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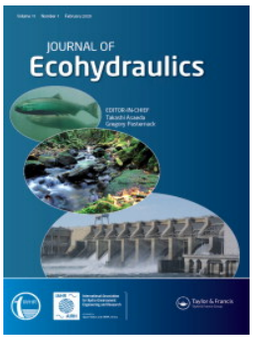

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Response of downstream moving European eel (*Anguilla anguilla*) to hydrodynamic conditions created by channel constrictions

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ABSTRACT

The efficacy of bypass channels that provide safe routes of passage for downstream moving fish at river infrastructure can be compromised if fish avoid the hydrodynamics encountered at the entrance. Using an open-channel flume, avoidance exhibited by European eel (*Anguilla anguilla*) was investigated in response to: (1) hydrodynamics created by a smooth tapered constriction under three discharge regimes (low, medium, high); and (2) a smooth tapered and sharp angled constriction under the low discharge. Although eel exhibited avoidance on encountering the smooth tapered constriction, the prevalence and magnitude of response was not influenced by flow acceleration, the hydrodynamic factor often considered responsible for deterring fish. Eel more frequently rejected the sharp angled compared to the smooth tapered channel by retreating upstream, delaying downstream progress. This was likely due to flow recirculation (i.e. the occurrence of flow reversal upstream and downstream of the constriction) that was generated only at the sharp angled entrance. Flow accelerated at both constriction geometries, suggesting that recirculation had a greater influence on behaviour and subsequent rate of downstream movement. Minimising areas of flow recirculation, a seldom considered factor, as well as rates of acceleration at bypass entrances is likely to enhance their efficiency.

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Introduction

Fresh waters are likely the most threatened of all ecosystems (Dudgeon et al. 2006; Gozlan et al. 2019) due to numerous persistent and emerging anthropogenic threats (Reid et al. 2019). As a consequence, freshwater fish are experiencing among the highest extinction rates of all vertebrates (WWF 2018). Freshwater habitat fragmentation, e.g. by dams and weirs, is a major cause of declining fish populations and their high conservation concern (Liermann et al. 2012; Fan et al. 2015; Best 2019). River infrastructure can prevent or limit critical seasonal and life-stage specific migrations, recolonization following disturbance, climate-mediated shifts in distribution and the exchange of genetic information between subpopulations (Wilkes et al. 2019). Although methods have been developed to mitigate the impacts of river infrastructure on fish movements, primarily through the construction of passage facilities (such as fishways and bypasses) that theoretically restore habitat connectivity, their effectiveness is highly variable and can be very low (Noonan et al. 2012; Bunt et al. 2016). As such, fish passage facilities are in many instances failing to achieve intended conservation goals (Brown et al. 2013).

A primary explanation for the low efficacy of fish passage facilities relates to a lack of understanding (or consideration) of fish behaviour in their design and operation (Williams et al. 2012). For example, determining the swimming performance of target species is essential for establishing water velocity design criteria for upstream fishways (or fish passes) (Vowles et al. 2013). The swim chambers used to obtain these data, however, prevent fish from expressing natural performance enhancing behaviours (such as burst-coast swimming) leading to inaccurate estimates (Peake and Farrell 2006; Tudorache et al. 2007; Vezza et al. 2020). Furthermore, where water velocities are within the limits of fish swimming performance, upstream passage success can be variable or remain low (e.g. Goerig and Castro-Santos 2017; Vowles et al. 2018). These examples suggest behaviour has a significant influence on fish passage efficiency and highlights

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the importance of improving understanding to maximise the efficacy of mitigation technology to conserve freshwater fish.

When fish migrate downstream, dams, weirs, and other impoundments can delay progress, increasing energetic costs and predation risk (Schilt 2007; Kemp 2015). Passage at infrastructure comprising mechanical elements, such as hydropower turbines or abstraction pumps, can also cause direct injury or mortality due to blade strike, rapid pressure change, cavitation, and high shear stresses (Coutant and Whitney 2000). Downstream bypass systems provide a potential means of mitigating these impacts and typically consist of physical (Kemp 2016) and/or behavioural (Noatch and Suski 2012) screens designed to prevent entrainment at intakes and guide fish to alternative routes. Prompt access to bypass channels is important if delay or risk of passing *via* more hazardous routes is to be minimised (Castro-Santos and Haro 2003), driving the need to create conditions conducive to entry, rather than those that might deter it. Yet, behavioural avoidance leading to delayed or low probability of bypass entry is common (e.g. Johnson and Moursund 2000; Nyqvist et al. 2017; Ovidio et al. 2017). Although there are several factors (e.g. acoustics, Duarte et al. 2019; light, Tétard et al. 2019) that may explain the elicitation of an avoidance response in fish as they encounter river infrastructure, hydrodynamic cues, such as the abrupt transitions of flow (i.e. accelerating water velocity) commonly occurring at the bypass entrance, are often provided as the main explanation (e.g. Kemp et al. 2005 and Vowles, Anderson, et al. 2014 for salmonids [*Oncorhynchus* spp]; de Bie et al. 2018 for cyprinids [*Squalius cephalus*], Piper et al. 2015 for eel [*Anguilla anguilla*]). Hydrodynamics in the real world are complex, however, and while abrupt transitions in flow velocity occur when channel geometry changes (e.g. at constrictions), there are other confounding variables, such as flow recirculation in proximity to the point of constriction, leading to flow reversal and generation of vorticity hot spots. These factors are seldom considered or referred to in detail in design criteria/guidance for such mitigation technology (Piper and Wright 2017; Fjeldstad et al. 2018; Calles et al. 2021). To enhance the efficacy of fish passage solutions, such as bypass systems for downstream moving fish, there is a need to better understand the relative importance of different hydrodynamic components of flow on triggering behaviours that are undesirable from a conservation management perspective.

To help improve the design and performance of fish bypass systems, this study investigated the relative importance of flow acceleration and recirculation in eliciting avoidance behaviour in downstream moving fish. To achieve this, we quantified the behavioural response and delay of downstream moving fish as they: (1) encountered different magnitudes of flow acceleration created by a smooth tapered channel constriction under three (low, medium, and high) discharge regimes, and compared the influence of: (2) acceleration and recirculation created respectively by a smooth tapered and sharp angled channel constriction under a single discharge. In addition to flow acceleration, the sharp angled geometry generated areas of flow recirculation that were absent under the smooth tapered design. The European eel was used as the model species as it is of high conservation concern (listed as "critically endangered" by the IUCN Red List of Threatened Species, Pike et al. 2020) and is known to exhibit avoidance when encountering channel constrictions during their downstream migration (Newbold et al. 2015; Piper et al. 2015). It was predicted that: (1) magnitude of behavioural avoidance would be positively related to flow acceleration, and (2) that flow recirculation would further enhance levels of avoidance and delay downstream progress.

Materials and methods

Study species

The European eel is a catadromous species that as adults migrate from freshwater to ocean spawning grounds in the Sargasso Sea (Miller et al. 2019; Wright et al. 2022). The larvae (leptocephali) use ocean currents to return to continental waters before entering estuaries and embarking on their upstream river migration as juveniles (glass eel and then elvers) and rearing (for the most part) in freshwater environments as the yellow phase eel, during which most growth occurs (Chadwick et al. 2007). Maturation into the silver phase eel precedes their downstream spawning migration that occurs mainly during the autumn (Vøllestad et al. 1986). European eel are critically endangered due to dramatic declines in recruitment (> 98% in some parts of its range) over recent decades (ICES 2019). River infrastructure is considered an important threat as it impedes eel migration and elevates mortality risk, particularly during passage through mechanical elements, such as turbines and pumps. Eel are considered particularly vulnerable at such sites due to their large adult size and elongated body morphology that increases the probability of blade strike (Montén 1985; Vowles, Karlsson, et al. 2014).

European eel used in this study were captured during their downstream migration by commercial fishermen on the River Test, Hampshire

(50°55.714'N 01°29.232'W; on 5 November 2015 and 21 November 2016) and transported in aerated river water to the International Centre for Ecohydraulics Research (ICER) facility at the University of Southampton (UK). Fish were held at low stocking density in seven tanks (~1200 L) fitted with aeration and filtration systems. Water quality parameters were monitored daily (ammonia $\leq$ 0.25 ppm; nitrite $\leq$ 0.50 ppm; nitrate $\leq$ 60 ppm) using an API Freshwater Test Kit. Increases in water quality parameters were reduced through partial exchange with dechlorinated tap water to maintain fish health.

Experimental setup and protocol

Experiments were conducted in an indoor open channel recirculatory flume (21.4 m long, 1.4 m wide, and 0.6 m deep) at the ICER facility. Two constriction geometries, defined as smooth tapered (Figure 1(a)) and sharp angled (Figure 1(b)) (0.4 m wide and installed ~12 m downstream of the flume inlet), were used to accelerate the flow without and with generating flow recirculation, respectively. To understand how differing magnitudes of acceleration influenced eel response, in 2015 experiments were conducted under three flow conditions, defined as low (100 l s^{-1}), medium (120 l s^{-1}), and high (160 l s^{-1}), using a single constricted channel geometry (smooth tapered) (Table 1; Figure 2). To compare the influence of acceleration and recirculation, in 2016 the experiments were conducted using two constricted channel geometries (sharp angled and smooth tapered) under a standardised (low) discharge (Table 1; Figure 2). The three flow conditions were selected to create distinct levels of flow acceleration within the range downstream migrating European eel might experience at channel constrictions in the wild (Piper et al. 2015). Within the flume, two polycarbonate tubular flow straighteners were installed 10 and 12 m upstream of the constrictions to create a 2 m long area in which eel were allowed to acclimate before the start of a replicate. An infrared video camera (Swann®) installed centrally and ~3 m above the base of the flume recorded eel behaviour in an "observation zone" spanning 2.0 m upstream and 0.5 m downstream of the entrance to the constriction (Figure 1).

Approximately 30 replicates were conducted for each treatment (Table 1) between 9–15 December 2015 and 22–27 November 2016. All replicates were conducted during hours of darkness (between 1800 and 0300 h) as this is when downstream migrating eel tend to naturally move and would be expected to encounter channel constrictions at river infrastructure (e.g. Evans et al. 2024). An individual eel

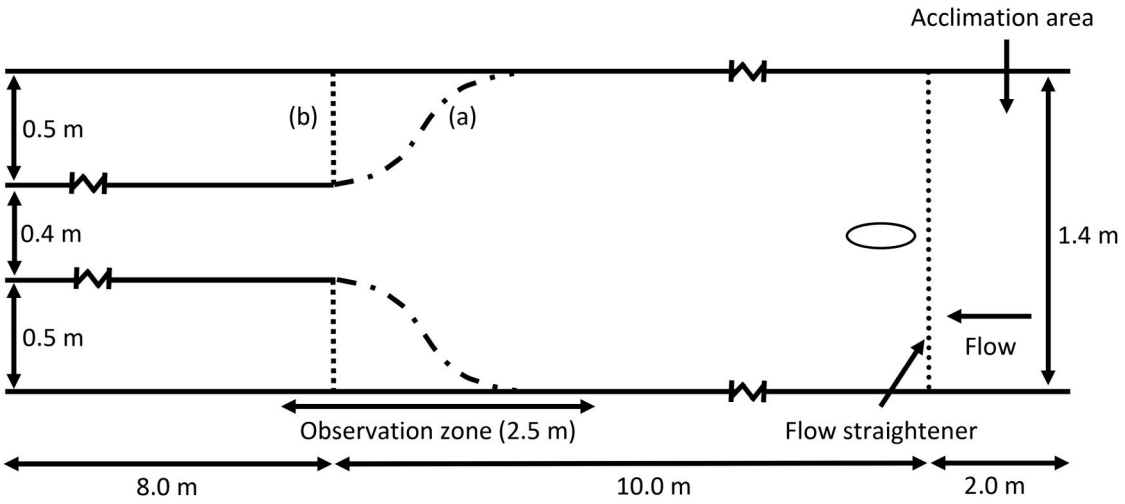

Figure 1. Plan view of a smooth tapered (a—dot-dashed line) and sharp angled (b—dotted line) channel constriction installed in a flume to determine the behavioural response of downstream moving European eel (*Anguilla anguilla*) to accelerating water velocities with (b) and without (a) flow recirculation. The centrally located oval immediately downstream of the flow straightener denotes the eel release location.

Table 1. Summary data across the experimental treatments used to determine the behavioural response of eel to flow acceleration and recirculation.

Channel constriction	Discharge	Year	Number of replicates	Eel length, mm (mean ± *SD*)	Eel wet mass, g (mean ± *SD*)
Smooth tapered	Low (100 L s^{-1})	2015	31 (27)	527.6 (±87.1)	262.6 (±125.6)
	Medium (120 L s^{-1})	2015	30 (29)	566.0 (±98.8)	355.2 (±229.8)
	High (160 L s^{-1})	2015	30 (29)	566.5 (±68.3)	349.6 (±171.4)
Smooth tapered	Low (100 L s^{-1})	2016	54 (52)	504.8 (±70.9)	244.1 (±92.6)
Sharp angled	Low (100 L s^{-1})	2016	30 (29)	507.5 (±79.4)	252.3 (±99.1)

For "number of replicates", the values in parentheses indicate those remaining after nine eel were excluded from the analysis due to corrupted video files or evidence of potential inadvertent observer influence.

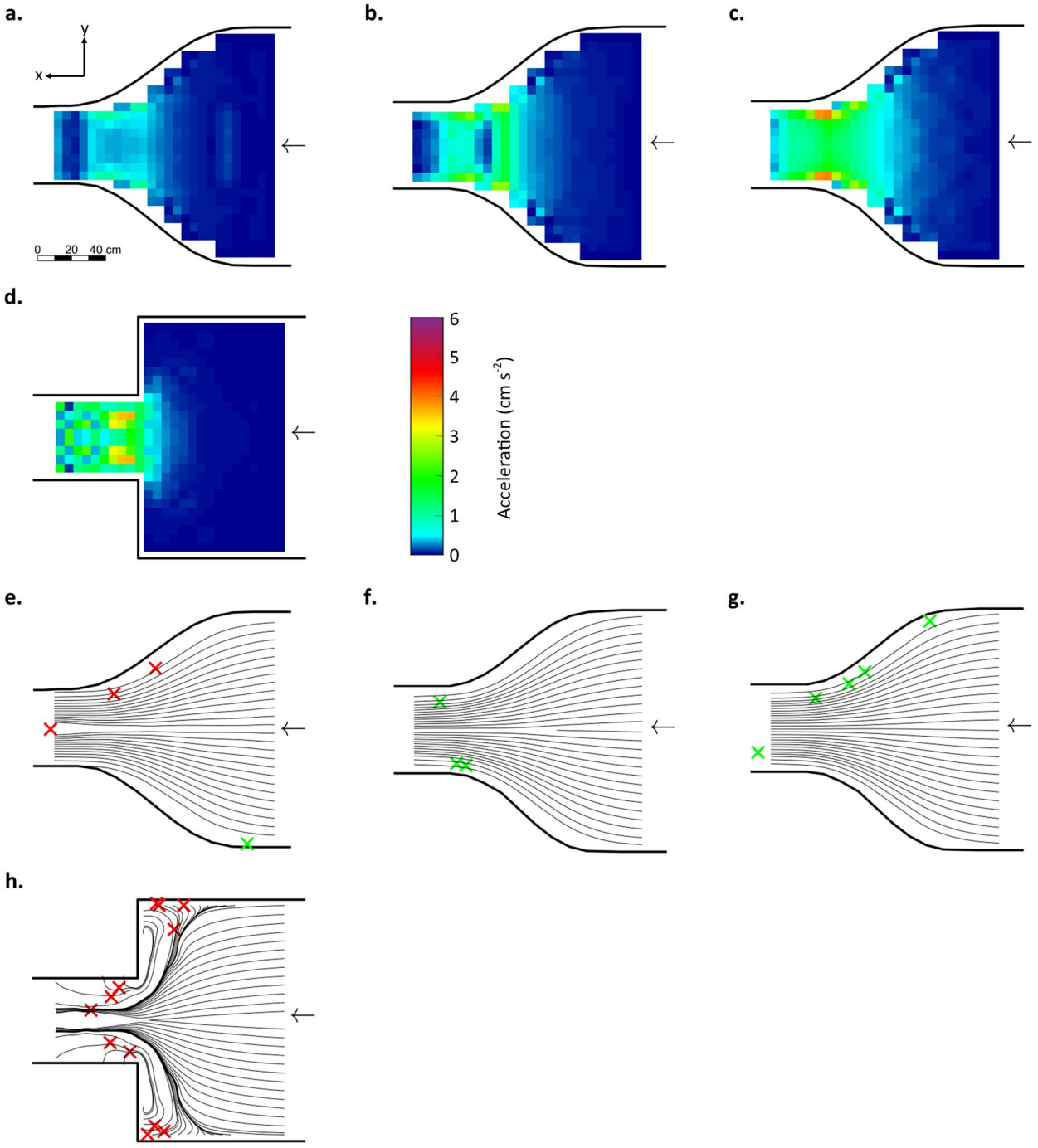

Figure 2. Flow acceleration (cm s^{-2}) (see Equation 1) at the entrance to the smooth tapered (a–c for low, medium, and high discharge, respectively) and sharp angled (d. low discharge) constrictions installed in the open-channel flume. Spatial discretization to calculate flow acceleration was 5 cm. The smoothed tapered constriction was designed to create negligible flow recirculation that is visualised using streamlines in (e–g) for low, medium, and high discharge, respectively. The sharp angled constriction designed to create strong flow recirculation under low discharge is shown in (h). The thick streamline helps visualise the spatial extent of flow recirculation immediately up- and down-stream of the constriction. Green and red crosses show eel rejection locations in 2015 and 2016, respectively.

was used in one replicate only. Up to 32 eels were placed into the acclimation area in the morning before the replicates commencing. After a minimum of 12 h, one eel was carefully netted from the acclimation area and released centrally into the flume, ~9.5 m upstream of the constriction (Figure 1). In 2015, each replicate lasted until the eel approached the constricted entrance and exhibited a behavioural response. In 2016, each replicate lasted until the eel passed through the constricted section of the flume, or until 20 min had elapsed, enabling comparison of delay to downstream movement between the two constriction geometries. At the end of each replicate, the eel was removed from the flume before being measured (total length, mm) and weighed (mass, g). The length (2015: $\chi^2 = 3.01$, d.f. = 2, $p = 0.222$; 2016:

$W = 818$, $p = 0.718$) and mass (2015: $\chi^2 = 5.45$, d.f. = 2, $p = 0.066$; 2016: $W = 838$, $p = 0.578$) of eel did not differ between treatments (Table 1). Mean (± *SD*) flume water temperature, measured at the beginning of each experimental evening, was 10.9 °C (± 0.6). One treatment was tested per night.

Hydrodynamic conditions

The smooth tapered (Figures 2(a–c)) and sharp angled (Figure 2(d)) channel constrictions generated the different flow fields of interest in this study. The smooth tapered channel created different magnitudes of flow acceleration under the three flow conditions tested, while at the low flow, a change in the geometry of the channel generated negligible (smooth tapered) to strong (sharp angled) levels of flow recirculation (Figure 2).

The hydrodynamic conditions created during each treatment were measured 5 cm from the channel floor on a 10 cm grid using an Acoustic Doppler Velocimeter (ADV, Vectrino+, Nortek, Norway) at a sampling rate of 50 Hz, with a sampling volume of ~1 cm^3 and duration of 60 s. Post-processing of the velocity time-series indicated that 60 s was enough to reach a statistically robust estimation of the time averaged velocity. Flow acceleration was estimated from the time-averaged velocities, in which the velocity vector was defined as $U(u, v)$, where u and v were the velocity components along the longitudinal (x) and transverse (y) axes of the flume, respectively (Figures 2(a–d)). The modulus of the flow acceleration at each point was estimated as:

$$|\boldsymbol{a}(x,y)| = \sqrt{a_x^2 + a_y^2}, \tag{1}$$

where $a_x = u(\partial u/\partial x) + v(\partial u/\partial y)$ and $a_y = u(\partial v/\partial x) + v(\partial v/\partial y)$ are the components of the acceleration a along x and y axes, respectively. Spatial discretization $(\Delta x, \Delta y)$ to calculate flow acceleration was 5 cm. In addition to flow acceleration, mean velocity components were used to plot streamlines (a curve tangent to the flow velocity vector) and visualise the associated 2-dimensional flow field. Streamlines allowed depiction of the mean paths of fluid particles (in steady flows, as in this study, streamlines and pathlines coincide). This highlights the lack of recirculating flow at the smooth tapered constriction (Figures 2(e–g)) and the spatial extent of the recirculating flow in the sharp angled constriction (Figure 2(h)). Under this geometry, recirculation occurs at multiple locations; first, immediately upstream of the constriction and second, immediately downstream of the channel constriction entrance (Figure 2(h)).

Data analysis

Nine eel (5.1%) were excluded from the analysis due to corrupted video files or evidence of potential inadvertent observer influence (Table 1). Reviewing the remaining video footage of eel (1) entering the observation zone and (2) first approaching the entrance to the channel constrictions allowed their behavioural response to (i) an open (control) and (ii) constricted (treatment) channel to be categorised as either *no response*, *reaction* or *rejection*. A *no response* was defined when an eel passed downstream without exhibiting any counter streamwise movement or switch in rheotactic orientation. A *reaction* was recorded when an eel exhibited some counter streamwise movement (increase in tail beat frequency/backward swimming) or switched to a positive rheotactic orientation (turn angle 90–180° from the predominant flow direction) on entering the observation zone or passing the constriction. A *rejection* was deemed to have occurred when eel exhibited a clear escape response by either swimming backwards or switching to a positive rheotactic orientation and actively swimming in a counter streamwise direction for at least 0.5 body lengths.

A Fisher's exact test of independence was used to determine whether the flow acceleration (positively related to discharge) influenced eel behaviour as they approached the smooth tapered constriction (2015 data). The same statistical method was used to compare eel behaviour as they approached the smooth tapered and sharp angled channel constriction under the single (low) discharge (2016 data). For statistical analysis, exhibition of *no response* or *reaction* behaviours were combined to enable comparison between the number of eel that rejected or passed the constricted channel on their first approach.

In 2016, the time between the body length of the eel entering and exiting the "observation zone" for both channel constrictions was used to quantify the *time to pass*. Exiting the observation zone involved moving downstream 0.5 m beyond the constricted channel entrance without immediately returning. Eel exhibiting a *rejection* could re-approach and exit or remain in, or upstream of, the observation zone until the end of the replicate. A Kaplan Meier estimator and Log Rank (Mantel-Cox) test statistic was used to identify differences in *time to pass* the smooth tapered compared to square angled constriction under a single (low) discharge. Kaplan Meier estimators and the global Log Rank tests were generated using the "survival" package in RStudio (v3.6.0; R Core Team 2019). Fish that approached the constrictions but failed to pass within the 20 min maximum replicate time were included in the analysis as right censored data. This statistical

approach is considered appropriate for analysis of fish passage data as individuals that fail to pass a constriction within the replicate time are included, enabling unbiased estimates of *time to pass* to be calculated (Castro-Santos and Perry 2012).

Results

Response to flow acceleration

In 2015, as eel moved down the open (control) channel and entered the observation zone, the vast majority (97.6%) exhibited *no response* under all discharge regimes, with most (83.5%) remaining unresponsive when they approached the smooth tapered constriction. Although the percentage of *rejections* increased with discharge (low: 3.7%, medium: 10.3%, high: 17.2%), the difference was not statistically detected ($p = 0.28$), indicating the magnitude of flow acceleration at the constriction entrance did not influence frequency of *rejection* (Figure 2 for *rejection* locations; Figure 3).

Response to flow recirculation

As eel moved downstream through the open (control) channel in 2016, the vast majority (97.5%) exhibited *no response* as they entered the observation zone under both constriction geometries. When approaching the constriction, eel behaviour was influenced by channel geometry ($p < 0.001$), with more rejections on approach to the sharp angled (41.4%) than the smooth tapered (5.8%) constriction (Figure 2 for *rejection* locations; Figure 4).

Time to pass downstream was influenced by channel geometry (Mantel Cox $\chi^2 = 10.5$, d.f. = 1, $p = 0.001$), being greater for the sharp angled (e.g. 75.9% probability of passage [PP] after 5 min) than the smooth tapered constriction (e.g. 96.2% PP after 5 min; Figure 5).



Figure 3. Behavioural response of European eel as they moved downstream in an open-channel flume and approached a smooth tapered constriction under a low, medium, and high discharge (2015 data). Eel exhibiting a *reaction* or *no response* passed through the constricted channel on their first approach.

Discussion

The reconnection of fluvial habitat fragmented by centuries of river engineering and the protection of fish as they encounter river infrastructure represent major conservation challenges (Thieme et al. 2024). A lack of understanding of fish behaviour in response to the hydrodynamics created at fishways, such as bypass systems for downstream moving fish, is a common explanation for why they are often

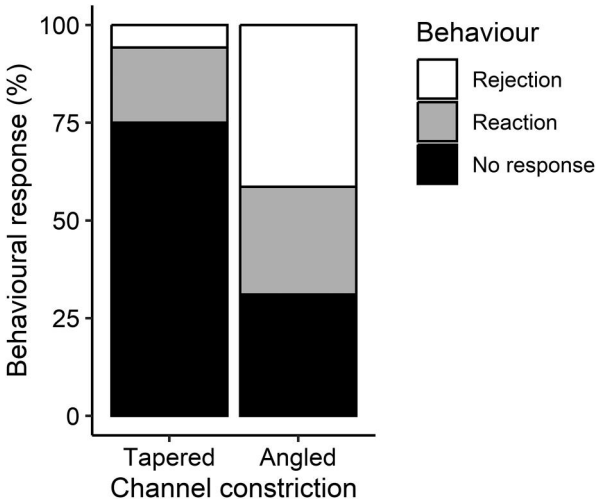

Figure 4. Behavioural response of European eel as they moved downstream in an open-channel flume under a single (low) discharge regime and approached a smooth tapered or sharp angled constriction in which flow recirculation was respectively absent and present (2016 data).

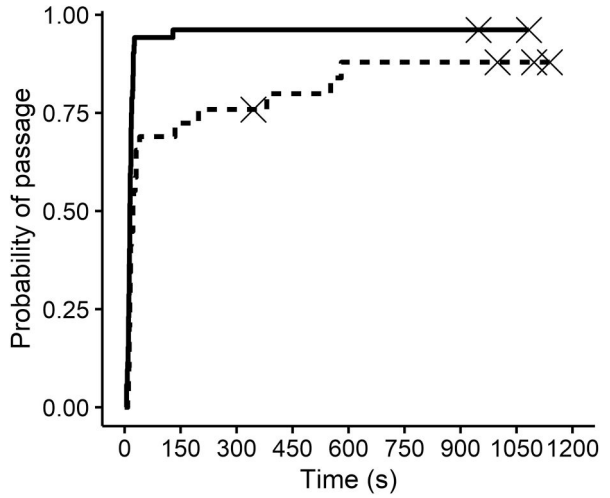

Figure 5. Cumulative probability of passing a sharp angled or smooth tapered constriction that did (dashed line) and did not (solid line) create flow recirculation, respectively, under a single (low) discharge (2016 data). Crosses represent right censored data.

ineffective (Kemp et al. 2008). The constricted flow at the entrance to bypass systems has been observed to elicit avoidance behaviour in fish, resulting in delayed movements, compromising conservation efforts (Ovidio et al. 2017). Abrupt accelerations of flow are commonly considered an important hydrodynamic feature governing avoidance behaviours, while other characteristics of flow are less frequently considered. For example, the flow field created due to the separation of flow at the channel constriction, here referred to as flow recirculation, also has the potential to impede the downstream movement of fish but is seldom considered (Silva et al. 2016). This study quantified the behaviour of downstream moving European eel (*Anguilla anguilla*) as they encountered channel constrictions in an experimental flume that: (1) generated different levels of flow acceleration; and (2) divorced the confounding effects of acceleration and recirculation to enable comparison of the influence of the two factors.

European eel tended to remain relatively unresponsive when encountering the smooth tapered constriction, indicating limited influence of flow acceleration (at least within the range of acceleration values herein investigated), contrary to our first prediction. Note that spatial discretization to compute flow acceleration was relatively small scale (0.05 m), compared to other studies available in literature (Piper et al. 2015; Enders et al. 2012 using cell size up to 0.25 and 0.15 m respectively). This means that the levels of acceleration (up to $\sim$0.05 m s^{-2}) observed in this study are of greater ecological relevance and within the range where eel might be expected to elicit a response in rivers. When acceleration was experienced in combination with recirculation there was greater rejection of the sharp angled geometry, supporting our second prediction. Avoidance was characterised by a clear escape response in which downstream moving eel rejected the channel constriction by moving back upstream, either by swimming backwards against the flow, or by switching orientation to swim upstream for more than half a body length. Accelerating flow was generated in both constriction treatments, whilst recirculation only occurred at the sharp angled constriction, suggesting the latter was the primary hydrodynamic factor influencing avoidance and subsequent rate of downstream movement. This finding should be incorporated into the design of fish bypass systems, particularly in relation to enhancing entrance efficiency, to help better achieve conservation management targets.

The influence of abrupt accelerations of flow on the behaviour of downstream migrating European eel has previously been reported. For example, the magnitude of response, characterised by the exhibition of rejection behaviour in which eel retreated back upstream before re-approaching, was positively related to flow acceleration at a redundant turbine intake on the River Stour (Dorset, UK) (Piper et al. 2015). Rejections occurred several metres upstream of a physical trash rack, providing strong evidence that observed behaviour was triggered by features of the flow fields rather than after physical contact with structure (Piper et al. 2015). In our experimental study, eel exhibited similar rejection behaviour under all treatments tested. Levels of rejection were low (10.6% when considering all three flow conditions: 2015 data) and uninfluenced by discharge, which was positively related to acceleration, when the entrance to the constriction was smooth tapered, resulting in a gradual acceleration of flow. This suggests that flow acceleration, while important in the elicitation of avoidance in eel, is unlikely to be the primary hydrodynamic cue responsible.

In addition to acceleration, the flow fields created at the entrance to the sharp angled constriction included multiple regions of recirculation. These occurred immediately upstream and downstream of the constriction and were the regions within which all rejection behaviours were initiated (Figure 2). This avoidance response delayed rate of downstream movement (supporting prediction 2). Similar observations have been reported by others (Silva et al. 2016) in relation to downstream passage of eel at an experimental vertical spillway that also created flow recirculation and caused downstream movement and passage success to be lower than for a modified sloped spillway. Areas of recirculation, vorticity or large scale turbulence more generally can affect fish swimming performance and stability (Tritico and Cotel 2010), and in some scenarios is utilised by fish to reduce energetic costs (Taguchi and Liao 2011). The results from Silva et al. (2016) and those reported in this study provide strong evidence that downstream moving European eel avoid aspects of turbulent flow at channel constrictions. The reasons for this are unclear but could relate to perceived risk associated with areas that could cause disorientation or lack of control during downstream movement. It should also be recognised, however, that multiple sensory modalities are likely involved in the downstream movement of eel; the sharp angled constriction also presented a greater physical barrier in terms of the walls of the channel opening being perpendicular to the bulk flow. Eel is known to be thigmotactic, reacting on contact with physical structure (Russon and Kemp 2011). In this study, the behavioural response observed was commonly associated with some physical contact with the sharp angled channel constriction, and so while responses

occurred in areas of hydrodynamic transition (rather than immediately following physical contact with the flume boundary), a combination of hydrodynamic and physical cues may have been important in eliciting greater avoidance and delay for this geometry than for the smooth tapered constriction.

To facilitate efficient entry of European eel into downstream bypass channels, current guidance recommends a tapered entrance that creates a smooth velocity transition based on evidence of eel reacting strongly to abrupt accelerations (Environment Agency 2011; Piper and Wright 2017). Additionally, bypass entrance geometries should avoid sharp bends and rough surfaces (Environment Agency 2011), which appears logical, but is not underpinned by an understanding of fish behaviour. Results from this study help disentangle the hydrodynamic characteristics influencing behaviour and should be applied to maximise efficacy of mitigation. Areas of flow recirculation should be minimised if unwanted avoidance behaviour and associated delay in downstream passage are to be reduced. This study provides further evidence that recirculating flow is an important hydrodynamic factor that can limit entrance efficiency of bypass channels for downstream moving eel.

Interestingly, the probability of channel rejection and delayed downstream movement were not associated with rate of flow acceleration. This is beneficial from a fish passage perspective as it suggests well designed bypass channels (e.g. those that minimise areas of recirculation and create smooth velocity transition) may function effectively over a wide range of flows. The extent to which this holds true under higher flows than those tested here and that may be encountered in the field requires further study. The findings of this empirical study should be of value to regulatory agencies, conservationists, and ecological engineers tasked with the design of environmental impact mitigation technology, such as fish bypasses and screens. Conversely, areas of recirculation and abrupt discontinuities in channel shape could be used strategically to deter fish from hazardous routes, such as turbine or pump intakes. Utilising our increasing understanding of fish behaviour in response to physical, hydrodynamic, and other (e.g. acoustic, electric, and light) stimuli should be applied to enhance efforts aimed at advancing freshwater fish conservation.

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