T3 (40 %) had statistically the same passage success of T1 (20 %) and C3 (30 %), (GLM, $p = 0.09$ and $p = 0.59$ respectively). There was a significant correlation between passage success and fish length (GLM, $p < 0.001$); larger fish were more likely to pass upstream than smaller fish. Time to pass (measured from the beginning of the experiment to the successful passage of the focal fish) did not vary between treatments, and there was no link between fish length and time to pass (GLM, $p = 0.19$).

The maximum distance upstream of the release area was calculated for every fish based on the tile number reached and provides a metric to evaluate performance that is less discretised than passage (Fig. 6). The maximum distance reached for the control treatment with a single fish (C1) was lower than C3 and T3 (GLM, $p < 0.03$) but not lower than T1 (GLM, $p = 0.12$). Larger fish were more likely to progress further than smaller fish (GLM, $p = 0.004$) further indicating that stickleback swimming performance increases with size.

Spills occur when a fish experiences a destabilisation while swimming; this is distinct from a change of direction by being clearly involuntary and often occurring while station holding. In the control treatments, a negligible number of spills was recorded when compared to the tile conditions where 190 spills were recorded overall, with T1 and T3 significantly different to control treatments (GLM, $p < 0.0002$) but not significantly different from each other. Fish length was correlated with number of spills indicating that smaller fish were more likely to spill (GLM, $p = 0.009$), since spilling is often related to turbulence this correlation is probably affected by turbulent parameters in a particular area. The more time a fish spent swimming, the more likely it was to spill (GLM, $p < 0.0001$). This might also be the reason that spill number was negatively correlated with passage success (GLM, $p = 0.03$). Most spills occurred within the large protrusion areas of the tiles compared to all other areas of the flume (GLM, $p < 0.006$).

The time spent resting was highest in the C1 and C3 treatments, and least in T3 (GLM, $p < 0.05$), whilst T1 was not significantly different to any other treatment. In the tiled treatments, resting did not only occur against the downstream flow straightener, but also within the small protrusions as the spacing allowed the fish to rest their body on consecutive protrusions or between protrusions and the sidewall without the need to swim. Despite increased resting opportunities the fish rested less with the tiles compared to the controls. The time spent

impinging was the lowest in treatments T1 and T3, specifically, less time was spent impinging in T1 than C1 (ZINB, $p = 0.002$) and less time was spent impinging in T3 than C1 and C3 (ZINB, $p < 0.02$). There was no significant correlation between fish length and time spent resting or being impinged.

In the control conditions, the only area available for the fish was the open channel so this was not analysed in terms of where fish spent most time. The fish in the control conditions did swim primarily near the walls where the flow is the slowest (around 0.2 ms^{-1} , equivalent to 57 % of the bulk velocity). In the tile conditions, the fish did not spend significantly different amounts of time above the tiles, on the side of the tiles, in the large protrusions, in the small protrusions or in the open channel when comparing T1 and T3, showing that shoaling did not have an impact on area selection. Larger fish, however, were less likely to spend time in the small protrusions than smaller fish (GLM, $p = 0.006$).

In treatment T1, the sticklebacks spent more time in and around the tiles than they did in the open channel (GLM, $p < 0.0001$). More specifically, more time was spent in the small protrusions than in the open channel, tile side and above tiles areas (GLM, $p < 0.002$) but not significantly different than in the large protrusions (GLM, $p > 0.8$). More time was spent among the large protrusions compared to any other area with the exception of the small protrusions (GLM, $p < 0.004$). The areas above the tiles and on the side of the tiles were used more than the open channel when summed (GLM $p = 0.02$) but not significantly if considered individually (GLM, $p > 0.05$). Similar results can be seen in treatment T3, the fish spent more time cumulatively in and around the tiles compared to the open channel (GLM, $p < 0.0001$). The time spent in the small and large protrusions individually was greater than for the open channel for both (GLM, $p < 0.0002$) but the tile side and above tiles areas did not have a significantly different amount of time to the open channel (GLM, $p > 0.5$). The time spent in the small protrusions was also significantly more than the time spent in the above tile and tile side areas (GLM, $p < 0.002$) but not different compared to the large protrusions (GLM, $p = 0.87$). More time was also spent in the large protrusions than in the above tile and tile side areas (GLM, $p < 0.001$) but there was no difference in time spent between the above tile and side tile areas (GLM, $p = 0.2$).

3.3. Shoaling behaviour

Overall, there was no significant difference in the total time spent

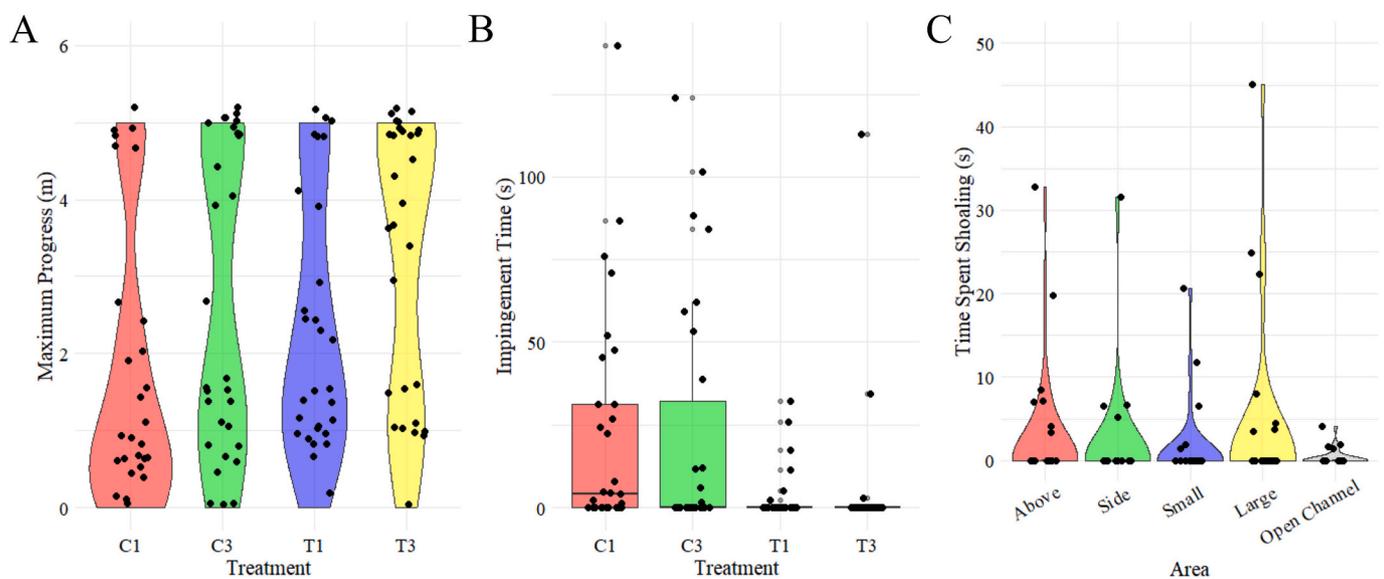


Fig. 6. (A) Maximum distance from the downstream end of the flume reached by the focal fish, beyond five metres a fish was considered to have passed upstream as the tiles ended there. (B) Total impingement time data for each fish. Boxes represent interquartile range and whiskers represent the 95 % range. (C) The amount of time spent in the company of at least one other fish by area. This is exclusively for the shoaling conditions with the tiles.

shoaling between the control C3 (32 % of time) and tile T3 conditions (21 % of time; GLM, $p = 0.3$), there was also no correlation with fish length (GLM, $p = 0.42$). There were no differences in the time spent in shoals of 2 fish or shoals of 3 fish between the two shoaling treatments (GLM, $p > 0.18$). In treatment T3, the focal fish spent significantly more time alone (not shoaling) than in shoals of 2 or 3 fish (GLM, $p < 0.0001$), and significantly more time in a shoal of 2 compared to shoal of 3 fish (GLM, $p = 0.02$). In treatment C3, the fish spent less time shoaling than either in shoals of 2 or 3 fish (GLM, $p < 0.0001$), but there was no significant difference between the time spent in shoals of 2 or 3 fish (GLM, $p = 0.18$). For treatment T3, we also analysed shoaling time per area; fish shoaled most in the area with small protrusions, this area was significantly different to all other areas (GLM, $p < 0.004$) except for the large protrusion area (GLM, $p = 0.09$).

4. Discussion

4.1. Hydrodynamics

Eel tiles are effective at reducing velocities but they also create moderate levels of turbulence. This is encouraging when viewed through the lens of potential fish passage. The complex flow in this study features multiple shear layers combined with the dual protrusion density of the tile. The established field of vegetated canopy flow in open channels is a helpful tool for analysing the hydrodynamics under investigation here because vegetation is often modelled as arrays or clusters of rigid cylinders in a flume, which resembles the current experimental setup. Furthermore, the overall solid volume fraction of the submerged tile ($\phi = 0.09$) matches ϕ values investigated in previous studies between 0.02 and 0.1 (Nepf and Ghisalberti, 2008; Unigarro Villota et al., 2023; White and Nepf, 2007). The velocity profiles through the water column are similar to those found in submerged vegetation canopies, with slow flow within the canopy rapidly increasing at the interface and reaching a more constant higher value at the top of the water column. This is typical of canopy flow and the inflection point in the profile points to the potential presence of a Kelvin-Helmholtz (KH) instability (Ghisalberti and Nepf, 2005; Nepf and Ghisalberti, 2008; White and Nepf, 2007). Although less well characterised, the cross-channel velocity profile also has similarities to canopy flow. Plots of horizontal Reynolds shear stress are also closely matched with literature, the peak being slightly below the top of the canopy and confirming the presence of a shear layer (Nepf and Vivoni, 2000).

Previously Ghisalberti (2002) established that 10 canopy heights (h) downstream of the leading edge, the canopy scale vortices remain the same size and have the same horizontal penetration into the canopy. In the case of the tiles, this is roughly equivalent to the length of one tile from the leading edge. Predictions can be made for the vertical penetration depth into the canopy based on C_{Dah} (Nepf, 2012), in this case ($C_{Dah} = 0.56$, where C_D is the drag coefficient, a is the frontal area per volume of the canopy, and h is the canopy height). $C_{Dah} > 0.23$ indicates that the penetration will be less than the protrusion height, which is further compounded by the shallow flow ($H/h < 2$) over the tiles reducing the size and strength of these large scale vortices (Nepf, 2012).

The turbulent structures identified in previous work have been extensively studied, the KH instability generates coherent canopy scale vortices that, according to the relative submergence, the canopy density and other factors, will penetrate within the canopy to different depths (Ghisalberti and Nepf, 2005; Nepf and Ghisalberti, 2008; Nepf, 2011, 2012). Conversely, in the current study, the large-scale turbulent structures recorded were non coherent ejections and fluctuations that were not strictly periodic. Ghisalberti and Nepf (2006) found that vortices were shed at the shear layer at 0.11 Hz so there is a possibility that the primary shedding frequency of the fluctuations in the current study was not detected because the sampling time was too short to detect it. Penetration of the turbulent structures was correctly predicted by Nepf (2012) such that the turbulence was penetrating the canopy but the

depth of the turbulence was less than the height of the protrusions, having a solid volume fraction of above 0.23 and being damped by the shallow water depth ($H/h < 3$). This may have implications for swimming stability of fish due to the Kelvin-Helmholtz fluctuations produced depending on the flow depth and bulk velocity conditions.

A potential issue of the tiles is that the low velocities may cause sediment deposition, causing them to become blocked. Deposition will largely depend on the sediment load of the water approaching the tiles, bed shear stress, and the flow velocity. During low flows, the base of the tiles should provide a barrier to the lowest velocities depositing sediment and higher flows may initiate it into resuspension. Turbulence generated by canopies can enhance sediment mobility and create scour within the canopy, especially with higher levels of turbulent kinetic energy which could potentially keep the tiles clean (Chen et al., 2012; Liu et al., 2021; Nepf, 2012). There is also the opportunity to lessen the scour downstream of the tiles due to the lower velocities immediately downstream of the tiles which could help with preventing culvert overhangs forming between the downstream end of culverts and the riverbed. Anecdotal evidence from practitioners who have installed these tiles report that they are easy to maintain and keep sediment free, especially when compared to other available solutions like elver brushes.

The tiles need to create favourable conditions for fish passage at high-speed barriers, primarily for eels but also for other species, to maximise habitat restoration and connectivity. The tiles produce significant velocity reductions within them and in their vicinity and do so consistently under varied flow conditions. This comes at the expense of generating turbulence which can be detrimental to swimming fish. Many studies have attempted to characterise fish responses to turbulence and have found that in specific situations, fish can utilize turbulence to their benefit if the turbulence is discrete, in the correct plane and shed at the correct frequency (Liao et al., 2003; Liao, 2007; Stewart et al., 2016; Harvey et al., 2022). Vortices can destabilise fish, causing them to 'spill' (Tritico and Cotel, 2010; Webb and Cotel, 2011; Smith et al., 2014; Muhawenimana et al., 2019; Zha et al., 2021) depending on the orientation of the eddy. The size of the vortices is important to fish stability, eddies the same length scale as the fish are more likely to cause spills (Muhawenimana et al., 2019). Reviewing the findings of studies on fish stability, the canopy scale turbulence produced by the tiles should not be strong, coherent or periodical enough for most fish to be either destabilised by it or to benefit from it. The stem scale turbulence however, would be the correct length scale for small fish (50 mm or below) to be destabilised if it were strong and discrete enough. Overall, the flow in and around the tiles seems suitable for fish passage and any fish species which find the conditions suboptimal will have the remainder of the channel to pass upstream as the tiles only partially cover the channel width. Furthermore, the tiles in SP configuration (with small protrusions near the flume wall) have very little influence on the rest of the channel, benefitting other species that may not need the tiles and reducing the impact of the tiles on the flow through a culvert or similar structure. The recommended mounting for the tiles is therefore to place the small protrusions next to the stream bank or culvert vertical wall.

4.2. Stickleback passage

The passage success of three spined sticklebacks was positively affected by the presence of shoalmates. Sticklebacks achieved the highest number of upstream passes when shoaling and in the presence of tiles. Behavioural data suggest that the effects of the tiles may be greater than is evident from the passage data. The sticklebacks impinged on the downstream flow straightener less with the tiles which may explain why the tiles did not appear to have a greater positive impact on passage. If a fish was impinged during this experiment after attempting to swim, it indicated exhaustion as the fish was unable to carry on swimming; in the control conditions most fish either passed quickly or impinged within the 10 min experimental period as they quickly became exhausted. In

contrast, with the tiles fish commonly spent the entire time in the tiles and were not exhausted by the end of the experiment. The tiles also allowed the fish to rest among the small protrusions at any distance from the downstream end (therefore conserving any progress made at the time of resting) so given a long timeframe for the experimental trials, it is likely that the sticklebacks would be able to eventually pass upstream. Overall, this suggests that the current study underestimates the potential for stickleback passage using the tiles, similar to findings by a previous study on the tiles that point to an underestimation of passage (Sonnino Sorisio et al., 2024). The ability for fish to rest anywhere on the tiles not only allows them to maintain progress already made without being swept downstream but it also means that the resting fish will be more evenly distributed, decreasing the likelihood of many fish resting in one place, thus creating a focal predation opportunity (Jepsen et al., 2010). The increased ability to rest within the tiles and the decrease in impingement also point to a probable decrease in energy expenditure, increasing the chances for the fish to be productive once they have passed. Sticklebacks are naturally found in highly vegetated areas with slow flows and many refugia (NatureServe., 2019; Arai et al., 2020), a bare culvert provides none of these and is therefore much less attractive to a stickleback so not only are the fish less likely to succeed in passing a velocity barrier, they might also not attempt to do so in the first place. The tiles provide cover, resting areas and refugia so the sticklebacks are more likely to use them and pass upstream. In the current study, the sticklebacks were released directly into the flume and they had no choice regarding the terrain so the comparative performance of the tiles is potentially further underestimated here.

The tiles also have the potential to aid stickleback swimming by modifying the flow dynamics below the protrusions and around the tiles. Clearly flow reduction is advantageous and here the tiles work well in two ways; they accommodate areas where the fish can station hold and rest and at the same time provide areas of slightly faster (but still reduced) flow for the sticklebacks to progress upstream. The large-scale turbulence recorded above and on the side of the tiles did not seem to affect the stability of stickleback swimming, evidenced by the low number of spills in these areas. This is probably due to the turbulent length scale being too large and rarefied to affect the fish. Fish can be destabilised by vortices in the range of >0.75 body lengths (Tritico and Cotel, 2010; Muhawenimana et al., 2019); the large-scale turbulence of the current study falls outside these parameters. However, the small-scale vortices shed by the large protrusions are within range for spills to occur. Most spills did occur within the large protrusions as the sticklebacks often held station behind a protrusion and the chance of spilling decreased with increasing fish size. This is a potential drawback of the tiles as increased spilling produced a decreased likelihood of passage but this may be a result of the fact that fish that passed quickly spent less time in the tiles and therefore had reduced chances of spilling. The fish still showed the ability to make progress in the large protrusions despite the destabilisations but more commonly would use this area to hold station and then move to the side of the tile or above the tile to swim further upstream. This contrasts with the control conditions where the fish rarely swam for the 10 min of the experiment, either passing upstream before that or in most cases, impinging on the flow straightener. This indicates that the flow conditions were on the limit of the swimming performance of these fish.

Shoaling had a significant effect on fish behaviour and sticklebacks were more likely to pass if they had shoalmates. There are multiple potential explanations for why the presence of two shoalmates helped performance; firstly, sticklebacks are a naturally shoaling fish and this behaviour is associated with reduced energy expenditure (Johansen et al., 2010), isolated sticklebacks lose this advantage and may potentially experience stress as a result of not being in a shoal. In the wild, stickleback shoals are usually larger (Barber and Ruxton, 2000; Mehliis et al., 2015) than used in the current experiment so we would expect the effects observed here with just three fish per shoal to be even more marked. Sticklebacks can tell the difference between shoals of different

sizes and always choose the larger group (Mehliis et al., 2015). Shoaling provides more social interactions (Cushing and Jones, 1968) reduces predation risk and increases foraging opportunities (Mayer, 2010). When subjected to flow, however, fish shoal more closely (de Bie et al., 2020) and when migrating shoal sizes are at their largest (Mayer, 2010). A combination of these mechanisms is the likely cause of the increased success of the stickleback shoals in this experiment but the hydrodynamic benefit is the most obvious and direct explanation in this case. It must also be considered that the sticklebacks did not shoal all the time they were in the flume and spent more time alone. This may be explained by several factors. Firstly, the flow conditions were not suited to shoaling as in the control condition bulk velocity was at the limit of the stickleback capability which would eventually separate fish with different swimming abilities. With the tiles there was more turbulence to destabilise the fish, making coordinated swimming harder as constant position adjustments can increase energy expenditure (Johansen et al., 2010). The spacing of the protrusions of the tiles also made shoaling harder as fish could not easily fit close to each other and may have also lost sight of each other among the tiles. This suggests that although there may be a hydrodynamic benefit to shoaling, the presence of other shoalmates is likely affecting the motivation of the sticklebacks in other ways that increase their likelihood of successfully passing upstream. The sticklebacks were wild caught and despite being visually checked for disease the fish may have had cryptic infections. This is relevant since infection can cause decreased swimming performance (Stewart et al., 2018) and reduced shoaling (Ward et al., 2005; Rahn et al., 2015). The degree to which the sticklebacks in this study were familiar to each other is unclear, they were caught in the same location and housed in the same tank but the shoals were not given time alone to familiarise and this can impact shoaling (Barber and Ruxton, 2000). In considering all these factors, it is still evident from this study that shoaling aided passage; the mechanism is uncertain but likely a combination of the hydrodynamic and social benefits.

For the tiles to have the desired effect of reconnecting fish populations and habitats, they need to benefit multiple species and different sizes of fish. These tiles can be effective for eels (Sonnino Sorisio et al., 2024) and potentially sticklebacks, two species with diverse morphologies, swimming dynamics, and passage requirements, indicating that they have the potential to help more species, especially fish small enough to fit within the protrusions or that can exploit the low velocities surrounding the tiles. The tiles also have the advantage of being cheap to purchase, easy to install and importantly, do not affect the whole channel. The tiles need only cover part of the channel near the bank and do not affect the rest of the channel, leaving it to flow freely and allow high performance swimmers like salmonids that may not require the tiles to continue their journey undisturbed.

5. Conclusion

Eel tiles show promise as a passage solution for three spined sticklebacks by providing decreased flow velocities, moderate turbulence levels, refugia and resting opportunities. The presence of other sticklebacks in the flume was the factor with the largest effect on passage however harsh flow conditions can break up shoals. By being effective for multiple species, the tiles have the potential to reconnect habitats at high velocity barriers and by modifying the flow around them potentially help other species pass too.

CRedit authorship contribution statement

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

Catherine A.M.E. Wilson: 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. All authors declare no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

links to the data are in the manuscript

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