Behavioural response of downstream migrating European eel (*Anguilla anguilla*) to electric fields under static and flowing water conditions

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Abstract

Like many other species of diadromous fish, the European eel (*Anguilla anguilla*) is threatened by entrainment at hydropower intakes and resultant injury and mortality during passage through turbines. Historically, physical screens have been installed to prevent European eel access to intakes but these are not wholly effective and can incur high costs of construction and maintenance, especially when regulations require screen retrofits with increasingly fine mesh. There is interest in the use of potentially less expensive behavioural guidance methods to block or guide eel movements. Electric barriers have been developed to guide several species of fish, but information relating to their effectiveness for European eel is limited. In this study, two experiments were conducted to quantify the response of downstream migrating adult (silver phase) European eel to electric fields and the effectiveness of electricity to block movements. First, a static water tank was used to identify the field strengths (Vcm^{-1}) required to induce threshold responses for three key behaviours (*twitch*, *loss of orientation* and *tetany)* across three different pulsed direct current (PDC) electric waveforms (single pulse-2 Hz, double pulse-2 Hz and single pulse-10 Hz) (Experiment 1). Second, a recirculatory flume was used to investigate how avoidance responses (*acceleration*, *change in orientation* and *rejection*) differed between two water velocity regimes [0.5 ms^{-1} and 1.0 ms^{-1}] and two field strengths [$\approx$ 0.15 Vcm^{-1} and $\approx$ 0.3 Vcm^{-1}] identified during the first experiment (Experiment 2). In Experiment 1, lower electric field strengths were needed to elicit *tetany* under the single pulse-10 Hz and single pulse-2 Hz compared to the double pulse-2 Hz waveform, but there was no effect of waveform for the other behaviours. In Experiment 2, avoidance was less frequent (31.4%) under the high compared with the low (74.5%) velocity, but electric field strength did not influence the response exhibited. This study provides insights into the potential use of electric fields to deter European eel. The effectiveness of electric barriers to block downstream migrating eel are likely limited at higher water velocities.

Keywords: *Anguilliform; behaviour; electric fields; migration; pulsed direct current*

1. Introduction

River infrastructure, such as dams and weirs, can impede the movement of aquatic organisms, fragment habitat, and disrupt fluvial processes (Kemp, 2015). Water intakes, such as those at hydropower plants, irrigation systems and pumping stations, can negatively impact animals that enter them. For example, fish can be injured or killed by striking physical structures, including striking the moving turbine blades, or as a result of shear stress, rapid decompression, and cavitation (Čada, 2001; Becker *et al*. 2003; Wiśniewolski, 2008; Larinier, 2008). Furthermore, fish can be damaged (e.g. descaling) or suffocate if impinged on debris racks or physical screens designed to block and divert them at the entrances to intakes (Calles *et al.* 2010). Although the decommissioning of river water withdrawal infrastructure is an option, the maintenance of existing facilities is sometimes essential, including the supply of water and generation of electricity (Schilt, 2007). The challenge is to reduce and mitigate the environmental impacts of existing and future facilities.

Behavioural barriers and guidance devices, such as those based on light (Hamel *et al.* 2008), acoustics (Piper *et al.* 2019), bubbles (Zielinkski *et al.* 2014) and electrical stimuli (Savino *et al.* 2001), have been developed in an effort to enhance the effectiveness of screening systems, either in combination with traditional physical screens, or as an alternative to them. Behavioural devices are employed to manipulate fish movement and guide them to preferred routes of passage (Adams *et al.* 2001; Noatch and Suski, 2012), and have advantages over physical barriers as they can do so with minimal alterations to water flow or navigation (Noatch and Suski, 2012; Kim and Mandrak, 2017). In addition, behavioural deterrents are beneficial particularly for small bodied or weak swimming fish that may pass through the mesh of traditional physical screens or become trapped on them and suffocate if unable to escape (Calles *et al.* 2010; Kemp *et al.* 2012).

European eel (*Anguilla anguilla;* hereafter referred to as “eel” unless otherwise noted) has been classified as critically endangered throughout its range (Jacoby and Gollock, 2014; Drouineau *et al.,* 2018) because recruitment has declined by 90-99% since the 1980s (ICES, 2015). The decline has been attributed to a combination of factors, including non-native parasites (Kirk, 2003), pollution (Maes *et al.* 2013), habitat loss (Moriarty and Dekker, 1997), overfishing (Dekker, 2003) and obstruction of migration, e.g. by hydropower dams (Feunteun, 2002; Piper *et al*. 2013). Adult downstream migrating (silver) eel are at particular risk due to their relatively large size and elongated body morphology that increases probability of strike by turbine blades and impingement on racks and screens from which they may be unable to escape (Calles *et al.* 2010). Like many downstream migrating species, adult eel often follow the bulk flow (e.g., Russon and Kemp, 2011, but see Piper *et al.* 2017 for evidence to the contrary at a complex of water control structures), and so are frequently carried towards turbine intakes at hydropower stations, where in some instances, mortality can be as high as 100% (Larinier, 2008).

Behavioural guidance systems have been promoted as technologies to mitigate the negative effects of river infrastructure on downstream migrating eel but have shown mixed results and varying degrees of efficacy (e.g. Sand *et al.* 2000 versus MacNamara, 2012 in relation to infrasound). Electricity may provide a potential cost-effective and efficient deterrent to protect fish from anthropogenic activity (Parasiewicz *et al.* 2016), or indeed humans from fish (in the case of shark repellents, e.g. Huveneers *et al.* 2018). Some previous attempts to assess fish response and injury to electric fields have tested a variety of field characteristics, e.g. pulse frequency (Miranda and Dolan, 2003), width (Weber *et al.* 2016) and field strength (Nutile *et al.* 2013. For example, early designs intended to exclude or guide upstream migrants of other fish species tended to employ alternating current (AC) (e.g. McClain, 1957 for sea lamprey *Petromyzon marinus*), while later iterations converted to pulsed direct current (PDC) (e.g. Swink, 1999). This is largely owing to the lower injury and mortality rate of PDC compared to AC (Beaumont *et al.,* 2000). The nature of the electric field is especially important for downstream migrating fish because a response to an electric field that results in a reduced ability to orient and swim, e.g. due to being stunned, will increase the risk of the fish being swept into the intake or other hazardous area (Hartley and Simpson, 1967; Beaumont, 2016). In the case of downstream moving eel, some earlier success of an electrode array installed in the River Shannon (Ireland) is reported (McGrath *et al.* 1969), although details on guidance efficiencies or characteristics of the electric field are lacking. To date, comprehensive fundamental research to quantify the response of downstream migrating eel to electric field characteristics (e.g. pulse frequency and width, field strength) and other factors, such as water velocities, remains limited. Understanding of behavioural responses of eel to electric fields must be improved if effective electrical deterrence and guidance is to be advanced.

To help develop technology to protect European eel at water intakes in the field, this study aimed to explore the viability and potential for utilising PDC electric fields to deter downstream moving adults under experimental settings. The objectives of the study were to: (1) determine field strengths (Vcm^{-1}) at which a threshold for three specific neurophysiological responses (*twitch, loss of orientation* and *tetany)* were elicited under static water conditions with respect to pulse frequencies and width (Experiment 1); (2) examine how behavioural responses varies between two electric field strengths corresponding to the mean field strength eliciting *twitch* ($\approx$ 0.15 Vcm^{-1}) and *tetany* ($\approx$ 0.3 V cm^{-1}), under flowing water conditions (Experiment 2); (3) assess how behavioural response varies under two water velocities (0.5 ms^{-1} and 1.0 ms^{-1}) (Experiment 2). Covariates including temperature, water conductivity, body mass and length for both experiments were accounted for statistically.

2. Materials and Methods

2.1 Experimental setup

All experiments were conducted at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton, UK.

2.1.1 Experiment 1- static water tests

Experiments were conducted in a clear glass (10 mm thick) rectangular tank (1.5 m long x 0.60 m wide x 0.25 m deep) (**Fig. 1**). Two aluminium plate electrodes (0.5 m wide x 0.35 m high x 2 mm thick) were placed at either end of the tank 1.42 m apart. An electrically insulating mesh screen (0.56 m wide x 0.23 m high x 2 cm deep, mesh opening = 1 mm) was placed in front of each electrode to prevent eel directly contacting metal electrodes. Water (conditioned tap water) depth was maintained at 15 cm.

The electrodes were connected to an ETS ABP-2 backpack electrofisher (ETS Electrofishing Systems LLC) modified as a pulse generator (200 W average output; 600 V/10 A maximum peak outputs), powered by a 12 V DC battery.

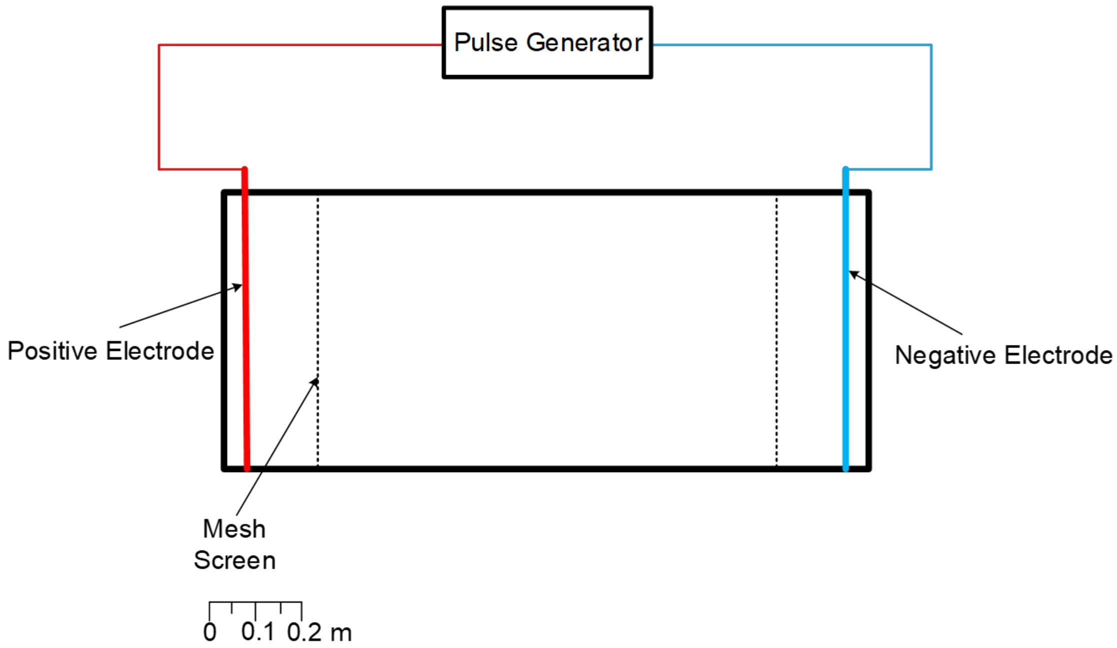

Fig. 1. Section of rectangular tank used to quantify thresholds of eel response to electric fields under static water conditions. Two aluminium electrodes were placed at either end of the tank and connected to a voltage pulse generator used to create the electric field.

Fish behaviour was monitored using four CCTV system cameras (Swann 1080p; 1920 X 1080 pixel resolution): two overhead (1 m above the tank rim); and two side-facing (34 to 39 cm away from the tank side). Two infrared lights (780-850 nm wavelength) were placed above the tank (70 cm from each camera) to provide illumination during periods of darkness.

The electric field was mapped using a potential probe consisting of two-point conductors 27 mm apart connected to an oscilloscope (Gwinstek GDS-1052-U) via a differential probe module (Probemaster Model 4232). Measurements were taken in a grid at a spacing of 10 cm in the x and y direction and at two depths (5 and 10 cm depth from the water surface) (**Fig. 2**) to record peak-to-peak voltage. Electric field maps were generated for all output voltages and waveforms.

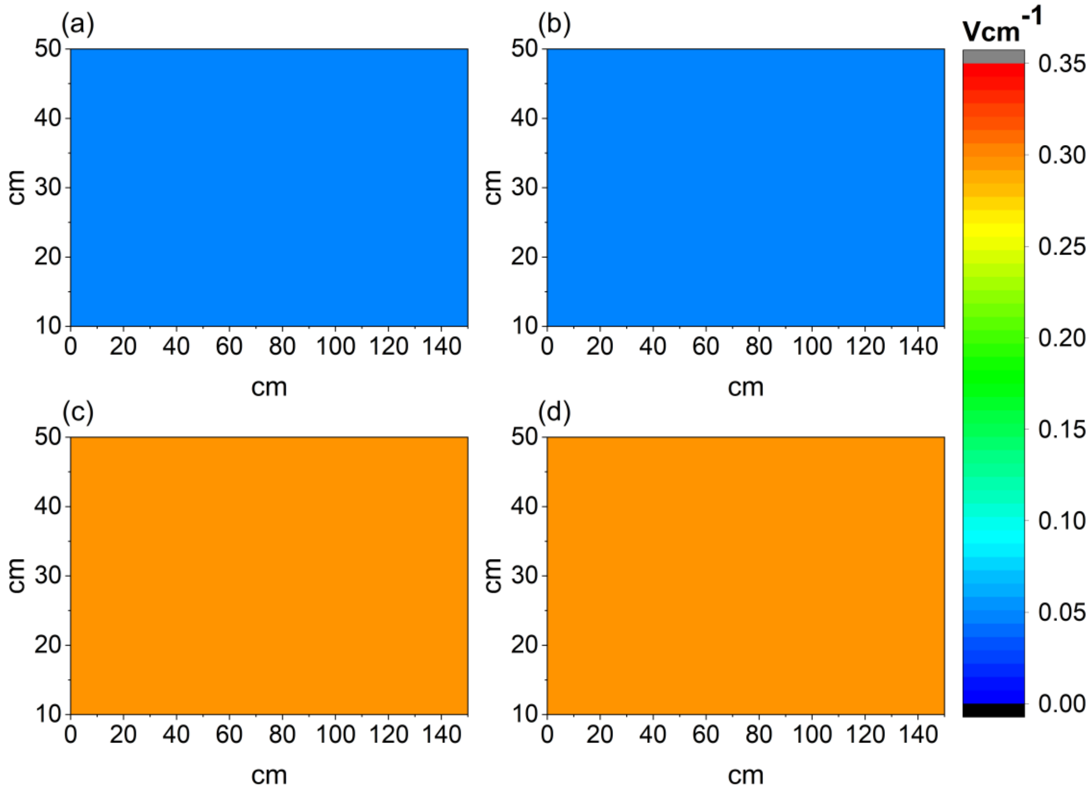

Fig. 2. Electric field (Vcm^{-1}) generated in the static water tank. (a) and (b) represent field strengths obtained with a pulse generator output of 7 V. (c) and (d) represent field strengths obtained with a pulse generator output of 42 V. (a) and (c) were measured at 5 cm depth and (b) and (d) at 10 cm depth from the water surface. Electric field strength was uniform across the tank and proportional to input voltage.

2.1.2 Experiment 2- flowing water tests

Experiments were conducted in an indoor glass-walled recirculatory flume (21.4 m long x 1.4 m wide x 0.6 m deep) filled with conditioned tap water (**Fig. 3**). Flow straighteners (100 mm wide polycarbonate honeycomb-structured screen with elongated tubular porosity- 7 mm diameter) were installed at 3.5 and 5.0 m from the upstream end of the flume to linearize flows and retain the eel during acclimatisation. Black plastic sheeting was installed along the length of the flume to prevent disturbance by observers.

The electric field was generated using three arrays of four steel rod electrodes (80 cm long x 1 cm diameter) fixed to wooden frames 27 cm apart. Each electrode was positioned 1 cm above the flume floor and insulated with fabric mesh to prevent eel contact. The first and third array were earthed to prevent the electric field extending up or downstream.

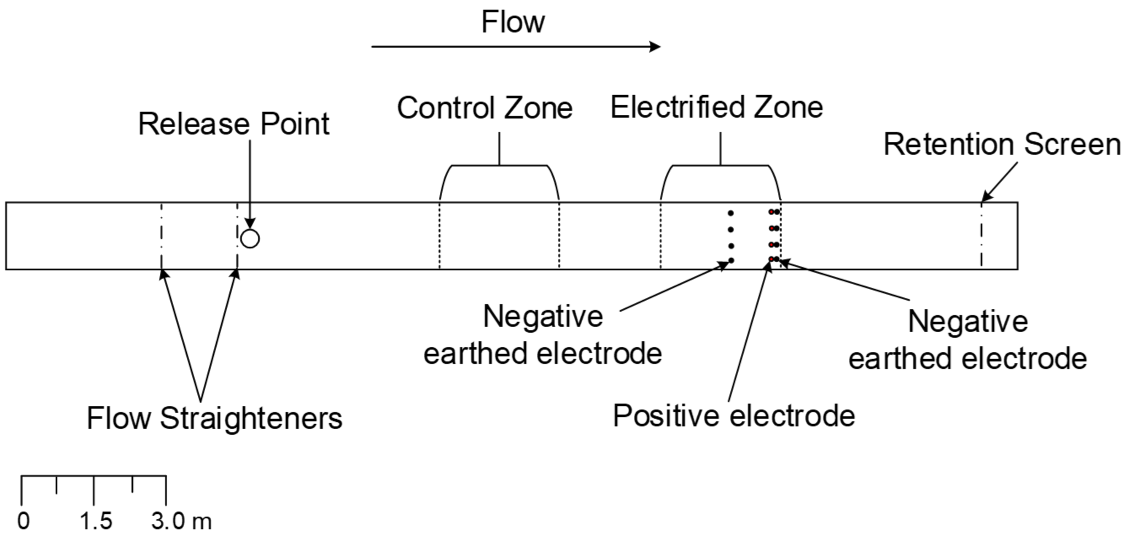

Fig. 3. Plan of the flume set-up for flowing water tests with the 3-electrode array used to investigate eel response to electric fields. The first (negative) and second (positive)

electrode arrays were separated by 1.0 m and the third (negative) 0.1 m downstream of this. Each electrode (80 cm long x 1 cm diameter) was separated by 27 cm and extended down to 1 cm above the flume floor. The first and third electrode array were earthed to avoid stray fields farther upstream.

Trials were conducted under two water velocities (0.5 ms^{-1} and 1.0 ms^{-1}), which might typically be encountered at water intakes (e.g. Turnpenny *et al.* 1998; Hadderingh and Jager, 2002). The 0.5 ms^{-1} velocity regime was achieved using two electrical pumps (0.09 m^3s^{-1} and 0.15 m^3s^{-1}) and by raising a weir at the downstream end of the flume. This produced a mean [± SE] upstream and downstream water depth of 32.4 [± 0.47] cm and 37.2 [± 0.20] cm, respectively. The 1.0 ms^{-1} water velocity was achieved by switching on a third pump (0.23 m^3 s^{-1}; total discharge 0.47 m^3 s^{-1}) and by tilting the flume 0.4 degrees downstream. The downstream weir was lowered for the higher water velocity to produce mean [± SE] upstream and downstream water depths of 29.5 [± 0.31] cm and 37.8 [± 0.21] cm, respectively. Water velocities were recorded and verified as point measurements across the width of the flume (upstream, downstream and within the electrode array) at the start of every five trials using an electromagnetic flow meter (Valeport Ltd Model 801).

Fish behaviour was recorded using eight CCTV digital video cameras (Swann 720p; 1280 X 720 pixel resolution) mounted above the flume. Two observation areas were defined: a 2.5 m control zone, 5.5 m from the release point where no electric field was detected (**Fig. 3**), and a 2.5 m electrified zone, 10.1 m from the release point. To provide sufficient illumination to enable video analysis during periods of darkness, 20 infrared lights were positioned above the flume. Behaviour of fish was recorded using a Swann digital video recorder at a resolution of 1280 x 720 with a frame rate of 25 frames s^{-1}.

The electric field was mapped using the same instrumentation as for static water testing and for both output voltages. Measurements were taken in a grid at a spacing of 10 cm in the x and y direction and at two depths (5 and 30 cm from the water surface) (**Fig. 4**).

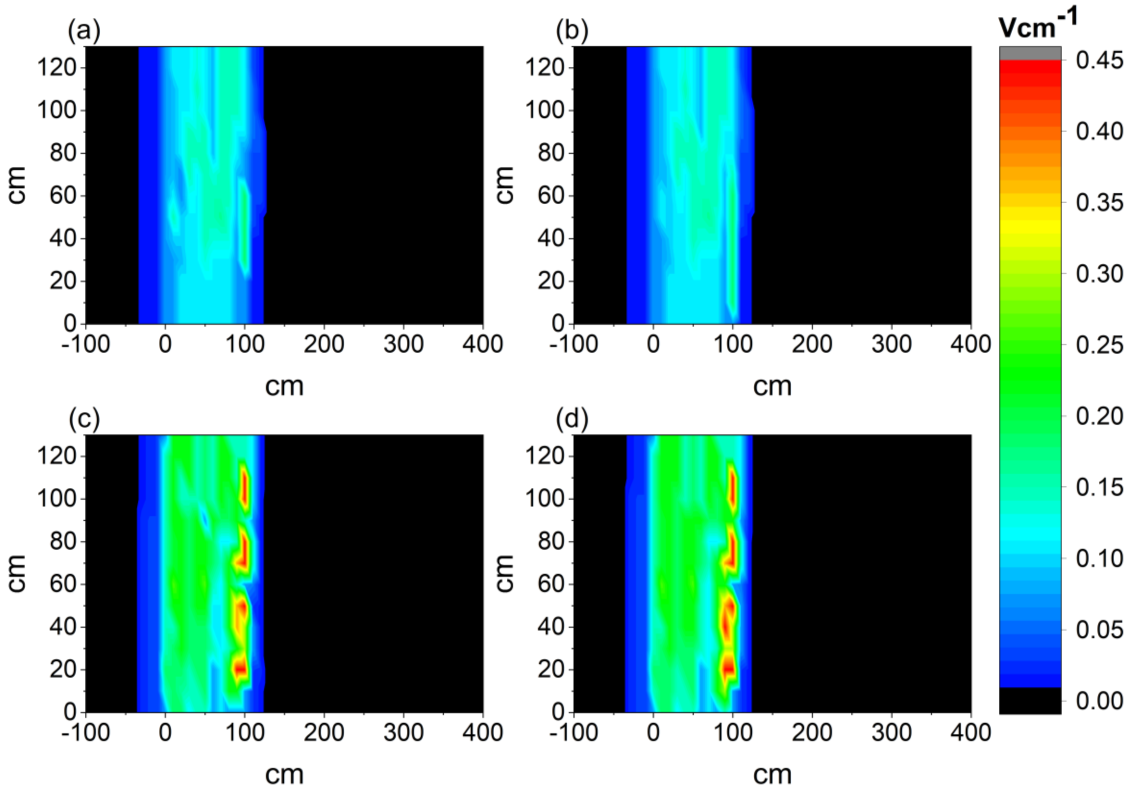

Fig. 4. Electric field (Vcm^{-1}) generated during the flowing water tests. (a) and (b) represent mean *twitch* condition and (c) and (d) represent mean *tetany* condition. Flow direction is from left to right. The x axis represent the longitudinal distance along the

flume; 1 m upstream (x = -100) and 4 m downstream of the last set of electrodes (x = 400). The three sets of electrodes were at x = 0, 100 and 110 cm and at y = 27.4, 54.8, 82.8 and 109.6 cm across the flume. (a) and (c) represent 5 cm depth and (b) and (d) 30 cm depth from the water surface.

2.2 Fish husbandry

Adult silver-phase eel were collected in three batches from the River Humber by a commercial fisherman using fyke nets. Eel were inspected for distinct characteristics of "silvering" (silver lateral coloration, large eyes and black fins/fin margins) and transported to the ICER facility in aerated river water. Forty eel were collected for Experiment 1 on 26 October 2017. A further 60 were collected on 24 November 2017 and 55 on 15 December 2017 for Experiment 2 (Table 1.). The eel were held in equal densities in four 3000 litre outdoor tanks (≤ 30 per tank) filled with conditioned tap water and fitted with gravity fed external filters with UV filtration capabilities. A venturi system on the filter outlets provided aeration, supplemented by large capacity air pumps. Fish health, water quality (pH: 7.8 - 8.4, ammonia: 0 ppm, nitrite: 0 ppm, nitrate: < 40 ppm) and temperature were monitored daily. Eel were transferred from outdoor to indoor holding tanks 24 hours prior to testing to allow suitable time for acclimatisation (mean holding tank temperature [± SE] (Experiment 1) = 12.8 [± 0.19] °C, (Experiment 2) = 9.75 [± 0.2] °C). Note temperatures here reflect the two experiments independently and were not related to collection batch.

Experiments were terminated if the temperatures of the indoor holding tanks and experimental tank/flume differed by more than 2°C. A single eel was used in each trial and tested once only.

Table 1. Collection date and numbers of adult (silver) European eel used in experiments to investigate behaviour in response to exposure to electric fields under static water (Experiment 1) and flowing water (Experiment 2). The mean temperature of the holding and experimental tank / flume temperatures are provided.

Date collected	Number	Experiment	Experimental Period	Mean holding tank temperature [± SE] (°C)	Mean experimental temperature [± SE] (°C)
26 October 2017	40	1	2-8 November	13.20 [± 0.15] °C	13.40 ± [0.11] °C

24 November 2017	60	1 + 2	28 November-6 December	Experiment 1: 10.7 °C Experiment 2: 10.87 [± 0.12] °C	Experiment 1: 10.7 [± 0.029] °C Experiment 2: 11.72 [± 0.14] °C
15 December 2017	55	2	18-20 December	9.13 [± 0.23] °C	9.81 [± 0.23] °C

2.3 Experimental procedure

All experimental trials were conducted during the hours of darkness (between 17:00 - 02:00 hr) to replicate conditions during the natural nocturnal downstream migration of adult eel (Tesch, 2003). Ambient light levels in testing facilities were less than 0.01 lux.

2.3.1 Experiment 1 - static water tests

The pulse generator was used to generate three square PDC waveforms: (a) single pulse-2 Hz (n = 17), (b) double pulse-2 Hz (n = 17), and (c) single pulse-

10 Hz (n = 6) (**Fig. 5**). Square PDC waveforms have been used in previous research (Dawson *et al.* 2006) and allow parameters (i.e. pulse width and voltage) to be quantified more easily (Beaumont, 2016). This range of frequency (≤ 15 Hz) was determined to compare differences while also reducing the chances of injuries (Sharber *et al.* 1994). Furthermore, comparisons between single and double pulse were performed as previous research has suggested this can elicit differences in behavioural responses (Bowen *et al.* 2003). The single and double pulse-2 Hz waveforms were alternated across trials (2 - 8 November 2017) and the single pulse-10 Hz was performed independently at a later date (28 November 2017).

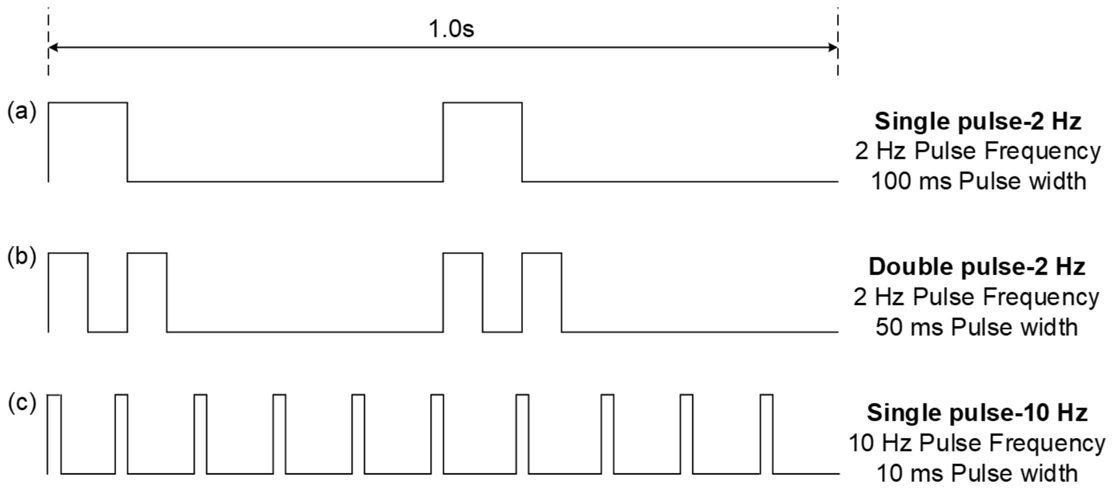

Fig. 5. Three PDC waveforms: (a) single pulse-2 Hz, (b) double pulse-2 Hz, and (c) single pulse-10 Hz waveforms used to investigate European eel (silver phase) response to electric fields under static water conditions (Experiment 1).

One eel was placed in the experimental area between the mesh screens (**Fig. 1**) and given 10 minutes to settle. This was followed by a 10 s control period (0 Vcm^{-1}) and a 10 s treatment of 0.05 Vcm^{-1} and subsequent 10 minutes recovery. The 10 s – 10 s treatment-control cycle was repeated with field strength increased in increments of 0.05 Vcm^{-1} for every cycle until *tetany* was observed. The behavioural response (*no response, twitch, loss of orientation, tetany*) was recorded for each treatment interval.

Water temperature was measured at the start and end of each trial (mean start temperature [± SE] = 13.0 [± 0.18] °C; mean end temperature [± SE] = 13.0 [± 0.18] °C). At the end of each trial fish (n=40) were weighed (mean mass [± SE] = 339.9 [± 14.2] g) and measured (mean total length [± SE] = 560.9 [± 7.86] mm).

2.3.2 Experiment 2 - flowing water tests

Eel were acclimatised in a holding tank filled with flume water for 45 minutes prior to the start of each trial, and then placed between the two flow straighteners for five minutes before released from that point (**Fig. 3**). Trials lasted a maximum of 60 minutes, or until the eel had passed the third set of electrodes, whichever occurred first. Flume temperature (mean start temperature [± SE] = 10.3 [± 0.22] °C; mean end temperature = 10.5 [± 0.21] °C) and water conductivity (HANNA HI98303 Conductivity Meter) (mean water conductivity [± SE] = 631.3[± 1.01] μS) were recorded at the start and end of each trial. Water depth (mean water depth downstream [± SE] = 37.4 [± 0.16] cm; mean water depth upstream [± SE] = 31.0 [± 0.46] cm) and water velocity were recorded every five trials. At the end of each trial, fish (n=98) were weighed (mean mass [± SE] = 338.3 [± 10.1] g) and measured (mean total length [± SE] = 566.2 [± 5.23] mm).

Tests were conducted under two electric field strengths identified during Experiment 1: (1) mean *twitch* (≈ 0.15 Vcm^{-1}) and (2) mean *tetany* (≈ 0.3 Vcm^{-1}). The single pulse-2 Hz waveform was used in the flowing water study and the two electric field strengths were alternated between trials. Two water velocities were tested: (1) low velocity (0.5 ms^{-1}) and (2) high velocity (1.0 ms^{-1}) and alternated across days (4 - 20 December 2017). This gave four treatments: (1) mean *twitch*, low velocity (n = 23), (2) mean *tetany*, low velocity (n = 24), (3) mean *twitch*, high velocity (n = 25), (4) mean *tetany*, high velocity (n = 26).

2.4 Fish Behaviour and Data Analysis

2.4.1 Experiment 1 - static water tests

The physiological metrics defined (Table 2) were based on experimental observations under the specified pulse frequencies and widths used. Note that the term *Tetany* is used to describe the muscular contraction of the whole body

(Lamarque, 1990), after which the fish immediately recovers once the stimulus is switched off.

Table 2. Definitions of physiological metrics exhibited by European eel in response to electric fields: *no response*, *twitch*, *loss of orientation* and *tetany* (Experiment 1: static water tests)

Metric	Definition
No response	No change or alteration in swimming movements on encountering an electric pulse
Twitch	Twitching or jerking movements of the eel body in synchrony with an electric pulse
Loss of orientation	Loss of vertical body orientation, rapid but uncontrolled swimming behaviour, collision with side walls of test tank
Tetany	Muscular contraction of entire body and cessation of swimming, fish recover immediately after stimulus removed

The lowest field strength voltage measured that elicited each behaviour was quantified as the threshold strength for that individual.

Statistical analyses were conducted using the R 3.5.1 (R Core Team 2018) programme package. Tests of normality were performed using the Shapiro-Wilk normality test. Attempts were made to transform non-parametric data to meet normality criteria of parametric tests; if this was unsuccessful, non-parametric tests were performed. Differences between the mean threshold field strength for *twitch*, *loss of orientation* and *tetany* were analysed using Kruskal-Wallis Rank Sum tests on pairs of treatments. Post-hoc comparisons were performed using the Dunn's Test.

2.4.2 Experiment 2 - flowing water tests

Image analysis software (LoggerPro Version 3.8.2, Vernier Software) was used to manually track 2D positions (x and y spatial coordinates) of fish on a frame-by-frame basis within the control (2.5 m) and electrified zones (2.5 m; 1.4 m approach and 1.1 m electrode array), with the control section positioned upstream. Dummy electrodes were not installed in the control section because inadvertent contact of the eel with the rods may have influenced behaviour of the fish as they entered the electrified zone. Furthermore, pilot tests indicated that the eel did not respond to the presence of rods in the electrified zone per se, presumably because visual cues were absent under conditions of darkness.

Fish velocities as they passed the observation zone (2.5 m control and electrified zones) were calculated by digitizing x and y positions (nearest cm) of the tip of the nose, creating a track for each fish. Distances within the zones were calibrated using a scale bar and corrected for parallax. The distance (D) between consecutive frame coordinates was calculated using the formula:

$$D = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2}$$

where:

x = x coordinate

y = y coordinate

1 = time step 1 (frame 1)

2 = time step 2 (frame 2)

Total distance travelled was calculated by summing distances between successive frames (**Table 3**). This value was divided by the total time required to traverse the 2.5 m control or electrified zone (*transit time*) to provide mean *ground speed* over the entire track. The mean flume water velocity was subtracted from mean *ground speed* to calculate mean *swimming speed*.

Table 3. Definitions of behavioural metrics; *total distance travelled*, *transit time*, *ground speed* and *swimming speed* obtained from tracking analysis of European eel (Experiment 2: flowing water tests).

Metric	Definition
Total distance travelled (m)	Distance travelled through the 2.5 m electrified or control zone
Transit Time (s)	Total time required to pass the 2.5 m electrified or control zone
Ground speed (ms^{-1})	*Total distance travelled*/*Transit time*
Swimming speed (ms^{-1})	Mean *ground speed* – water velocity

Within the flume, behaviour was characterized and quantified from video recordings as fish passed through the control and electrified zones using the following metrics based on observations (**Table 4**).

Table 4. Definitions of behavioural metrics; *no change*, *acceleration*, *change in orientation* and *rejection* observed by experimental eel on encountering an electric stimulus (Experiment 2: flowing water tests).

Metric	Definition
No change	No change in swimming speed or body orientation
Acceleration	Increase in swimming speed
Change in orientation	90-360º turn in body position

Rejection	180º turn in body position and one upstream movement for at least one body length

Behavioural metrics (*no change, acceleration, change in orientation,* and *rejection)* were analysed (yes or no) using a generalised linear mixed model (GZLMM) fitted with a binomial distribution. Main effects included water velocity and electric field strength. Temperature, water conductivity, body mass and length were included as covariates. Day was included as a random effect. Optimal model selection was performed based on lowest Akaike information criterion (AIC) scores. *Total Distance travelled*, *swimming speed and transit time* was analysed using Kruskal-Wallis Rank sum tests on pairs of treatments.

3. Results

3.1 Experiment 1

3.1.1 Threshold field strengths for physiological responses across waveforms (objective 1)

The threshold field strength for *twitch* ($\chi^2(2) = 1.16$, $p = 0.56$) and *loss of orientation* ($\chi^2(2) = 3.62$, $p = 0.16$) did not differ across waveform treatments (**Fig. 6**). The threshold field strength for *tetany* was influenced by waveform

($\chi^2(2) = 12.62$, $p = 0.002$), with a lower threshold recorded for the single pulse-10 Hz than the double pulse-2 Hz waveform (Dunn's Test: $z = 3.47$, $p = 0.002$) and a slightly lower threshold for single pulse-2 Hz than double-2 Hz (Dunn's Test: $z = -1.98$, $p = 0.048$). Only six eel were tested under the single pulse-10 Hz waveform, and all exhibited the same threshold field strength for *tetany* under this treatment.

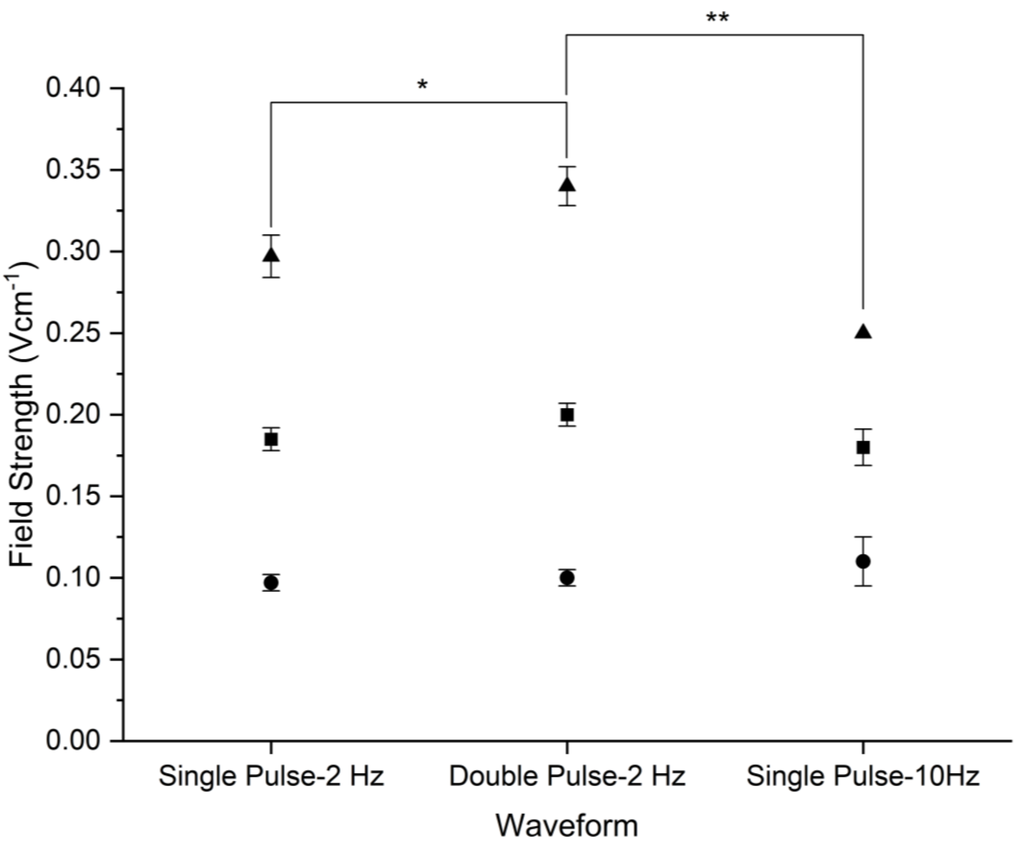

Fig. 6. Mean threshold field strengths [± SE] for three physiological responses; *twitch* (circles), *loss of orientation* (squares) and *tetany* (triangles) exhibited by downstream migrating European eel under three waveforms: single pulse-2 Hz, double pulse-2 Hz and single pulse-10 Hz. Note * denotes $p<0.05$ and ** denotes $p<0.01$.

3.2 Experiment 2

3.2.1 Effect of electric field strength on eel response under flowing water conditions (objective 2)

Of the 98 eel tested, 52% exhibited at least one avoidance response. Field strength (mean *twitch* vs. *tetany*) had no influence on behavioural response observed (GZLMM: *acceleration*: z = 0.55, p = 0.59, *change in orientation*: z = 0.78, p = 0.43, *rejection*: z = 0.50, p = 0.62 and *no change*: z = -1.38, p = 0.17) (**Fig. 7**). Field strength did not influence any of the tracking behavioural metrics (**Table 4**).

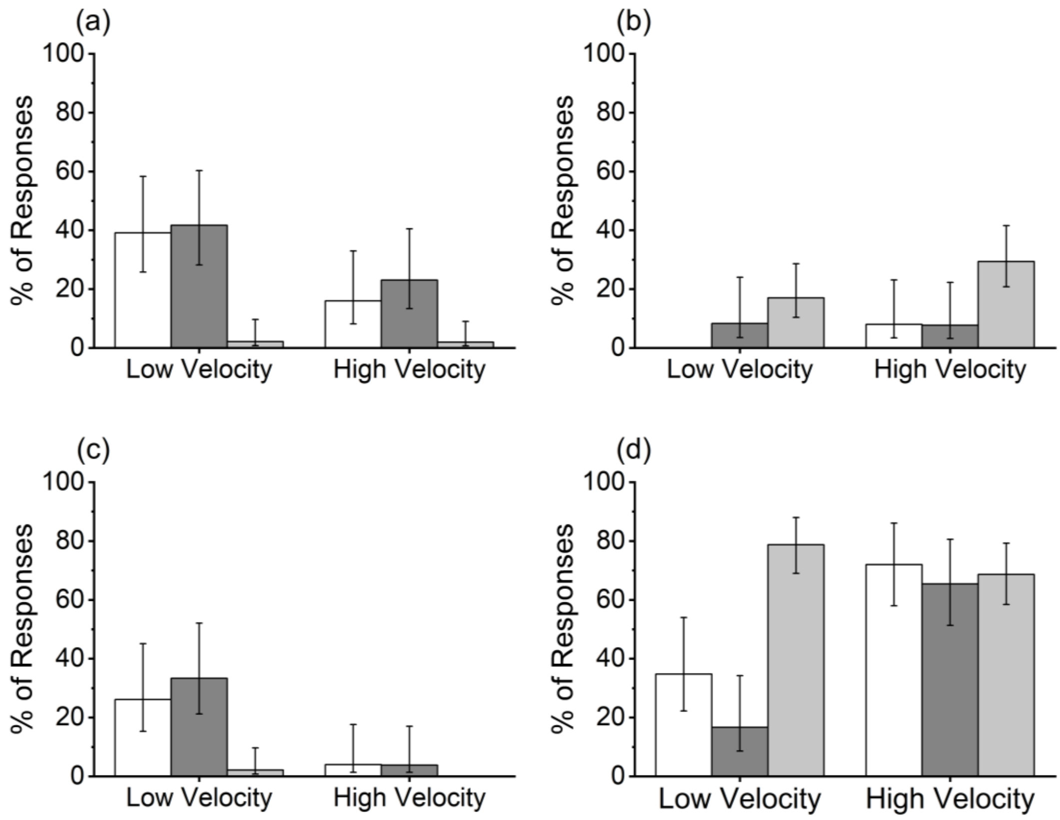

Fig. 7. Mean percentage of all initial responses (± 95% CI) exhibited by European eel for the four behaviour metrics: (a) *acceleration*, (b) *change in orientation*, (c) *rejection* and (d) *no change* between the two treatment field strengths; mean *Twitch* (white bars), mean *Tetany* (dark grey bars) and control (light grey bars) under the low and high water velocity.

3.2.2 Effect of water velocity on eel response to electric fields (objective 3)

Acceleration and *rejection* was more common under the low than high velocity treatment (z = -2.22, p = 0.03, *rejection*: z = -2.83, p = 0.005), whereas *no change* was more frequent under the high than low velocity condition (*no change*: z = 2.63, p = 0.009) (**Fig. 8**). Water velocity had no effect on the occurrence of *change of orientation* (z = 0.73, p = 0.46).

Under the low velocity treatments (0.5 ms^{-1}), 74.5% of eel exhibited an avoidance response across both field strengths, whereas under the high velocity (1.0 ms^{-1}) only 31.4% did so. The highest percentage of initial response observed under low velocity was *acceleration* (40.4 %), followed by *rejection* (29.8 %), *no change* (25.5 %) and *change in orientation* (4.26 %) (**Fig. 8**). In contrast, under high velocity, *no change* was most common (68.6 %), followed by *acceleration* (19.6 %). A small proportion of eel exhibited a *change in orientation* (7.84 %) and *rejection* (3.92 %).

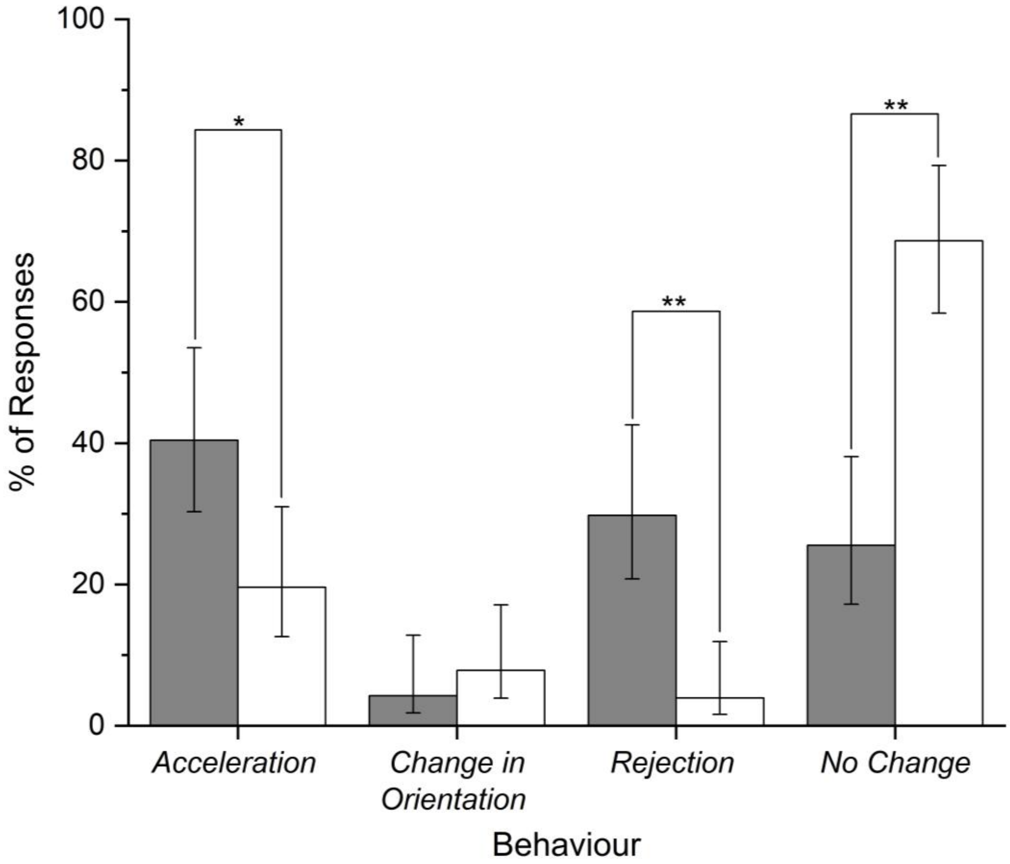

Fig. 8. Mean percentage of initial responses (± 95% CI) exhibited by downstream migrating European eel observed for the four behavioural metrics; *acceleration*, *change in orientation*, *rejection* and *no change* under the two water velocities; 0.5 ms^{-1} (grey bars) and 1.0 ms^{-1} (white bars) and aggregated across both field strengths (0.15 Vcm^{-1} and 0.3 Vcm^{-1}). Note * denotes p<0.05 and ** denotes p<0.01.

Both *total distance travelled* ($\chi^2(1) = 28.5$, $p < 0.0001$) and *transit time* were higher in the low velocity treatment (χ^2 (1) =43.9, $p < 0.001$) (**Table 4.**). In both high velocity treatments, the mean *swimming speed* was lower than under the low velocity conditions ($\chi^2(1) = 29.8$, $p < 0.0001$).

Table 4. Mean *total distance travelled*, *transit time*, *ground speed* and *swimming speed* ± SE, obtained from tracking analysis, across the six treatment groups.

Treatment	Mean *Total Distance Travelled* [± SE], (m)	Mean *Transit Time* [± SE], (s)	Mean *Ground Speed* [± SE], (ms^{-1})	Mean *Swimming Speed* [± SE], (ms^{-1})
Low Velocity, Mean *Twitch*	5.50 [± 0.88]	10.6 [± 2.26]	0.62 [± 0.05]	0.12 [± 0.05]
Low Velocity, Mean *Tetany*	7.41 [± 1.48]	16.4 [± 4.78]	0.61 [± 0.06]	0.11 [± 0.06]
High Velocity, Mean *Twitch*	3.15 [± 0.10]	4.25 [± 0.29]	0.80 [± 0.04]	-0.20 [± 0.04]
High Velocity, Mean *Tetany*	3.68 [± 0.30]	4.65 [± 0.64]	0.86 [± 0.03]	-0.14 [± 0.03]
Control (Low Velocity, 0 Vcm^{-1})	4.50 [± 0.55]	26.7 [± 8.07]	0.37 [± 0.02]	-0.13 [± 0.02]
Control (High Velocity, 0 Vcm^{-1})	3.68 [± 0.18]	6.96 [± 0.96]	0.78 [± 0.06]	-0.21 [± 0.06]

4. Discussion

Migratory (silver) phase adult European eel exhibited both involuntary physiological responses (*twitch*, *loss of orientation*, and *tetany*) and modified their behaviour (e.g., *acceleration, change in orientation, rejection*) when experiencing electric fields. The nature of the response varied depending on the characteristics of the electric field (frequency, pulse width, field strength) and presence of flow. As expected, based on the results of previous studies relating to other species (Bearlin *et al.* 2008), eel exhibited a hierarchy of physiological response, with thresholds for *twitch* and *tetany* occurring at the lowest and highest field strengths, respectively, under static water conditions. Interestingly, *tetany* was elicited at lower field strengths when a single-pulse 10 Hz waveform was employed. When behavioural response was tested in the flowing water tests, eel were less likely to exhibit avoidance, and swam more slowly, under a higher velocity.

The observation that the three physiological responses were consistently elicited over a relatively narrow range of field strengths that did not overlap is promising in terms of the application to behavioural deterrents. An efficient deterrent should induce avoidance in the target species (or group of species) so that they may be directed to some alternative route, without injury or rendering them unable to respond (Hartley and Simpson, 1967), e.g. as would occur during *tetany*. The distinct difference between the field strengths that induced the different responses will enable development of guidance criteria that reduces the risk of unwanted negative effects. The greatest difference between field strengths that induced *twitch* (the preferred response) and *tetany* (an undesirable response) was observed for the double pulse-2 Hz waveform. Conversely, the smallest difference in threshold field strength between *twitch* and *tetany* was observed for the single pulse-10 Hz waveform, indicating that this is the least preferred option to advance in deterrent development. The smaller range of field strengths seen under the single pulse-10 Hz waveform is likely due to more severe and more frequent myoclonic jerks seen at higher frequencies which has been suggested to result in more extreme physiological responses (Sharber *et al.* 1994).

Waveform shape, frequency, and pulse width are known to affect fish response (Beaumont *et al.* 2000; Miranda and Kidwell, 2010). Previous research has focused on determining the least harmful waveform shapes (e.g. exponential, square wave, gated burst) for electrofishing, but there is a lack of consensus relating to the optimal shape used (Sharber and Carothers, 1988). Furthermore, fish physiological response to PDC is variable due to the interaction of the different parameters of the electric field (i.e. type of current, field strength, pulse width and frequency), which are not standardised across studies. While the field strength and magnitude of response is expected to be positively related, other interacting parameters influence the nature of the physiological behaviour exhibited, and severity of the response observed (Bearlin *et al.* 2008). This study shows that different pulse frequencies affect physiological responses of eel, with the mean threshold response for *tetany* being elicited at a lower field strength under the single pulse-10 Hz waveform than the double pulse-2 Hz waveform. Under higher frequencies the electrical current pulses are transferred more frequently to the body of the eel, likely explaining the observation of *tetany* at a lower field strength. Higher pulse frequencies are more likely to injure fish, including eel (Reynolds and Holliman, 2004), particularly in relation to spinal damage (Sharber *et al.* 1994). This, and the fact that higher frequency fields are more effective at stunning fish, an undesirable response in the development of deterrents, indicate lower frequency fields are preferred when fish are required to exhibit active muscle control for orientation and locomotion (Holliman *et al.* 2015). It is crucial however, that studies report parameters (i.e pulse frequency and width, voltage) of the electric field so direct comparisons can be made.

Focusing on the two low frequency treatments, a lower threshold field strength for *tetany* was observed under the single pulse-2 Hz condition than for the double pulse-2 Hz field. This likely reflects the difference in pulse width, with the single pulse-2 Hz being twice that of the double pulse-2 Hz stimuli (100 versus 50 ms). Longer pulse widths result in greater electrical power transmitted to the fish (Beaumont, 2016), likely as a result of greater time, and thus opportunity, available for the current to exponentially rise during each pulse to its maximum level. Thus, under the same frequency and where the exhibition of *tetany* in unwanted, shorter pulses are preferred. Conversely, there was no evidence that the field strengths for *twitch* or *loss of orientation* varied across waveforms.

Under flowing water conditions typically experienced during natural migrations of eel in rivers, there was no evidence of differences in behaviour in response to two different field strengths selected based on the results of static water tests. In the flume study, eel were provided greater opportunity to volitionally avoid the gradient generated by the electric field, e.g. by returning upstream or rapidly accelerating through it, over a greater distance compared to the constrained conditions experienced while in the static water tank. As a result, eel never exhibited *tetany* under flowing conditions and were less likely to alter their behaviour on encountering the electric field under the high velocity treatments, resulting in lower occurrences of *acceleration* and *rejection*. It is possible that a rapidly moving eel may have passed through the test zone before it had been exposed to a sufficient number of electrical pulses to elicit a response. The single pulse-2 Hz waveform produced two 100 ms pulses every second, with a 400 ms gap between each. This is sufficient time for eel moving with the bulk flow at a higher *ground speed* under high velocity treatments to have passed some considerable distance through the 1.1 m zone between the first and third set of electrodes. Therefore, water velocity through an electrical array, electric field size and configuration, and pulse rate may be as critical as field strength and waveform in an electrical guidance array.

This study indicates that adult European eel exhibit both physiological and behavioural responses when exposed to electric fields. Furthermore, in terms of the use of electric fields for behavioural guidance, a high percentage of eel exhibited avoidance under low velocity. However, the effectiveness of electric deterrents may be low in areas where velocity is high if eel have limited opportunity to elicit volitional behaviour. Similar observations have been recorded for other species. For example, the guidance efficiency of electric fields for outmigrating sea lamprey were limited when water velocities increased above 0.25 ms^{-1} (Johnson and Miehls, 2014; Miehls *et al.* 2017). Compared to upstream swimming migrants, the development of electrical guidance devices for downstream moving fish is considered a greater challenge because a response to an electric field that results in a reduced ability to orient and swim, e.g. as a result of being stunned, will increase the risk of being swept into the hazardous areas (Hartley and Simpson, 1967; Beaumont, 2016). In other words, it is crucial that the deterrent effects of any mitigation device outweigh the impacts; e.g. if stunned fish come into close contact with the strong electrical fields at the electrodes, which in extreme cases may induce stress, haemorrhaging, and spinal and notochord injuries (Holliman and Reynolds, 2002; Schreer *et al.* 2004), and/or experience greater risk of being entrained through turbines or impinged on screens. Therefore, the use of electrical deterrents when water velocities regularly exceed the escape capabilities of the target species might not be appropriate, e.g. when targeting small and weak swimming fish, or those that utilise currents to migrate downstream, if there is insufficient time to avoid the field. Further research is warranted to better define the physiological and behavioural responses of fish to electric fields in relation to their characteristics (i.e. pulse frequency and width, voltage, waveform type) and to investigate the possibility of using additional multi-modal stimuli to improve guidance efficiency.

5. Conclusions

- Under static water conditions (Experiment 1), eel exhibited three key physiological responses (*twitch*, l*oss of orientation* and *tetany*) at distinct electric field strengths.
- The higher frequency single pulse-10 Hz waveform elicited *tetany* at a lower electric field strength.
- Slightly lower electric field strength elicited *tetany* for the single pulse-2 Hz than double pulse-2 Hz waveform.
- We recommend the use of waveforms with lower frequencies and shorter pulse widths for guidance of eel.
- Under flowing water conditions (Experiment 2), 74.5% of eel exhibited at least one avoidance behaviour under low velocity, while only 31.4% did so under high velocity.
- The effectiveness of electric barriers to block downstream migrating adult eel is likely to be limited by water velocity, especially under very high velocities when opportunity for volitional behaviour is reduced.
- Further research should explore the use of electric fields to investigate waveform characteristics to guide a range of eel life-stages under experimental (e.g. choice tests) and field (e.g. a real-world bypass system) settings.

- In addition, future work could investigate the use of multi-modal deterrents such as electricity and light or acoustics or in conjunction with physical screens to enhance efficiency.

Ethical Note

This study was performed after approval from the University of Southampton's Ethics and Research Governance Office (Ethics ID 30639).

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***Declaration of Interest Statement**

Declaration of interests

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

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