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Water and Environmental Engineering

Response of fish to electric fields: implications for guidance systems

by

MHAIRI MILLER

Thesis for the degree of DOCTOR OF PHILOSOPHY

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Abstract

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River infrastructure such as dams, weirs and hydropower facilities can reduce habitat connectivity and lead to direct mortality of fish species. Physical devices (e.g. screens or fish passes) designed to mitigate these negative impacts are not wholly effective and can be costly. Behavioural stimuli such as electric fields offer an alternative or enhancement to traditional physical devices. This thesis addresses the response of fish to electric fields through experimental studies conducted under both static and flowing water conditions.

Assessing the response of European eel to electric fields has received limited attention. Threshold field strengths (i.e. electrosensitivity) of key physiological responses (*twitch*, *loss of orientation* and *tetany*) were quantified with respect to pulse frequency and width, for the critically endangered European eel (*Anguilla anguilla*) under static water conditions. Lower field strengths were required to elicit *tetany* under a higher pulse frequency and longer pulse widths.

Research into eel guidance systems has largely focused on downstream migrating adult (silver-phase) using light and acoustics with mixed success. To gain insights into the potential effectiveness of electric fields for guidance, the behavioural responses of three life-stages of European eel (glass, yellow- and silver-phase) were assessed under flowing water conditions. All life-stages showed avoidance to electric fields, with largely more occurring under higher field strengths for juvenile (glass) eel. Avoidance in downstream migrating adults was reduced under a higher water velocity (1.0 ms^{-1}) and yellow-phase eel were more likely to respond when travelling upstream. Evidence of any successful guidance by electric fields was only observed for upstream migrating juvenile (glass) eel and efficiency was improved under lower frequencies (2 Hz) and higher field strengths.

Ensuring species selective guidance systems is the next challenge for fisheries management in areas where desirable and invasive species co-exist. A direct comparison of electrosensitivity between two known invasive cyprinids, grass carp (*Ctenopharyngodon idella*) and common carp (*Cyprinus carpio*), and adult eel was performed. Adult eel had a higher electrosensitivity than both cyprinids indicating the potential for electric fields to provide a species selective fish guidance system.

The research presented in this thesis has advanced scientific knowledge of both fundamental physiological and behavioural responses of fish to electric fields with respect to parameters tested. This research will guide future work to optimise parameters of the electric field to translate avoidance behaviours more effectively into reliable guidance for fisheries management.

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Research Thesis: Declaration of Authorship

Mhairi Miller

Response of fish to electric fields: implications for guidance systems

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
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6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
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Miller, M., de Bie, J., Sharkh, S.M. and Kemp, P.S. 2021. Behavioural response of downstream migrating European eel (*Anguilla anguilla*) to electric fields under static and flowing water conditions. *Ecological Engineering* 172, p. 106397.

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Signature: .... Date:..........................

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Glossary

A.1. Fish Families

Common Name	Latin Name
Carp and minnows	Cyprinidae
Catfish	Ictaluridae
Eel	Anguillidae
Lamprey	Petromyzontidae
Perch	Percidae
Righteye flounders	Pleuronectidae
Salmon	Salmonidae
Smelt	Osmeridae
Sturgeon	Acipenseridae
Sunfish	Centrarchidae
True gobies	Gobiidae

A.2. Fish Species

Common Name	Latin Name
Alewife	*Alosa pseudoharengus*
American eel	*Anguilla rostrata*
American gizzard shad	*Dorosoma cepedianum*
Atlantic cod	*Gadus morhua*
Atlantic salmon	*Salmo salar*
Bighead carp	*Hypophthalmichthys nobilis*

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Black carp	*Mylopharyngodon piceus*
Black crappie	*Pomoxis nigromaculatus*
Bluegill	*Lepomis macrochirus*
Brook trout	*Salvelinus fontinalis*
Brown trout	*Salmo trutta*
Channel catfish	*Ictalurus punctatus*
Chinook salmon	*Oncorhynchus tshawytscha*
Common carp	*Cyprinus carpio*
Common dab	*Limanda limanda*
Cutthroat trout	*Oncorhynchus clarkii bouvieri*
Delta smelt	*Hypomesus transpacificus*
Eurasian ruffe	*Gymnocephalus cernuus*
European eel	*Anguilla anguilla*
European perch	*Perca fluviatilis*
European plaice	*Pleuronectes platessa*
Goldfish	*Carassius auratus*
Grass carp	*Ctenopharyngodon idella*
Ide	*Leuciscus idus*
Lake sturgeon	*Acipenser fulvescens*
Largemouth bass	*Micropterus salmoides*
Lemon sole	*Microstomus kitt*
Longspine porgy	*Stenotomus caprinus*
Murray cod	*Maccullochella peelii peelii*
Pacific lamprey	*Entosphenus tridentatus*

Rainbow smelt	*Osmerus mordax*
Rainbow trout/steelhead	*Oncorhynchus mykiss*
Round goby	*Neogobius melanostomus*
Sacramento squawfish	*Ptychocheilus grandis*
Scaled sardine	*Harengula jaguana*
Sea lamprey	*Petromyzon marinus*
Siberian sturgeon	*Acipenser baerii*
Silver carp	*Hypophthalmichthys molitrix*
Sockeye salmon	*Oncorhynchus nerka*
White sturgeon	*Acipenser transmontanus*

A.3. Non-fish family

Common name	Latin name
Freshwater crayfish	Astacidae
Freshwater mussels	Dreissenidae

A.4. Non-fish species

Common name	Latin name
Signal crayfish	*Pacifastacus leniusculus*
Zebra mussel	*Dreissena polymorpha*

B. General Terms

Abiotic: Non-living components of an ecosystem.

Acclimation: The physiological adjustment of an organisms to environmental conditions under laboratory settings.

Alternating current: continually reversing polarity (positive then negative).

Anadromous: Diadromous fish for which the majority of feeding and growth is undertaken in marine environments before the adults migrate to freshwater to spawn.

Anguilliform: Shaped like or resembling an eel. Also a swimming mode (see anguilliform locomotion).

Anguilliform locomotion: A swimming mode where the whole body participate sin large amplitude undulations. Since at least one complete wavelength of the propulsive wave is present along the body, lateral forces are adequately cancelled out, minimising any tendencies for the body to recoil.

Anthropogenic: Relates to an effect or object resulting from or induced by human activity.

Behavioural barrier: A system used to deter fish from certain locations (e.g. hydropower intakes) by using a stimulus that fish can detect or sense and respond to with either a repulsion or attraction behaviour.

Benthic: Bottom dwelling; living on or positioned near to the substrate of rivers.

Biotic: Living components of an ecosystem.

Blade strike: When a fish is struck by a rotating propeller/impeller.

Bypass: An alternative route for downstream moving fish, allowing them to bypass anthropogenic river barriers. Designed to be a safer or more benign route than that of the bulk flow of the river (e.g. where the majority of water may be passing through a hydropower turbine).

Catadromous: Diadromous fishes in which most feeding and growth take place within freshwater prior to migration of adults to the sea to reproduce.

Cavitation: The rapid formation and collapse of low-pressure bubbles in liquids by means of mechanical forces.

Conductivity: the ability of a unit volume of matter to conduct electricity. Measured in $S.m^{-1}$, but typically $\mu S.cm^{-1}$ in freshwater water.

Conservation: The principles and practice of the science of preventing species extinctions.

Direct current: unidirectional flow of electrons. Can be further split into: (1) continuous direct current (DC) where flow is continuous and (2) pulsed direct current (PDC) where flow passes in short bursts known as pulses.

Diadromous: Fish migrations that occur between fresh and marine environments.

Discharge: The rate at which a volume of water is flowing per unit time, typically measured in m^3s^{-1} or Ls^{-1}.

Duty cycle: the percentage (%) of time that current is flowing within one cycle.

Electrode: A conductor by which electricity enters or leaves an object, substance or region.

Elver: the juvenile life-stage of an eel between glass and yellow-phase eel. Individuals are larger than glass eel and pigmented.

Entrainment: fish passage through a physical screen, intake, structure, hydropower or pumping facility, typically non-volitionally.

Escapement: The passage from freshwater to marine environments of adult seaward migrating eel for the purpose of reproduction.

Fish pass: A structure (such as a series of stepped pools), that water flows down, located on or around anthropogenic barriers and designed to allow fish to pass upstream of the barrier (e.g. dam or weir). Fish pass is synonymous with 'fishway', which is the more commonly used term in North America.

Fishway: See fish pass.

Freshwater fish: Fish that live all or a critical part of their life history in fresh, inland or brackish waters, including estuaries and mangrove swamps.

Glass eel: The life-stage of an eel between the leptocephali larvae and elver stage. Individuals conform to the elongated eel morphology but are unpigmented.

Habitat: An area that provides the resources (e.g. food, space) necessary for the existence of an organism or particular life-stage.

Habitat connectivity: The size and distribution of suitable habitat patches and the ease with which a species can move through the landscape between patches.

Habitat fragmentation: The subdivision of a specific habitat into smaller and more isolated fragments or patches, through both natural and anthropogenic activities (although typically in reference to anthropogenic activities in this thesis), resulting in changes to the landscape composition, structure and function.

Habituation: A reduction in the magnitude of a response to a stimulus after repeat encounter or exposure to it.

Hybridisation: Reproduction between two distinct populations or species.

Impingement: The non-volitional entrapment of a fish against a structure.

Interspecific: In reference to between different species.

Intraspecific: In reference to within the same species.

Leptocephali: A colourless, transparent, flattened larva, especially of certain eel and ocean fishes.

Migrant: The life-stage of a fish (including resident species) which moves from one location, habitat or system (e.g. river or ocean) to another.

Migrating: Moving from one area of residence to another.

Migration: The seasonal movement of an animal from one area to another.

Mitigation: An action intended to reduce the adverse impact of a specific project, development, or activity.

Panmixia: random mating within a breeding population.

Physical screen: A device used to excluded, deflect or guide fish from hazardous locations, such as water abstraction points or hydropower intakes, and towards more benign routes / locations (such as bypasses). A large number of alternative designs (e.g. passive mesh screens, rotary disc screens) exist; see Turnpenny and O'Keeffe (2005) for more information.

Pulse frequency: the number of pulses per second, measured in Hz.

Pulse width: duration of time that the current is flowing, measured in milliseconds (ms).

Rheotaxis: The behavioural orientation of fish to water currents. Positive rheotaxis refers to fish facing head first into the current and negative rheotaxis to those moving downstream head first.

Semelparous: species that reproduce once during their life-cycle.

Shear stress: When two parallel layers of water masses have opposite forces due to their velocities.

Silver-phase eel: Eel at the end of the growth phase which have undergone reproductive and osmoregulatory changes in preparation for migration to spawning grounds. During these changes individuals take on a silver hue.

Smolt: The juvenile life-stage of an anadromous salmonid that has undergone physiological adaptation for saline environments.

Voltage gradient: the difference in voltage between two points (in water), measured in Vcm^{-1}.

Water velocity: The speed with which water is flowing, typically measured in cm s^{-1} or ms^{-1}.

Waveform: shape of the voltage, when plotted over time. Typically three types, alternating current (AC), direct current (DC) and pulsed direct current (PDC).

Yellow-phase eel: Growth stage of catadromous eel. Individuals are usually dark in colour with yellow hue.

Structure of the thesis

This research project was performed to assess both the fundamental responses of fish to electric fields and provide initial insights into its potential as a guidance system.

The individual chapters in this thesis are all linked. Chapter 1 provides an initial introduction to the importance and challenges faced by freshwater ecosystems notably the impact of river infrastructure on fish movement and survival whilst highlighting mitigation strategies such as behavioural guidance systems including electric fields. Chapter 2 provides a detailed literature review, discussing research trends, biases and gaps in knowledge in terms of conservation of European eel, invasive species management for grass and common carp and response of fish to electric fields. The information in Chapter 1 and 2 guided the formation of research aims and objectives (Chapter 3).

Chapters 4 – 7 present the results, the first of which explores the physiological and behavioural responses of a species of conservation concern, the adult (silver-phase) European eel in static and flowing water conditions when exposed to electric fields. In Chapter 5, the behavioural response of upstream migrating juvenile (glass) eel was quantified in response to field strength and pulse frequency. Chapter 6, quantified the behavioural responses of both yellow- and silver-phase European eel under flowing water conditions to a two-choice test with respect to electric field parameters (e.g. field strength, pulse frequency). In Chapter 7, quantification of physiological responses (i.e. electrosensitivity) of two known invasive cyprinids (grass and common carp) combined with a direct comparison to the results obtained for adult eel (Chapter 4) was performed. The final chapter (Chapter 8) provides an overall discussion and conclusions from the results obtained through this thesis as well as recommendations for management and future research.

Chapter 1 Thesis introduction

Freshwater constitutes 0.01% of the world's water with lakes, reservoirs and rivers covering around 2.3% of the global land surface area (Lehner and Döll, 2004; Reid *et al.*, 2019). The Freshwater Animal Biodiversity Assessment (FABA) (Balian *et al.*, 2008) estimates these ecosystems represent habitat for approximately 9.5% of known animal species. Furthermore, around 40% of the global fish diversity live in freshwater and due to difficulties in assessing biodiversity in developing and remote areas this is likely to be a conservative estimate (Lundberg *et al.*, 2000; Cooke *et al.,* 2012). Fish are a key part of aquatic food webs and strongly contribute to ecosystem functioning in many ways such as influencing nutrient cycles (Janetski *et al.*, 2009), modifying physical landscape (Moore, 2006) and biodiversity (Lynch *et al.*, 2016). For humans, fish are essential in terms of economic security and cultural services (Lynch *et al.*, 2016). In addition, fish are a main source of protein and income for hundreds of million people worldwide, a large percentage of whom are impoverished (Bailey *et al.,* 2015; Cooke *et al.*, 2016). For example, the Lower Mekong river basin accounts for 47 – 80% of the total animal protein consumed by the residents (Cambodia = 79.9%, Laos = 48.2%, Thailand = 46.8% and Vietnam = 59.0%) (Hortle, 2007) and represents the world's largest inland fishery, estimated to be worth between $4.3 – 7.8 billion US dollars on retail markets (Hortle, 2009).

Humans have been modifying freshwater ecosystems for many centuries for example, through the construction of river infrastructure which has enabled progress in agriculture, urbanisation and industrialisation through flood defence, waste disposal, supply of water, power production, transport and navigation (Goudie, 2013; Kemp, 2015). This modification has predominately been through damming, channelization or water abstraction (Goudie, 2013). River modification has continued to increase over the years with only 37% of rivers longer than 1000 km free flowing (Grill *et al.*, 2019) and almost half of global river volume altered by flow regulation and or fragmentation (Grill *et al.*, 2015). Furthermore, as the world population grows there will be a disproportionate increase in water and energy consumption which will lead to further habitat alterations (Kemp, 2015). For example, around 3700 major hydropower dams are either in planning or under construction (Zarfl *et al.*, 2015) which would result in 93% of all river volume to be affected by flow regulation or fragmentation (Grill *et al.*, 2015). This proposed construction is also largely focused in species-rich catchments in South America, South and East Asia and Africa (Zarfl *et al.*, 2019). Whilst these modifications have been justified to improve human life they can also result in significant ecological consequences on riverine populations and biodiversity (Vörösmarty *et al.*, 2010).

Freshwater habitats are thought to be particularly sensitive to anthropogenic activity for example, in riverine systems the unidirectional flow means that activity upstream (e.g. pollution, barriers) directly influences downstream areas (Malmqvist and Rundle, 2002; Dudgeon *et al.*, 2006). Additionally, the life-history strategies of many freshwater fish include specific environmental tolerances and habitat requirements especially for spawning and juvenile life-stages (Moyle and Leidy, 1992). For example, the catadromous European eel (*Anguilla anguilla*) is a species which undertakes migrations as both adults and juveniles of around 6000 km between spawning grounds (presumed to be Sargasso sea) and freshwater habitats in Europe, northern Africa and Mediterranean Asia (Van Ginneken and Maes, 2005). The impact of this infrastructure on fish populations varies not only by the type and size of the structure but also with environmental factors including river hydrology, swimming capabilities, behaviour and timing of migration (Northcote, 1998).

River infrastructure (e.g. dams and weirs) can block, restrict or delay fish from accessing key refuge, feeding or reproductive habitats through the fragmentation of previously connected ecosystems (Arnekleiv and Rønning, 2004; Katano *et al.*, 2006; Marschall *et al.*, 2011; Piper *et al.*, 2013; Schmutz and Moog, 2018). The accumulation of fish at impassable barriers can prolong stress, increase the chance of disease and may attract predators and harvesters (Schilt, 2007; Garcia de Leaniz, 2008; Castro-Santos *et al.,* 2009). Consequently fish may incur additional energetic costs which will have a large impact on non-feeding migrants (e.g. adult anadromous salmonids and catadromous eel) and simultaneously reduce survival and increase fitness costs (Jepsen *et al.*, 1998; Venditti *et al.,* 2000; Caudill *et al.*, 2007; Nestler *et al.*, 2008; Nyqvist *et al.*, 2017). Fish can also pass into other water offtakes (e.g. irrigation and land drainage) and become lost from the main river population (Prince, 1923; Rago, 1984).

Injury and mortality can also occur due to river infrastructure as fish pass through turbines (Calles *et al.*, 2010; Mueller *et al.,* 2017) at hydroelectric power stations or entrainment at water abstraction points (Piper *et al.*, 2013). Direct mortality can occur through several different methods: blade strike, grinding, abrasion, barotrauma due to rapid changes in pressure, cavitation, shear stress or turbulence (Clay, 1995; Čada *et al.,* 1997; Coutant and Whitney, 2000;

Kemp, 2015). Blade strike occurs if fish collide with turbine blades and the impact and likelihood is dependent on the characteristics of the structure (i.e. turbine dimensions) and fish (i.e. body length) (Čada *et al.,* 1997; Turnpenny *et al.,* 1998; Deng *et al.*, 2007; EPRI, 2008, 2011). Grinding refers to when fish are squeezed through narrow gaps between moving and fixed structures (Čada, 2001). Abrasion can occur from rubbing contact with moving or stationary objects (USACE, 1995) which can cause the loss of protective mucus coating, descaling or damage to skin and consequently lead to infection and delayed mortality. The movement of fish from high to low pressure areas during turbine passage can lead to ruptured or distended swim bladders due to expansion (Čada, 1997; Brown *et al.*, 2009, 2012). Due to extremely low pressures within the turbine, cavitation can occur where vapour bubbles violently collapse (Čada, 1990) which can lead to localised shock waves capable of pitting turbine machinery and potentially causing physical damage to the fish. Shear stress can occur when high and varying flow velocities produced by two bodies of water move past one another (Čada, 1990). Shearing forces applied parallel to a fish's body can lead to severe physical damage with typical injuries resulting in torn opercular and damaged eyes (Neitzel *et al.*, 2004; Deng *et al.*, 2005). Fluctuations in water motion known as turbulence has the potential to cause localised injury to fish (e.g. scale loss, fin tears, bruises) (Mueller *et al.,* 2017) and large scale turbulence can lead to disorientation and subsequent increase in predation risk especially in the tailrace of turbines (Larinier and Travade, 2002; Økland *et al.,* 2017). Alternatively, there might be non-lethal injuries or disorientation which could increase the chance of subsequent death from predation or infection (Čada, 2001; Kemp, 2015). River infrastructure has been identified as a key contributor to the decline of several species including the critically endangered European eel (Feunteun, 2002; Dekker *et al.,* 2007; Verhelst *et al.*, 2018b; Pike *et al.,* 2020). These structures have been reported to cause injuries (Bruijs and Durif, 2009), direct mortality (Calles *et al.*, 2010; Pedersen *et al.*, 2012) and migration delay or failure (Besson *et al.*, 2016; Trancart *et al.*, 2018) of eel. In addition, due to the long elongated body morphology and low swimming capabilities of eel it is particularly susceptible to injury and mortality (Boubée and Williams, 2006; Calles *et al.*, 2010; Russon *et al.,* 2010; Radinger *et al.,* 2021).

Designing suitable mitigation strategies to restore fish populations is often difficult due to limited knowledge of life history and taxonomy, fish flow relationship, seasonal aspects of behaviour and difficulties in sampling sites (Cooke *et al.,* 2012). Barrier removal is the most obvious mitigation strategy (McRae *et al*., 2012) but this is often undesirable due to the benefits of such structures including flood control, irrigation and recreation (Ficke *et al.,* 2011; Katopodis and Williams, 2012), possible environmental risks (e.g. sediment transport) and economic concerns (e.g.

removal/decommissioning costs) (Shuman, 1995; Bednarek, 2001; Stanley and Doyle, 2003). Another proposed strategy is through the use of fish passes (Clay, 1995) which are often considered the most feasible option to increase or restore connectivity (Branco *et al.*, 2013) but these can have variable efficiency (Brown *et al.*, 2013; Bunt *et al.,* 2016). In addition, both barrier removal and construction of fish passes risk inadvertently allowing the spread of invasive species (Mclaughlin *et al.*, 2013). This raises the “connectivity conundrum” (Zielinski *et al*., 2020) which refers to the tension between facilitating passage of desirable (native) species whilst restricting or blocking the passage of potentially ecologically and economically harmful invasive species (Fausch *et al.*, 2009).

Physical barriers (e.g. vertical or horizontal bars, barrier nets, physical screens, and low-head dams) are another mitigation strategy implemented to block and guide fish movements (Taft, 2000). However, these barriers can incur high construction and maintenance costs as they are prone to fouling (Kim and Mandrak, 2017). Furthermore, fish can also become impinged on physical screens and bars which can lead to mortality (Hadderingh and Jager, 2002; Greenwood, 2008). The use of behavioural stimuli offers an alternative approach to achieve guidance of fish either to safer routes of passage (i.e. bypasses) and/or to block invasive species. Although behavioural guidance systems are reported to only have marginal success (Hocutt, 1980), freshwater fish are restricted to a network of waterways so there should be large potential to control movements using behavioural stimuli (Kolar and Lodge, 2002). Several types of stimuli have been proposed for fish guidance including light (Hansen *et al*., 2018), acoustics (Maes *et al.*, 2004), bubbles (Zielinski and Sorensen, 2016) and electricity (Dawson *et al.,* 2006). Whilst eliciting a consistent change in behaviour and high effectiveness (100%) might be challenging there are large research gaps which could be explored to achieve suitable efficiencies.

Electric fields have been used in fisheries management for many years (e.g. electrofishing) and has gained attention as a potential method for fish guidance but limited research has been performed to date (see Parasiewicz *et al.*, 2016; Kowalski *et al.,* 2022). Further, the majority of this research has focused on using electric fields to block/divert invasive species both in laboratory (e.g. Holliman *et al.,* 2015; silver carp, *Hypophthalmichthys molitrix*) and field (e.g. Johnson *et al*., 2016; sea lamprey, *Petromyzon marinus*) settings. In contrast, little research has been performed on guiding native or species of conservation concern (e.g. Stoot *et al.*, 2018; lake sturgeon, *Acipenser fulvescens*) to less hazardous routes and with limited effectiveness. For example, only 5 - 28% of native Atlantic salmon smolts (*Salmo salar*) were successfully guided to a bypass using electric fields (Gosset and Travade, 1999). However, parameters associated with electric fields have been shown to influence fish responses such as pulse frequency (Larson *et al.,* 2014), pulse width (Layhee *et al.*, 2016) and type of current (Simpson *et al.,* 2016) which could help explain limited success to date.

In order to optimise the effectiveness of electric barriers, more thorough and extensive testing of parameters with respect to the morphological characteristics of fish (i.e. body size) and specifics of the site (i.e. water velocity, species assemblages) is required. Moreover, the limited research that has been performed on electric guidance systems has sometimes failed to quantify parameters used and so drawing conclusions and making comparisons can be difficult. Hence, ensuring the accurate quantification of parameters tested is a crucial first step for fish guidance management strategies. Subsequently, the design of an effective electric field guidance system should then be considered within the context of the site. For example, areas with higher water velocities could limit the effectiveness of an electric barrier (Johnson and Miehls, 2014; Miehls *et al.,* 2017). In addition, previous work has tended to focus on a single management application, either guiding native fish or blocking the further spread of invasive species. However, in areas where invasive and native species occur in sympatry it is particularly important that the species composition be assessed to ensure electric barriers are effective for the desired management needs and to minimise potential harmful effects on non-target species. In this way, differences in electrosensitivity could be exploited to design species-selective mitigation strategies for guidance. Whilst the use of electric fields is a growing and promising area of research there are still large research gaps to address if it is to be adopted as a management strategy.

Due to the associated problems surrounding traditional mitigation strategies (e.g. cost, risk of impingement and spread of invasive species) there is an increasing need to investigate other methods to control fish movements. This thesis aims to advance the understanding of fundamental responses and guidance efficiency of fish to electric fields to provide initial recommendations for management strategies for the conservation of fish and to prevent further spread of invasive species whilst also considering situations where both applications are needed. Hence, a species of conservation concern, the critically endangered European eel (*Anguilla anguilla*) and two known invasive cyprinids; grass (*Ctenopharyngodon idella*) and common carp (*Cyprinus carpio*) were selected for this research.

1.1 Initial research aim and objectives

The broad overall aim of this thesis is to:

1) Advance scientific knowledge in the response of fish to electric fields as a potential guidance system.

To meet this aim, an initial objective have been formulated:

1) Review current literature to identify research trends, biases, and knowledge gaps on the conservation of European eel, cyprinid invasive species management and fish response to electric fields.

Chapter 2 Literature review

2.1 European eel: life-history, stocks and management

Anguillidae are globally distributed in over 150 countries and inhabit freshwater, brackish estuaries and coastal waters (Pike *et al.,* 2020). They have a complex life-history with multiple life-stages (Figure 2.1), semelparity and panmixia (Aida *et al.,* 2003; Van Ginneken and Maes, 2005). The European eel (*Anguilla anguilla*) is a catadromous species which spawns in the ocean and matures in rivers (Tesch, 2003). Spawning is thought to take place in the Sargasso Sea and the larvae (Leptocephali) drift around 6000 km to the European continent using ocean currents (Schmidt, 1922; Tesch, 2003; Van Ginneken and Maes, 2005; Dekker, 2008; Aarestrup *et al.*, 2009; Bruijs and Durif, 2009). This is a long (between 10 months to over 2 years) and passive trans-oceanic drift and consequently the distribution of eel is very large (Schmidt, 1922; Tesch, 2003; Bonhommeau *et al.*, 2009). The laterally flattened Leptocephalus transforms into a rounded unpigmented glass eel at the continental shelf edge (Dekker, 2008). Glass eel then migrate upstream into coastal waters, estuaries and rivers and then into lakes and streams using Selective Tidal Stream Transport (STST) (Beaulaton and Castelnaud, 2005; Dekker, 2008). During ebb tides the fish remain at the water bottom and during flood tides they rise into the water column enabling a net migration into freshwater (Harrison *et al.*, 2014; Cresci, 2020). This is a mechanism which enables fish with low swimming capabilities to move upstream using tidal currents to save energy (McCleave and Kleckner, 1982; Gascuel, 1986; Beaulaton and Castelnaud, 2005). Flow direction and olfactory cues are thought to be the primary navigation cues for juvenile immigration into estuaries and rivers (Deelder, 1954; Crivelli *et al.*, 2008). The detection of freshwater is crucial for both orientation and stimulating migration (Sola, 1995; Briand *et al.,* 2002; Huertas *et al.*, 2007). Glass eel then metamorphose into pigmented elvers and continue to grow and feed to mature into yellow-phase eel and this stage lasts usually between 8 - 15 years (females) and 3 - 12 years (males) (Aprahamian, 1988; Feunteun, 2002). The yellow-phase life-stage exhibits a great deal of phenotypic plasticity for habitat and inter-habitat migrations (Feunteun *et al*., 2003; Tesch, 2003; Daverat *et al*., 2006). This life-stage can be sedentary in a small home range or they can continue to make upstream movements during the spring and summer months (Feunteun *et al.*, 2003). Sex determination also occurs during this stage and, although not fully understood, is suggested to be dependent on local stock density (Dekker, 2008). After this growth phase, eel undergo further metamorphosis (silvering) involving a number of reproductive and osmoregulatory changes to prepare for migration to spawning grounds as adult silver-phase eel (Van den Thillart and Dufour, 2009). Adult eel migrate downstream to the Sargasso Sea to spawn and subsequently die (Dekker, 2008; Egg *et al.*, 2017).

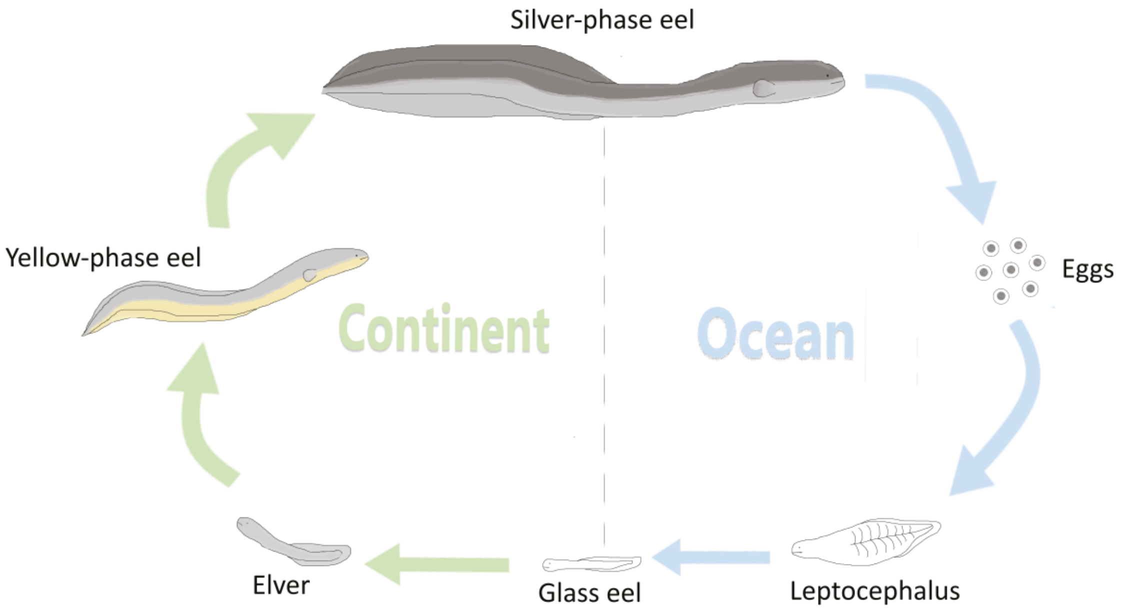


Figure 2.1. Life-cycle of the European eel.

The European eel is now classified as critically endangered by the International Union for Conservation of Nature (IUCN) (Pike *et al.,* 2020). Since the 1970s, the recruitment of European eel has declined substantially for example, by 70% in some areas (e.g. Bristol Channel and Severn Estuary) and by over 90% in others (e.g. river Thames) (Bark *et al.,* 2007; Gollock *et al.,* 2011; Dekker and Casselman, 2014). Although, European eel recruitment indices between 2011 – 2020 appear to be on an increasing trend they are still below 10% of the baseline of 1960 – 1979 (ICES, 2021) and the stock is not showing signs of long-lasting recovery (Righton *et al.*, 2021). Before the 1980s there was a perceived high abundance of European eel and consequently several factors attributed to their decline have only recently started receiving attention (Piper *et al.*, 2013). These factors include pollution (Maes *et al.*, 2005; Geeraerts and Belpaire, 2010), overfishing (Aalto *et al.*, 2016) introduction of parasites (Køie, 1991), climate change (Knights, 2003; Bonhommeau *et al.*, 2008), habitat modification (Kettle *et al.,* 2011), man-made barriers (Trancart *et al.*, 2020) and direct mortality from turbine blades (Heisey *et al.*, 2019). All these factors are well-accepted but the relative contribution of each to the decline is unclear (Feunteun, 2002; Wirth and Bernatchez, 2003; Dekker, 2004).

As European eel stock is considered outside safe biological limits (i.e. mortality exceeds recruitment and growth) legislation has been developed to establish measures for its recovery (ICES, 2007, 2011b). The European Union have adopted council Regulation 1100/2007/EC (Eel Recovery Plan) which requires states to prepare eel management plans (EMPs) into mitigating the impact of anthropogenic barriers on eel migration to help stock recovery (EU, 2007; ICES, 2011a; Vowles *et al.*, 2015). The EMPs for each state is required to detail how the target, of an escapement of silver eel biomass to the sea of equal to or more than 40% of the estimated escapement in the absence of anthropogenic structures, will be achieved (EU, 2007). Furthermore, the UK have developed The Eels (England and Wales) Regulations 2009 to prevent the ingress of eel into potentially harmful water abstraction points (those capable of pumping less/or equal to 20 m^3/day) by screening (2 – 20 mm gap spacing, depending on life-stage present), a measure that will restrict the recruitment of juvenile eel into reservoirs via pumped inputs. However, whilst legislation is important for the recovery of eel, post-evaluations in 2012 (ICES, 2013) and 2015 (ICES, 2016) suggest goals have not been fully achieved (ICES, 2016; Dekker, 2016; European Commission, 2020) with no substantial improvement in stocks or reduction in mortality.

Whilst legislation has been implemented to recover eel stocks there are several reasons which makes conservation particularly challenging. Firstly, implementing and designing conservation measures for a fish species with multiple life-stages across a wide geographical area is complex (Mcdowall, 1992). Moreover, for eel, the large distances between the marine spawning areas and freshwater habitats makes monitoring eel movements difficult and hence poses constraints on evaluating conservation measures (Mcdowall, 1992; Aida *et al.,* 2003; Tesch, 2003). Secondly, it can be difficult to ascertain which stage or stages of the life-cycle have been affected (Feunteun, 2002; Kettle *et al.,* 2011), or whether the origin of the decline is the result of freshwater, inshore or oceanic influences (Dekker, 2008). Hence, all life-stages should be investigated and considered for effective management strategies (White and Knights, 1997; Feunteun *et al*., 1998; Briand *et al*., 2005; Bult and Dekker, 2007; Laffaille *et al.,* 2007; Watz *et al*., 2019). Thirdly, a variety of methods are used to obtain accurate estimates or measures of recruitment, population size and escapement and inconsistences in the data make it hard to draw conclusions to assess the effectiveness of management strategies (Bevacqua *et al.*, 2015; Jacoby *et al.*, 2015; Righton *et al.*, 2021). Consequently, focus has been placed on implementing actions (i.e. closing fisheries) rather than evaluating if measures are successful (e.g. increase in escapement) (Schiavina *et al.*, 2015). Finally, whilst local management efforts are important, due to the complex life-cycle of eel, in order to achieve measurable change of population recovery a broad integrated collaboration from national and international stakeholders is required (Jacoby *et al.*, 2015).

River infrastructure is a key contributor to the decline of European eel and in Europe, around 33% of the estimated potential eel habitat (123,800 km^2) is inaccessible due to man-made barriers (Moriarty and Dekker, 1997). More recent estimates suggest between 50 – 90% of eel habitat was inaccessible by the end of the twentieth century in Europe (Feunteun, 2002). The Iberian Peninsula is one area that has been particularly effected by large dam constructions and eel are thought to have lost over 80% of their habitat in that region (Clavero and Hermoso, 2015). In the UK alone there is over 26,000 potential anthropogenic barriers to fish migration and an estimated 500 are considered to severely restrict free passage (Environment Agency, 2011a). Furthermore, due to the catadromous nature of eel this infrastructure can lead to blocks and delays to migration for both downstream seaward migrating silver-phase eel and inward upstream migrating (glass) juveniles (Feunteun, 2002; Bruijs and Durif, 2009; Verhelst *et al.*, 2018b).

As eel mature into adults (silvering) they cease feeding as they begin their downstream migration and delays (due to barriers) to this can lead to an increased risk of predation, disease and depletion of energy stores thus reducing the chance of successful migration and spawning (Tesch, 2003; Garcia de Leaniz, 2008; Piper *et al.*, 2013). One study in the heavily regulated river Stour in the UK found these delays to downstream migration could be up to 68.5 days (Piper *et al.*, 2013). These migration delays have resulted in the reversion of the silvering process back to yellow-phase which might cause eel to miss an environmentally favourable migration period (Durif *et al*., 2003, 2005). Whilst the exact energetic consequences of delayed migration have not been quantified, it is likely that the long-term viability of spawners would be reduced through the depletion of finite energy reserves that are required for successful oocyte production and long oceanic migration (5000 – 6000 km) (Haro *et al.,* 2000; Behrmann-Godel and Eckmann, 2003; Travade *et al.*, 2010; Trancart *et al.,* 2020). In addition, adult silver-phase eel can tend to, though not always (see Piper *et al.*, 2017), follow the bulk flow which increases the chance they will encounter water intakes as these often have a large proportion of the flow (Jansen *et al.*, 2007; Bruijs and Durif, 2009; Piper *et al.*, 2013). Furthermore, the elongated body morphology and relatively poor burst swimming capabilities of adult silver eel increases the chances of impingement on screens and entrainment at pumps and turbines (Calles *et al.*, 2010; Russon *et al.,* 2010; Radinger *et al.,* 2021). Mortality due to entrainment can occur in a variety of ways such as, turbine blade strike, cavitation, pressure differences and shear stress (Turnpenny *et al.,* 1998;

Schilt, 2007; Bruijs and Durif, 2009; Pracheil *et al.*, 2016). In some cases, the mortality rate of *Anguilla spp.* has been documented to be 100% (Boubée *et al.,* 2008; Carr and Whoriskey, 2008), but generally between 10 - 50% is more common (Jansen *et al.*, 2007; Larinier, 2008).

Upstream migrating juvenile (glass) eel also face risks from river infrastructure but these are generally not well understood and so often are ignored (Åström and Dekker, 2007). Whilst juvenile eel have the ability to climb moist surfaces, large dams can restrict upstream movement preventing migration (Hitt *et al.,* 2012). In addition, in obstructed river systems the water velocity might be inadequate to stimulate the positive rheotaxis for juveniles to move upstream (Gascuel, 1986). It is unlikely that juvenile eel would be attracted to water intakes due to their positive rheotactic behaviour as the flow direction is in the opposite direction to their migratory instinct. However, the relatively weak swimming capabilities of juveniles may result in non-volitional entrainment at these facilities (Environment Agency, 2011b). Additionally, at water discharge points the flow might attract individuals away from natural channels into harmful locations (e.g. fish farms, waste water treatment works and power stations) (Turnpenny and O'Keeffe, 2005). One study found mortality occurred in glass eel as a result of being drawn into water intakes at power plants causing entrainment (Bryhn *et al.,* 2014). As glass eel pass through the filters they are exposed to cooling water from power plants which can result in sharp changes in temperature and pressure and also potential mechanical harm (Bryhn *et al.,* 2014). Estimating the percentage mortality from these structures can be challenging but some estimates have been made; for example, one study found that 13.4% of glass eel captured after passage died (Bryhn *et al.,* 2014). Another study found that there was a cumulative mortality of 15% over a week as a result of eel being drawn into and through a water intake at the Blavais power station (Roqueplo *et al.*, 2000).

Most of the conservation efforts for European eel have focused on the migratory life-stages (i.e. glass and silver-phase eel) as they are considered most at risk from the impacts of river infrastructure. However, whilst the yellow-phase life-stage is not typically migratory and frequently considered sedentary (Laffaille *et al.,* 2005), it represents the bulk of the eel's life-cycle and exploratory behaviour during this stage could contribute to population decline. In addition, the habitat use and feeding ecology of the yellow-phase eel is still poorly understood (Van Liefferinge *et al.*, 2012) and they are thought to undertake seasonal movements between winter refuges and summer feeding habitats (Feunteun *et al*., 2003; Riley *et al*., 2011) indicating a high degree of plasticity (Ovidio *et al.*, 2013). This plasticity for habitat use is likely important so eel can access feeding habitats to obtain sufficient food resources to accumulate energy and lipid content to complete the downstream migration to spawn (Maes *et al.*, 2005; Belpaire *et al.*, 2009; Ovidio *et al.*, 2013). Furthermore, the body condition of yellow-phase eel has been shown to be negatively correlated with lateral connectivity (Lasne *et al*., 2008) possibly due to the inability to access habitats with higher nutritional quality food (Van Liefferinge *et al.*, 2012). Hence, if yellow-phase eel are unable to access suitable foraging habitat due to barriers they will not build up enough lipid content and silvering may not be initiated which will have consequences for the recovery of stock (Larsson *et al.,* 1990). Therefore, it is important that research be performed to design mitigation strategies for the impacts of river infrastructure on all life-stages of eel. Moreover, these mitigation strategies should be designed and tested for the specific life-stage of concern to account for differences in behaviour (i.e. swimming, feeding and migratory), morphology and/or physiology, which might result in variations in effectiveness.

For *Anguilla spp*. there is limited research to date for both physical and non-physical designs to mitigate the effects posed by river infrastructure (Bruijs and Durif, 2009; Boubée, 2014; Haro, 2014). However, historically the focus has been placed on physical designs including fish passes and screens. Eel specific passes often consist of narrowly inclined ramps lined with a climbing substrate (e.g. natural; stones, vegetation or artificial; bristles, plastic mouldings or studs) (Solomon and Beach, 2004; Vowles *et al*., 2015) but the efficiency is not always assessed (Birnie-Gauvin *et al.*, 2019). In addition, physical screens have been used to prevent eel movements down hazardous routes, but these are not wholly effective and can incur high costs from construction and maintenance (Hadderingh and Jager, 2002; Calles *et al.*, 2010). Juvenile eel are easily entrained which has resulted in the retrofitting of existing facilities with narrow-spaced designs (1-2mm, Sheridan *et al.*, 2014) which can incur high costs. Fish can also become impinged and suffocate on the screens if the velocity exceeds burst swimming capabilities (Calles *et al.*, 2010), or they can result in physical abrasion (Swanson *et al.,* 2005) leading to secondary infection and delayed mortality. Consequently, fish guidance systems using behavioural stimuli (e.g. light, bubbles, acoustics and electric fields) offer the potential to develop a cost-effective alternative to improve mitigation measures.

The use of behavioural stimuli could have several potential applications including blocking movements, guidance to fish passes or bypass channels and for collection or trapping. Light and acoustics have received the most attention for the guidance of eel and have shown some promise (Hadderingh *et al.,* 1992; Sand *et al.*, 2000). For example, downstream migrating silver-phase eel were deflected up to 85% using underwater light in one study (Hadderingh *et al.,* 1992) but another reported a lower deflection rate of 50 - 65% when using the same stimuli (Hadderingh *et al.*, 1999). For upstream migrating eel, a strobe light barrier was tested in the field and found to be 65 - 92% effective as a deterrent (Patrick *et al.,* 1982). Infrasound has also been investigated for eel guidance and showed success in the River Imsa, Norway (Sand *et al.*, 2000) but another study found limited avoidance response in an English river (Piper *et al.*, 2019). Therefore, it is clear that more studies need to be performed to analyse the effectiveness of stimuli and results may be site specific. Crucially, before implementation of behavioural guidance systems in the wild, fundamental responses of fish to stimuli needs to be accurately quantified under controlled settings. However, historically the focus has been placed on assessing which routes fish take at river infrastructure rather than the fundamental responses of how they respond (e.g. hydrodynamic cues) (Coutant, 1999). Designing a behavioural guidance system is challenging especially due to the possible factors that can influence responses such as species (Schilt, 2007), ontogenic stage (Lucas and Baras, 2001), motivation (Colgan, 1993), behavioural bias (Kemp *et al.,* 2012), prior experience, learning and habituation (Odling-Smee and Braithwaite, 2003). Hence testing eel guidance systems needs to be performed across multiple life-stages. The lack of agreement over the most efficient, applicable method for eel conservation coupled with the absence of crucial testing and validation presents a large challenge (Boubée, 2014; Haro, 2014).

2.2 Invasive species management of common carp and grass carp

As the human population increases, there is an ever-growing need to block and control the spread of invasive species. Human activities often result in invasive species being introduced into new areas (Ricciardi *et al*., 2000). For example, national economies are building more international relationships hence increasing globalisation which can cause the spread of exotic species (Hulme, 2009). Global climate change has also been linked with an increase in the rate of invasive species introduction in part due to altered thermal regimes, reduced ice cover and increased salinity (Hellmann *et al.*, 2008; Rahel and Olden, 2008). Furthermore, mitigation measures to alleviate the impacts of river infrastructure (e.g. fish passes) can inadvertently enable the spread of invasive species. Although, rates of establishment are relatively low there still are inherent risks that could have irreversible, catastrophic ecological consequences (Britton *et al.,* 2011).

Invasive species often inflict large economic and ecological burdens on the environment they invade including loss of ecosystem services and native species, ecosystem degradation and management costs (Pimentel *et al.,* 2005; Williams *et al.*, 2010; Ricciardi and MacIsaac, 2011). The negative environmental impacts of these species include spreading non-native parasites, destroying aquatic vegetation and increasing competition, predation and hybridisation (Courtenay and Moyle, 1992; Britton *et al.,* 2010; Gozlan *et al.*, 2010; Havel *et al.*, 2015). The estimated economic damages and associated costs of invasive species can be high; for example, $120 billion annually in the US (Pimentel *et al.,* 2005). In the UK, control costs for freshwater invasive species was estimated at £26.5 million per year (Oreska and Aldridge, 2011). These estimates are also likely conservative as data on damages and control costs are not always available (Pimentel *et al.,* 2005).

Common carp (*Cyprinus carpio*) and grass carp (*Ctenopharyngodon idella*) are two examples of species that have been introduced into many areas of the world. Common carp are native to Eurasia but have been introduced to all continents except Antarctica and are one of the most invasive and ecologically destructive fish in the world (Balon, 1995; Vilizzi *et al.,* 2015). These species are known to increase the turbidity of water and cause the destruction of submerged aquatic plants (Crivelli, 1983; Bajer *et al.,* 2009; Weber and Brown, 2009).There are several characteristics of common carp which have aided their success for example, rapid growth (Vilizzi and Walker, 1999; Phelps *et al.,* 2008), high fecundity (Swee and McCrimmon, 1966; Tempero *et al.*, 2006) and the ability to thrive under a variety of abiotic (i.e. temperature, dissolved oxygen, pH, turbidity) (Crivelli, 1981; Edwards and Twomey, 1982) and biotic (i.e. food resources) conditions (García-Berthou, 2001; Britton *et al.*, 2007).

Grass carp are part of a group of invasive species including bighead (*Hypophthalmichthys nobilis*), black (*Mylopharyngodon piceus*) and silver (*Hypophthalmichthys molitrix*) carp known collectively as Asian carp (Conover *et al.,* 2007). Grass carp are often stocked to control undesirable aquatic vegetation but due to their long-life span can completely remove all vegetation (Cassani, 1996). High densities of grass carp can also increase nutrient enrichment and eutrophication, spread of non-native parasites, increase interspecific competition and decrease available refugia for other organisms (Chilton and Muoneke, 1992). Asian carp have been shown to have widespread distribution and their success is, at least in part, due to their reported reproductive capability, population densities, generalist feeding, rapid growth, broad climate tolerance, mobility, and longevity (Cudmore and Mandrak, 2004; Nico *et al.,* 2005; Kolar *et al.,* 2007). In the Mississippi basin, Asian carp numbers have increased substantially and there is evidence of spawning (Embke *et al.*, 2016) and recruitment (Chapman *et al.*, 2013) already in the Great Lakes and so potential further spread is of concern (Cudmore, 2012, 2017). The Great Lakes represents the largest freshwater body in the world and is an area of huge biodiversity and economic importance (Mills *et al.*, 1993) and damage from invasive species in this region has been estimated at up to $138 million annually (Rothlisberger *et al.*, 2012). Consequently, control methods have been designed and are estimated to cost tens of millions of dollars annually for the prevention, control, and management of these invasive species (Rosaen *et al.,* 2012; MNDNR, 2015).

To minimise the impact of invasive species it is more effective to prevent the initial introduction of the species but often management strategies are only designed after this (Lodge *et al.*, 2006; Noatch and Suski, 2012). For both common and grass carp, management strategies have focused primarily on physical removal and treatment of lakes with toxin (e.g. rotenone) (Escobar *et al.*, 2018; Robinson *et al.*, 2021). These strategies have associated issues for example, physical removal is not effective on large scales and the use of toxins can kill all fish in the area (Escobar *et al.*, 2018). Physical barriers are also costly due to the substantial engineering and maintenance (Bajer *et al.*, 2018). Consequently, the use of behavioural stimuli, including electric fields, are being investigated to block and control invasive species. Behavioural stimuli are particularly advantageous in areas where physical barriers are not logistically possible (e.g. shipping canals) (Pegg and Chick, 2004). In particular, the use of electricity has been proposed as it is thought to produce a more consistent response pattern in species than light or acoustic stimuli (Bajer *et al.*, 2018). However, often these electric barriers do not account for the potential impacts on non-target fish (i.e. blocking migration and possible mortality, see Johnson *et al.*, 2021) in the area and so more fundamental knowledge and comparisons of electrosensitivities is needed.

2.3 Fish response to electric fields

Fish have widely been reported to respond to electricity (e.g. electrofishing) however, the exact mechanisms of how fish detect and sense electric fields are not fully understood. Local action theory states that brain-nerve-muscle pathway is disrupted when an electric field directly stimulates nerves and causes fish muscle to contract creating an involuntary response (Lamarque, 1990). In this way, at a certain threshold the direct current will initiate and maintain nerve excitation and the electric stimulus acts directly on the muscle (Lamarque, 1967; Stewart, 1990). These nerves or muscles can become excited or inhibited in the field as the fish's body has since become part of the electric field (Lamarque, 1967). The electric field causes the muscles to contract up to a certain threshold (maximum contraction rate) and above this the fish becomes immobilised (Stewart, 1990). Another proposed explanation is the responses observed in electroshocked fish are due to an epileptic seizure, which is an abnormal stimulation of the central nervous system (CNS) rather than local action on the nerves and muscles (Sharber and Sharber Black, 1999). The observed responses of electroshocked fish have been shown to correspond to well-known stages of epileptic seizure which offers support to this theory (Reynolds and Kolz, 2012). There could also be a combination of both the electrostimulation of the CNS and autonomous nervous system (ANS) with a direct response of muscles of the fish and induced epilepsy (Lamarque, 1967; Kolz, 1989; Sharber and Sharber Black, 1999). Although there are unknowns concerning the physiological mechanisms responsible for fish responses to electric fields, it offers an attractive solution for guidance at least in part because the predictability of responses is sufficient for its use extensively for sampling and integrated into commercial fishing gear (Von Brandt, 1972; FAO, 1978).

Fisheries management has been interested in controlling fish movement for two main reasons: containing invasive species and protecting fish at anthropogenic structures (O'Farrell *et al*., 2014). Since the early 20th century research has been performed investigating responses of fish to electric fields (McMillan, 1928; Hartley and Simpson, 1967; Simpson and Reynolds, 1977; Steinmetz, 1990; Vaux *et al.*, 2000). However, this research predominately focuses on effective methods for electrofishing (Schneider, 1992; Beaumont *et al.*, 2002) and there is limited work on accurately quantifying behaviour responses of fish in terms of guidance strategies. In addition, research which has been performed does not always quantify the parameters of the electric field accurately, which makes it difficult to compare results (Beaumont, 2011). Therefore, whilst electric barriers have been implemented in the wild to control the movements of fish there is a large research gap in terms of the electric field parameters (e.g. type of current, waveform type, pulse frequency and width), behaviour, species, size of fish and effectiveness (Reynolds, 1996; Noatch and Suski, 2012; Johnson *et al.*, 2014; Parker *et al.*, 2015). Hence, it is crucial that research is performed to assess fundamental responses before further implementation of electric barriers in the environment.

Investigating the responses of fish to electric fields relies on an understanding of the principles associated with electricity. When electrodes are connected to a power supply and placed in water the movement of electrons from a positively charged electrode (anode) to a negatively charged electrode (cathode) induces a current (I), measured in amperes (A). The difference in the electric charge will generate a potential difference, voltage (E) measured in volts (V), between the electrodes. The voltage gradient can also be calculated and refers to the difference in voltage between two points in water, measured in volts per centimetre (Vcm^{-1}). The opposition to electric current flow is known as the resistance which can be calculated though Ohm's law ($R = E/I$) and expressed in ohms (Ω). The reciprocal of resistance is conductance and refers to the ease with which electricity flows through the substance in which it is contained, measured in Siemens (S). Conductivity is the ability of a unit volume of matter to conduct electricity and is usually measured in micro-Siemens per centimetre ($\mu S.cm^{-1}$) in water. Power (P) is the rate at which electrical energy is transferred by an electric circuit ($P = EI$) and expressed in watts (W).

There are three main types of voltage waveforms that have been suggested for use in electric barriers; (1) alternating current (AC), (2) direct current (DC) and (3) pulsed direct current (PDC) (Figure 2.2). Historically, AC was predominately used as it is advantageous due to lower voltage gradients required to elicit responses which allowed smaller generators to be used reducing economic costs (Beaumont, 2011). Whilst species such as sea lamprey (*Petromyzon marinus*) have been successfully blocked and guided using AC (McLain *et al.,* 1965) the rapidly reversing polarity (positive to negative) and cyclic changes in voltage gradient are suggested to increase the risk of fish mortality (Sternin *et al.,* 1976; Beaumont, 2011). AC is considered the most lethal and injurious and its use for sampling fish in Europe is prohibited and is recommended against in North America unless death is needed and injury or mortality to other fish is of no concern (Snyder, 2003). A study comparing AC and DC showed that for brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*), 110 V AC waveform resulted in 11% mortality compared to 2% when using 230 V DC waveform (Pratt, 1955). A study using 115 V AC and 115 V DC waveform found less difference in mortality with 4.6% and 1.5% respectively for bluegills (*Lepomis macrochirus)* (Spencer, 1967). AC waveforms were not found to be more harmful to embryonic or alevin steelhead (migratory form of rainbow trout) but once they reached swim-up stage (absorption of the yolk sac) they became more sensitive to AC (Simpson *et al.,* 2016). Perhaps at the embryonic stage there is not sufficient muscle to cause contractions but once the fish has reached the juvenile or adult stage muscles have developed and so become more sensitive to AC (Simpson *et al.,* 2016). The electric field in DC and PDC is unidirectional as the positive and negative electrodes of the circuit remain the same (Reynolds, 1996). Negative charge carriers (electrons) are repelled from the negative cathode and attracted to positive anode (Reynolds, 1996; Beaumont, 2011). PDC consists of pulses of DC and the number of pulses per second is thought to be advantageous over DC as lower voltage gradients are required to elicit responses (Sharber *et al*., 1994; Beaumont, 2011). Hence, this should reduce power demand and solar panels and battery banks have been suggested as a feasible option to power these barriers (average power consumption 0.13 kW; Johnson *et al.*, 2021). Electric barriers are also considered fairly cost-effective for example, an electric barrier used for sea lamprey control was roughly $60,000 U.S. dollars to purchase and a few hundred dollars of electricity a year to operate (Johnson *et al.*, 2021). In addition, electric barriers can also be implemented using non-permanent structures which makes them easier to permit as they do not impound or divert water (Johnson *et al.*, 2016). Minimising injury and mortality is also achievable with PDC by using lower pulse frequencies (recommended < 15 Hz, e.g. McMichael, 1993; Sharber *et al.*, 1994; Snyder, 1995; Cooke *et al.,* 1998). In this way, more recent research into testing and designing electric fields for fish guidance has focused on PDC (e.g. Dawson *et al.,* 2006 for Eurasian ruffe, *Gymnocephalus cernuus* and Miehls *et al.,* 2017 for sea lamprey). Ultimately, however, minimising injury and mortality using electric fields is largely dependent on the duration, exposure and parameters set rather than the type of current (Snyder, 2003).

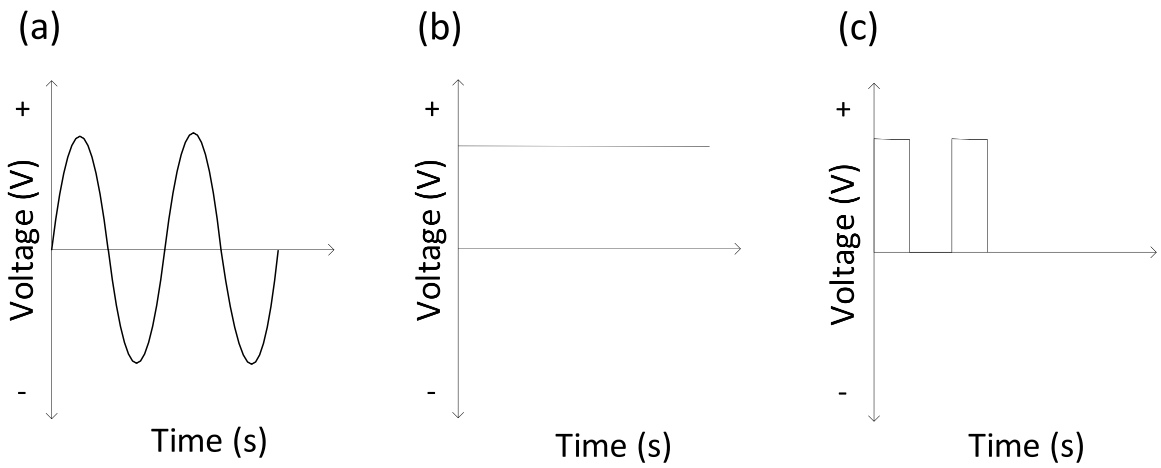


Figure 2.2. Diagram of examples of three types of electric current: (a) alternating current (AC), (b) direct current (DC) and (c) pulsed direct current (PDC).

The waveform type (e.g. square, exponential, sine) implemented can influence responses of fish to electric fields (Bird and Cowx, 1993; Beaumont *et al.,* 2000). Unfortunately, there is limited research addressing the response of fish under different waveforms. Some comparisons have been performed showing a higher injury rate under sine than both square and exponential waveforms in adult rainbow trout (Sharber and Carothers, 1988). However, previous work has sometimes neglected the accurate quantification of waveform shape which makes extrapolating results for future studies difficult (Snyder, 2003). Consequently, the effects of varying waveform shape are largely unknown (Bohlin *et al.*, 1989).

Pulse frequency is another variable which has been shown to affect the responses of fish to electric fields (Stewart, 1977). Increasing frequency reportedly increases fish conductivity due to a decrease in capacitance of fish muscle cell membrane allowing more current to pass through leading to higher injury rates (Sternin *et al.,* 1976). Furthermore, the power transfer theory (PTT) (Kolz, 1989) states that the effect of electricity on fish is dependent on the transfer of electric power and responses will only occur once specific power thresholds have been reached (Kolz, 1989; Kolz and Reynolds, 1989, 1990). Under higher pulse frequencies there will be a higher power density delivered into fish which increases the chances of injury (Kolz, 1989; Kolz and Reynolds, 1989, 1990). Several studies have confirmed this relationship with higher frequencies resulting in more injury and mortality of rainbow trout (Dalbey *et al.,* 1996; Ainslie *et al.,* 1998), black crappies (*Pomoxis nigromaculatus*) (Dolan *et al.,* 2002) and silver carp (Culver and Chick, 2015). Myoclonic jerks associated with shock-induced seizures are suggested to develop faster under higher frequencies which offers further explanation to increasing injury rates (Dolan *et al.,* 2002). One study showed if pulse frequency was increased from 11.5 to 20 Hz the occurrence of injuries in Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) was doubled at an electric weir used for trapping (Larson *et al.,* 2014). However, increasing pulse frequency by 1 Hz (from 2 to 3 Hz) was also found to be better in reducing passage success across an electric barrier for steelhead and Pacific lampreys (*Entosphenus tridentatus)* in a laboratory setting (Mesa and Copeland, 2009). Hence, selecting the most effective pulse frequency for guidance whilst minimising injury is a challenge for fisheries management.

Studies testing the influence of the pulse width of electric fields on fish responses has received less attention than frequency and is not fully understood. Nevertheless, it is generally thought that under longer pulse widths the mean, but not the peak, power transferred to the fish is greater (Beaumont, 2011) and so once a threshold in pulse width is reached increasing this further has no effect on fish response (Halsband, 1967; Sternin *et al.,* 1976). However, as pulse width increased, a lower voltage was found to elicit the same tension in muscle (Stewart, 1990). Furthermore, Stewart (1979) reported that the field strengths required to elicit responses decreased as pulse width increased (0.1 - 10 ms) for plaice (*Pleuronectes platessa*) and cod (*Gadus morhua*) muscle. In terms of assessing the effect on potential guidance, one study found that increasing pulse width reduced the passage success of rainbow trout (Layhee *et al.*, 2016) whilst another found no effect on escapement rate for walleye (*Sander vitreus*) (Weber *et al.,* 2016).

To successfully design electric field guidance systems care needs to be taken to test parameters (e.g. pulse frequency, width, voltage) in order to ascertain the desired behavioural response for management. For example, narcosis, defined as immobilization with prolonged post stimulus loss of consciousness (see Bearlin *et al.,* 2008), is thought to be elicited through the temporal summation of high-frequency pulses (Sharber and Sharber Black, 1999; Bearlin *et al.,* 2008). Hence, whilst higher frequencies are required to elicit narcosis, the electric parameters required to elicit other behaviours such as escape swimming might be different. In addition, altering these parameters independently might elicit different responses but it is also possible that there could be interactions between them (Bearlin *et al.,* 2008). For example, perhaps at lower frequencies and constant voltage gradients, higher pulse widths are required to pass the threshold to elicit a response. Alternatively, if lower pulse widths are used, higher voltage gradients might be required. This could make management strategies harder to design depending on the desired behaviours and predicting the parameters needed to elicit a response requires extensive testing with respect to species. There might also be trade-offs to consider with the economic efficiency of the most desired electric field parameters.

Species can respond to electrical fields in different ways due to body shape, skin characteristics, swimming motions, central and peripheral nervous system, scale thickness, sensitivity of the lateral line and stress responses (Sternin *et al.,* 1976; Dawson *et al.,* 2006). Additionally, any combination or possible unaccounted physiological differences between species could influence responses to electric fields. Limited species comparisons have been performed in terms of responses to electric fields, but the occurrence of haemorrhaging and spinal injury was found to be different between bluegill, channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) (Dolan and Miranda, 2004). These differences were suggested to be due to anatomical and morphological characteristics of the skeleton and scales (Dolan and Miranda, 2004). In addition to physiological traits of target species it is also important when testing electric fields, for fish guidance, that the specific behaviour is considered such as habitat preferences (i.e. pelagic, semi-pelagic and benthic fish). For example, in the case of a bottom dwelling species such as the European eel, the electric field would need to extend to the sediment floor to be effective

(Bohlin *et al.*, 1989). The life-stage of the target species is also likely to affect the responses observed. For example, the sensitivity of fish to DC has been shown to be higher for fish embryos (Dwyer and Erdahl, 1995; Henry and Grizzle, 2004; Bohl *et al.,* 2010) but reportedly cause the least injuries for adults (Reynolds, 1996; Muth and Ruppert, 1997; Henry *et al.,* 2003; Snyder, 2003; Bohl *et al.*, 2009). In addition, during periods of migration, spawning, feeding, predation or overcrowding swimming motivation will be heightened and so the effectiveness of an electric barrier might be reduced for these life-stages (Dawson *et al.,* 2006). However, one study found that even when food had been positively associated with a flashing light, a 50 V, 1 ms pulse width, 15 Hz barrier was effective in preventing several flatfish species (European plaice*;* lemon sole, *Microstomus kitt* and common dab, *Limanda limanda*) crossing the barrier to the light (Stewart, 1981). Another study in the Jordan river showed that a 2 ms pulse width, 10 Hz barrier was sufficient to completely block upstream migrating sea lamprey movement (Swink, 1999).

The size of fish is another factor which determines the sensitivity to the electric field. Large fish are more sensitive to electric fields (i.e. higher electrosensitivity) than small fish (Dolan and Miranda, 2003) because the voltage gradient is measured across the length or width (depending on orientation) of the fish (Reynolds, 1996). The voltage gradient is a function of both the field intensity and orientation of the fish relative to the field lines (Snyder, 2003). Hence, for longer fish the voltage gradient from the nose to tail (if parallel to field lines) will be greater as it will span more field lines. Another proposed reason for the increase sensitivity of larger fish is that they possess larger nerves (Lamarque, 1967). However, it is thought this might only be applicable for smaller fish as once nerves reach approximately 4 cm the threshold for stimulation remains stable (Lamarque and Charlon, 1973). In addition, the bigger muscles in larger fish could result in the inability for muscles to slacken in between pulses if the frequency is high enough (Halsband, 1967; Snyder, 2003). Larger fish have been shown to have higher electrosensitivity in laboratory studies, for example, smaller bighead carp were able to swim further into the electric barrier than larger individuals before an avoidance behaviour was observed (Holliman, 2011). Similarly, body length was negatively correlated to the voltage gradient required for immobilisation in grass carp (Briggs *et al.*, 2019). If the voltage gradient (i.e. the electric field strength) is high it is possible that whilst large fish will be blocked before reaching the area of maximum field strength, small fish may be able to continue and consequently more extreme behaviours (e.g. breaching) could be observed (Holliman, 2011; Parker *et al.*, 2015). Conversely, a study investigating responses of lake sturgeon (*Acipenser fulvescens*) found that larger fish were less susceptible to electric field exposure (Stoot *et al*., 2018). However, this could be explained by age-related differences such as scale and scute density, which can influence electrical conductivity rather than specific body length measurements (Stoot *et al.*, 2018).

The effectiveness of an electric barrier relies on the electricity to pass from the electrodes to the water and into the fish, making the design and placement of these important (Kolz, 1993; Beaumont, 2011). The placement and design of electrodes both effect the shape, size and distribution of the electric field (Copp, 1989). Typically, there are two types of electrode placement: horizontal and vertical. Vertical electrodes can be either fixed into the water bed or suspended by an overhead wire whilst horizontal electrodes are usually mounted on the river bed (Beaumont, 2011; Johnson *et al.*, 2014, 2016). Horizontal electrodes are thought to produce an electric field which is most intense at the substrate and then decreases as it gets closer to the surface (Ostrand *et al.*, 2009). One issue with horizontal electrodes is that they can be particularly affected during flooding events due to the notable reduction in electric field strength in the upper water column (Johnson *et al.*, 2014). Therefore, a higher voltage gradient would be needed to enable the field to extend from the substrate to the surface of the water which might elicit more extreme behaviours (Bajer *et al.*, 2018). This is an important consideration for application if the target species tend to swim throughout the water column. Furthermore, there is an added cost associated with embedding horizontal electrodes in the riverbed (Bajer *et al.*, 2018). Conversely, vertical electrodes produce an electric field which varies on the horizontal plane and so as distance from the electrodes increase, electric field strength decreases (Johnson *et al.*, 2014). However, if electrodes are fixed in place a mechanism is needed to remove debris as this can affect the efficiency and the power demand if the sediment is conductive (Beaumont, 2011).

The conductivity of the water, fish, and sediment are all other factors which can affect the characteristics of the electric field. Firstly, the surrounding water conducts the electric field to the organism and the extent to which this occurs is related to the resistivity which is the inverse of the conductivity (Gros*s et al*., 2015). Kolz and Reynolds (1989) determined the most efficient energy transfer from the pulser to organism is when the water conductivity and organism conductivities are equal. The efficiency of power transfer decreases exponentially with the ratio of fish to water conductivities (Kolz and Reynolds, 1990). At higher water conductivities more power is required to achieve a set field strength due to lower resistivity (Gross *et al.*, 2015). Hence, to generate desired field strengths in waters of high conductivity a more powerful generator is required (Bohlin *et al.*, 1989). If the water conductivity is higher than the organism's, the current will flow more easily through the water than through the fish (Gross *et al.*, 2015). In contrast, lower water conductivity will require the generation of higher field strengths as a result of higher resistance (Bohlin *et al.,* 1989). Secondly, in terms of recording fish conductivities there is limited research to date (see Reynolds, 2021) and no standardised methods nor established values (Kolz and Reynolds 1989; Miranda and Dolan 2003; Kolz, 2006). Furthermore, fish conductivities are not constant and are dependent on life-stage and will change with the electrical input as the nervous system will react differently (Kolz and Reynolds, 1989; Dolan *et al.,* 2002). Fish conductivity is also positively correlated with temperature and a study on common carp showed a five-time increase in temperature (5 - 25°C) was matched with a five-time conductivity (372 - 1969 $\mu S.cm^{-1}$) increase (Whitney and Pierce, 1957). Finally, the sediment conductivity is usually higher than that of water hence a bottom dwelling (i.e. near the sediment bed) species would feel a lower field strength (Sternin *et al.,* 1976).

Electric fields have been proposed for several different applications including blocking invasive species (Gross *et al*., 2015), guidance from hazardous routes (Burrows, 1957) and even to protect humans from fish in the case of shark repellents (Huveneers *et al.*, 2018). Most of the previous research using electric fields in fisheries management has focused on blocking invasive species. A key example of this is in the Chicago Sanitary Shipping Canal (hereafter; CSSC) which is 50 km long and connects the Great Lakes to the Mississippi river which can serve as a route for invasive species to spread (Moy *et al.,* 2011). The first electric barrier (Demonstration Barrier) was constructed there in 2002, originally to combat the downstream movement of round goby (*Neogobius melanostomus*) from the Great Lakes to the Illinois river (tributary of the Mississippi River) and was shown to be almost 100% effective (Savino *et al.,* 2001; Sparks *et al*., 2010; Moy *et al.,* 2011). In 2009, two further barriers (Barrier IIA and IIB) were conducted and now all three work over a larger area to tackle and block the upstream movements and expansion of Asian carp and common carp (Sparks *et al.*, 2010) from the Mississippi River into the Great Lakes (Veraldi *et al.*, 2011; Parker *et al.*, 2015). In this way there are two downstream wide arrays which emit a weak electric field and these are coupled with two upstream narrower arrays which generate the maximum field strengths (Holliman, 2011). These barriers use steel cable electrodes, pulse frequency 34 Hz and width 2.3 ms with field strengths of 0.79 - 0.91 Vcm^{-1} (USACE, 2011). These parameters were based on incapacitation rates of fish which increased at 0.91 Vcm^{-1} for bighead carp (Holliman, 2011) and 0.79 Vcm^{-1} for silver carp (Holliman *et al.,* 2015). This gradient in field strength should enable the fish enough time and distance to exhibit adverse reactions to the electric field and potentially stop movement before they reach the maximum field strength, which could cause a more uncontrolled shock response (Parker *et al.*, 2015). This uncontrolled response could result in the fish swimming further through the barrier due to shock (Hartley and Simpson, 1967; Parker *et al.*, 2015). Ultimately, the maximal field strength should be sufficient to block the smallest target species and the lower field strengths should sufficiently move the larger ones out of the area (Hartley and Simpson, 1967). Testing for a further barrier (Barrier I) is underway to determine the appropriate settings of field strength, pulse frequency and width and will be the first to be adjustable for these parameters (Egly *et al*., 2021).

The CSSC barriers have a high effectiveness and reportedly have incapacitated 97 - 100% of fish attempting to pass, but they also raise several concerns (Sparks *et al.*, 2010; Parker *et al.*, 2015). Firstly, the barrier requires continual power, which incurs high economic costs (Dettmers *et al.*, 2005; Moy *et al.,* 2011; Parker *et al.*, 2015). The demonstration barrier costs were estimated at $1.5 million for construction and monthly electricity costs $1,850 per month (Moy *et al.,* 2011). Secondly, the effectiveness against small fish has been questioned and the potential dangers to non-target species (Dettmers *et al.*, 2005; Moy *et al.,* 2011; Parker *et al.*, 2015). However, the parameters of the CSSC have largely been justified based on the lack of native species migrating through the canal (Moy *et al.,* 2011). Thirdly, the electric field is affected by metal hull barges due to their high conductance (Parker *et al.*, 2015). As a result, the electric field will be strongly attracted to the hull and direct observations have shown that a peak field strength of 0.91 Vcm^{-1} can be reduced to as low as 0.06 Vcm^{-1} near vessels (Parker and Finney, 2013; Parker *et al*., 2015). This may enable fish to swim further into the barrier area or become entrained beyond it (Dettmers *et al.*, 2005; Parker and Finney, 2013; Parker *et al.*, 2015). Finally, whilst the barrier is functioning and appears effective there is a lack of basic laboratory studies assessing fundamental responses of species to electric fields.

Promising results have also been found for other invasive species, including upstream migrating sea lamprey, where an electric field successfully guided 75% of individuals into a trap in the field (Johnson *et al*., 2016). This system only operated during the night in order to minimise non-target impacts and keep the annual cost low ($4, 800 U.S dollars) (Johnson *et al.*, 2016). In other laboratory and field trials 100% of upstream migrating lamprey were blocked, albeit with considerably higher power required for success in the field (0.3 mW/cm^3 vs ≥ 4.4 mW/cm^3, Johnson *et al.*, 2014). This study highlights the importance of confirming laboratory results in the wild. Other field studies have also been performed for example, the effectiveness of an electric barrier placed in an outlet stream to block common carp was assessed (Verrill and Berry, 1995). The fish were tagged and released downstream of the barrier and no fish were caught upstream (Verrill and Berry, 1995). Electric fields have also been shown to divert an average of 72% of upstream migrating common carp into a mock trap in a natural stream within 22 hours (Bajer *et al.*, 2018). Similarly, a study on grass carp tested an electric barrier in Lake Seminole, Florida and showed that escapement was reduced from 35 - 68% to 0% after the barrier was implemented (Maceina *et al.,* 1999). However, neither of these field studies provided details of the quantification of the electric field. The absence of accurate electric field quantification in studies makes comparison of the results and informing future research difficult.

Guiding downstream moving fish is considered a particularly difficult application of electric barriers (Burger *et al.,* 2012). Consequently, more focus has been placed on testing and implementing electric barriers for upstream than downstream moving fish. One reason for this is that designing electric barriers for upstream moving species is thought to be easier than downstream as if the fish turns away from the electric field it should be swept naturally by the flow out of the area (Beaumont, 2016). In contrast, for downstream electric barriers to be effective the fish needs to first experience discomfort to the field but still exhibit avoidance behaviour and move away (Beaumont, 2016). It is possible though that the fish may become incapacitated and be swept by the flow into the exclusion area (Beaumont, 2016). Furthermore, if downstream moving fish approach an electric barrier sideways, the voltage gradient will be felt across the width of their body. In contrast, if fish are actively approaching the barrier the voltage gradient will be felt anterior to posterior (i.e. maximum). Consequently, if the electric field on approach causes them to switch orientation from sideways to an active approach this will result in them experiencing a higher voltage gradient (i.e. anterior to posterior) and could cause sudden shock and incapacitation into the area of highest field strength (Beaumont, 2016). The optimal orientation for electro-stunning is reportedly when fish are perpendicular to the electrodes (i.e. actively approaching) and so in this situation undesirable responses such as stunning might occur rather than controlled avoidance out of the area (Rous *et al.*, 2015). However, some studies have been performed on downstream moving fish for example, vertical electrodes became less effective at guiding juvenile sea lamprey at water velocities greater than 0.1 ms^{-1} (Johnson and Miehls, 2014) and 0.25 ms^{-1} (Miehls *et al.,* 2017). Equally work on out-migrating salmonids concluded that electrical guidance was achievable where water velocity was < 0.3 ms^{-1} (Pugh *et al.,* 1970). In addition, a study at a pumping station revealed 72% of all fish inverted their swimming direction after approaching the electric fence, but again the mean velocity was low (0.05 ms^{-1}) (Egg *et al.*, 2019). In areas with still water, issues might also occur if there is no flow to sweep a fish out or away from the electrified area and extreme responses such as paralysis occur. An electric barrier (0.2 - 0.4 Vcm^{-1}) was sufficient to block common carp in still water but stunned individuals were still to be able to cross an electric field possibly due to sudden shock (Kim and

Mandrak, 2017). Hence the effectiveness of a barrier might be limited in still water areas and the parameters (e.g. frequency, voltage) set should not result in paralysis (Hartley and Simpson, 1967).

Assessing and quantifying behaviour responses whilst accounting for variables associated with real-life applications (e.g. water velocity) before implementation in the wild is crucial but not always possible in a laboratory setting. For example, fish are likely to repeatedly encounter an electric barrier in the field and so habituation or reduced sensitivity to the stimulus could occur. Whilst habituation has been reported for other stimuli (e.g. acoustics; Knudsen *et al.,* 1992; Murchy *et al*., 2017) very little is known about any similar relationship for electric fields. In addition, reduced effectiveness of already implemented barriers has not been reported although this could be due to inconsistent monitoring. One study did find evidence of reduced response to electric fields in lake sturgeon after a five-minute exposure to a low field strength was increased to a higher level (Stoot *et al*., 2018). This study only tested two exposures of the electric field separated by a 48-hour period and whilst fish showed reduced responses after the second, the effect of subsequent exposures does not mean habituation would occur. Additionally, it seems less likely that habituation will occur for a stimulus such as electric fields if it relies on an involuntary muscular response due to direct action on the nervous system (Stewart, 1990).

For any electric guidance system to be successful a combination of both initial laboratory and field studies are needed. However, due to the limited research performed to date assessing fundamental and applied behaviour with respect to parameters set, laboratory based work is needed as an initial assessment. Comparing results from studies poses difficulties as the same parameters are not always measured (Dwyer and Erdahl, 1995; Muth and Ruppert, 1997; Henry and Grizzle, 2004; Bohl *et al.*, 2009). Field studies are also challenging as these generally rely on coarse observations of fish which are marked or tagged (Parker *et al.*, 2015). Nonetheless, once initial laboratory trials have been performed field studies are needed to validate the results to provide information on long term affects such as altered habitat use, changes in migratory behaviour, feeding, reproductive behaviour and mortality as a result of continuous operation (Ostrand *et al.*, 2009). In this way, it is important that the test location is thoroughly assessed before deployment of any electric barrier (Ostrand *et al.*, 2009). This assessment should consider the species assemblages in the area including both native and invasive species. If electric field barriers are implemented to block invasive species without accurate knowledge of the effects on native populations, non-target mortality could be high. For example, whilst an electric barrier used to block sea lamprey was found to be effective, the non-target species mortality was also high (Johnson *et al.*, 2021).

2.4 Summary

There is a growing need to control fish movements to both guide native fish to safer routes and to block the further spread of invasive species. Electric fields are one proposed stimuli which could be utilised to control fish movements. This review has highlighted key biases and gaps in current knowledge involving both fundamental physiological fish responses to electric fields and its potential use for guidance. Firstly, whilst the threats of river infrastructure are well documented for European eel, the use of behavioural stimuli to mitigate these impacts has received limited attention. Further, the research that has been performed has focused on the use of acoustics and light. Thus, there is a lack of knowledge on both fundamental responses of eel to electric fields and its potential as a guidance system. Secondly, studies on behavioural stimuli for eel guidance has largely concerned downstream migrating adults. Meanwhile, upstream migrating juveniles (glass) and typically non-migratory yellow-phase life-stages have been neglected. Thirdly, most of the literature relating to fish responses to electric fields is in relation to optimising electrofishing (e.g. injury, capture efficiency). Whilst these studies provide initial outlooks on sensitivity of species to electric fields often the behaviours reported such as stunning will not be beneficial for developing electric guidance systems. Consequently, the results of these studies cannot be used as a direct comparison. Fourthly, accurate quantification of parameters (e.g. pulse frequency, width, voltage, waveform type) used in studies is sometimes lacking. In order to provide more robust comparisons and develop this area of research, assessing responses with respect to parameters set is crucial. Finally, research to date has tended to focus on the use of electric fields either for guiding native populations or blocking invasive species. However, direct comparisons between species and/or families to design selective fish guidance strategies is lacking. This is an important, but often missing, step in testing guidance systems before construction and implementation in the field.

Chapter 3 Finalised research aims & objectives

There is a growing need to develop effective mitigation strategies against the negative impacts of human modification on freshwater ecosystems. The use of behavioural stimuli such as electric fields could be used to guide native/desirable fish to safer routes of passage, to prevent the further spread of invasive species or alternatively a combination of both. Knowledge of the physiological and behavioural responses of fish to electric fields will ultimately aid management strategies.

The broad overall aim of this thesis was to:

1) Advance scientific knowledge in the response of fish to electric fields as a potential guidance system.

To meet this aim, an initial objective was formulated:

1) Review current literature to identify research trends, biases, and knowledge gaps on the conservation of European eel, cyprinid invasive species management and fish response to electric fields.

Through the completion of the objective 1, the following additional objectives were formulated to address current research gaps and meet the overall aim of this thesis:

2) Quantify the physiological responses of fish to PDC electric fields.
3) Quantify the behavioural responses of eel to PDC electric fields.
4) Assess the effectiveness of electric fields with respect to water velocity for downstream migrating silver-phase eel guidance.
5) Quantify the behavioural responses of yellow-phase eel to electric fields with respect to direction of travel.
6) Compare the electrosensitivity of cyprinid and anguillid species.

The research conducted in this thesis and how individual chapters meet set objectives are summarised in (Figure 3.1).

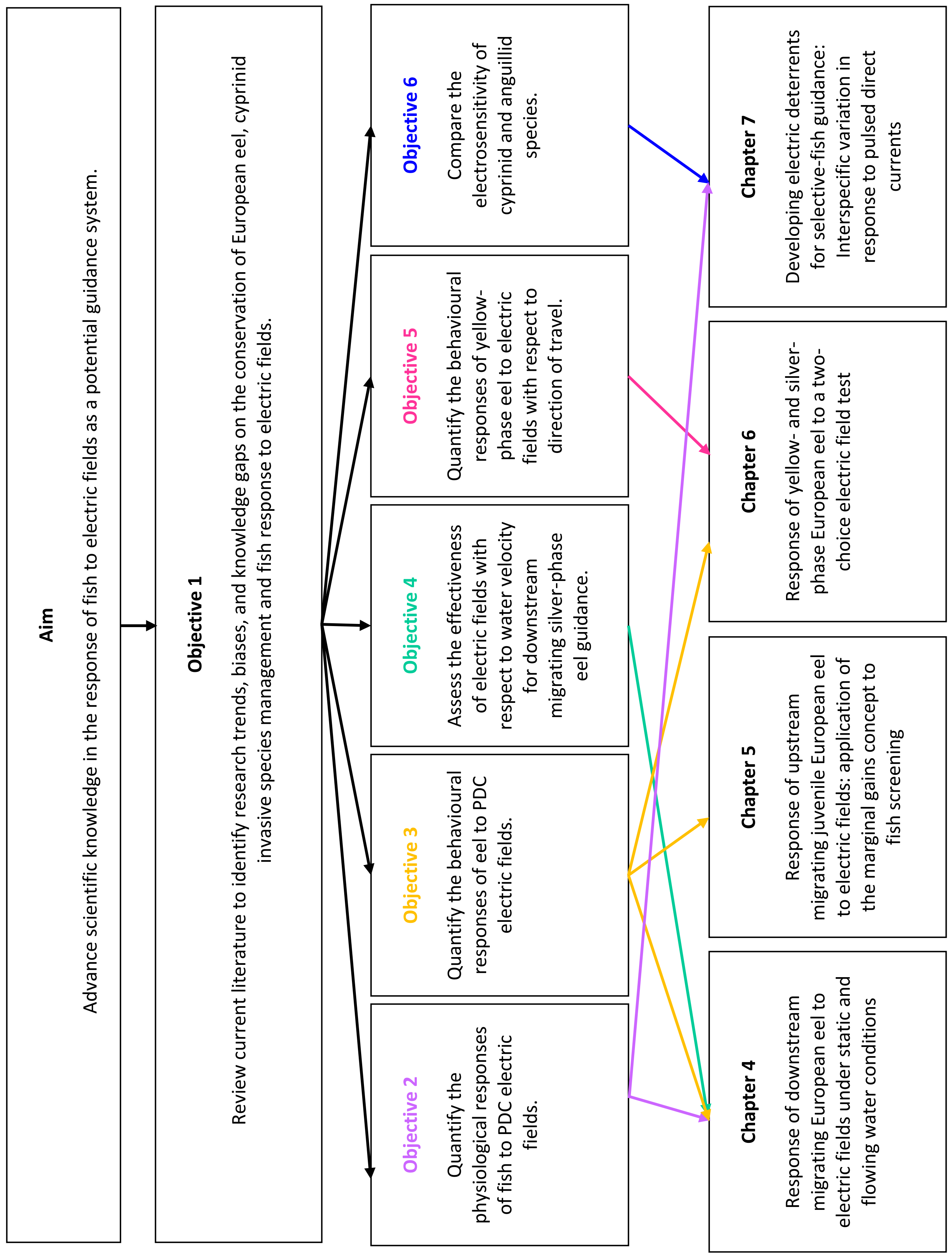


Figure 3.1. Schematic summary of thesis aim and objectives with corresponding results chapters (4 – 7) undertaken to meet these.

Chapter 4 Response of downstream migrating European eel to electric fields under static and flowing water conditions

4.1 Summary

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 (≈ 0.15 Vcm^{-1} and ≈ 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.

4.2 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; Larinier, 2008; Wiśniewolski, 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 (Vetter *et al.,* 2015), bubbles (Zielinski *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 has been classified as critically endangered throughout its range (Drouineau *et al.*, 2018; Pike *et al.,* 2020) because recruitment has declined by 90 – 99% since the 1980s (ICES, 2016). 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-phase) 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; Radinger *et al.,* 2021). 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 e*t 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. McLain, 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, 2016). 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 physiological 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* (≈ 0.15 Vcm^{-1}) and *tetany* (≈ 0.3 Vcm^{-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.

4.3 Methods

4.3.1 Experimental set-up

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

4.3.1.1 Experiment 1- static water tests

Experiments were conducted in a clear glass (10 mm thick) rectangular tank (1.5 m long x 0.6 m wide x 0.23 m deep) (Figure 4.1). 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 the eel directly contacting metal electrodes. Water (conditioned tap water) depth was maintained at 15 cm.

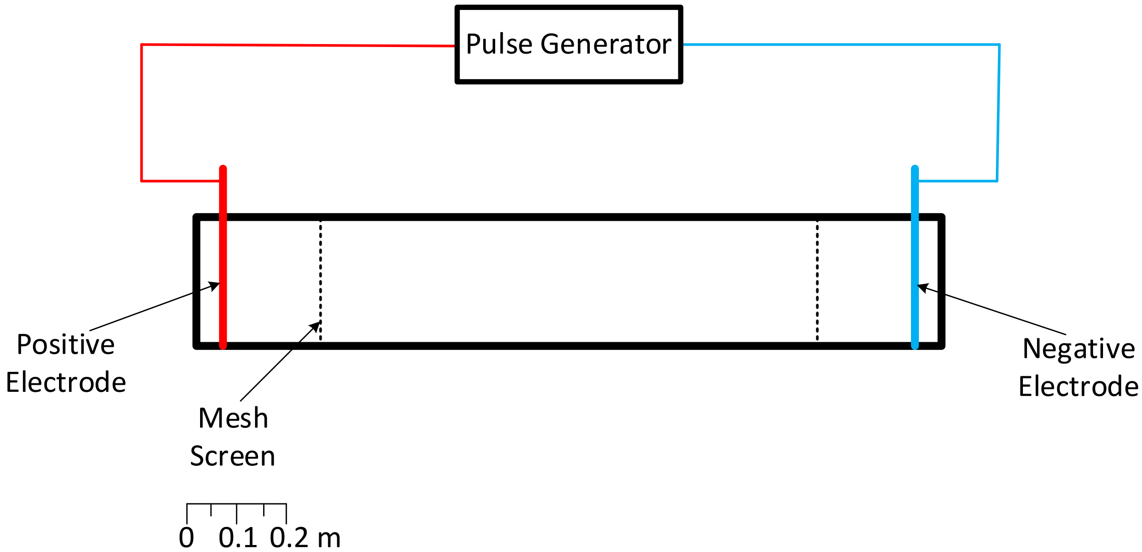


Figure 4.1. Section of rectangular tank used to quantify thresholds of eel response to electric fields under static water conditions. Two aluminium electrodes were placed at either end of the tank and connected to a voltage pulse generator used to create the electric field.

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.

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 (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) (Figure 4.2) to record peak-to-peak voltage. Electric field maps were generated for all output voltages and waveforms. Ambient water conductivity during mapping was 630 µS.cm^{-1}.

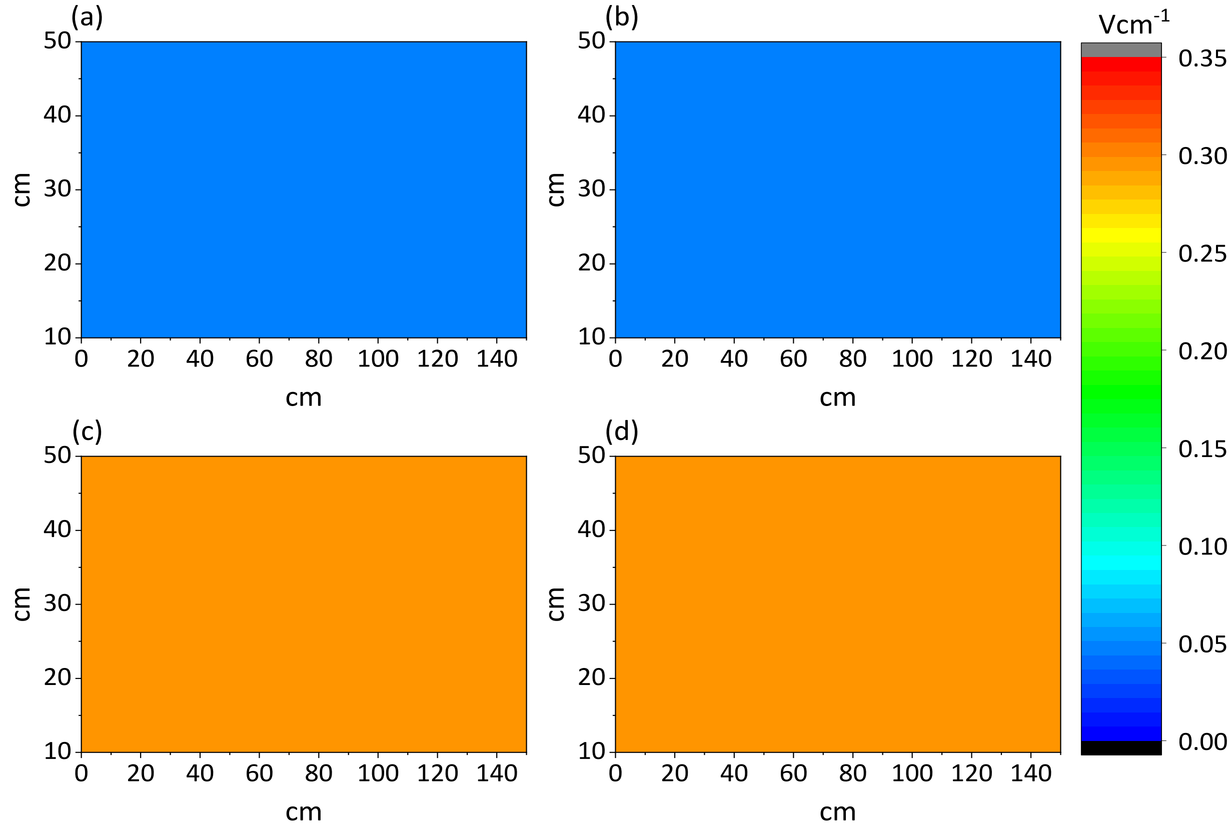


Figure 4.2. Electric field (Vcm^{-1}) generated in the static water tank. (a) and (b) represent field strengths obtained with a pulse generator output of 7 V. (c) and (d) represent field strengths obtained with a pulse generator output of 42 V. (a) and (c) were measured at 5 cm depth and (b) and (d) at 10 cm depth from the water surface. Electric field strength was uniform across the tank and proportional to input voltage.

4.3.1.2 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 (Figure 4.3). 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 electrical 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 1cm 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.

(b)

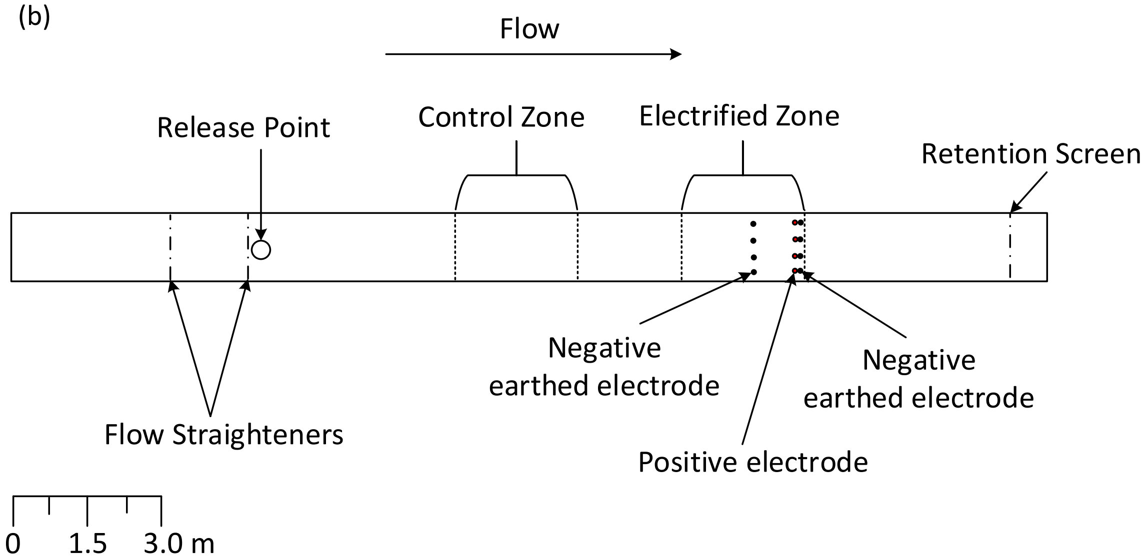


Figure 4.3. (a) Indoor 21 m recirculatory flume at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton and (b) Plan of the flume set-up for flowing water tests with the 3-electrode array used to investigate eel response to electric fields. The first (negative) 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 [± SD] upstream and downstream water depth of 32.4 [± 1.41] cm and 37.2 [± 0.61] cm, respectively. The 1.0 ms^{-1} water velocity was achieved by switching on a third pump (0.23 m^3s^{-1}; total discharge 0.47 m^3s^{-1}) and by tilting the flume 0.4 degrees downstream. The downstream weir was lowered for the higher water velocity to produce mean [± SD] upstream and downstream water depths of 29.5 [± 0.89] cm and 37.8 [± 0.60] 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; 25 frames s^{-1}) mounted above the flume to ensure complete coverage. Two observation areas were defined: a 2.5 m control zone, 5.5 m from the release point where no electric field was detected (Figure 4.3b), 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.

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) (Figure 4.4).

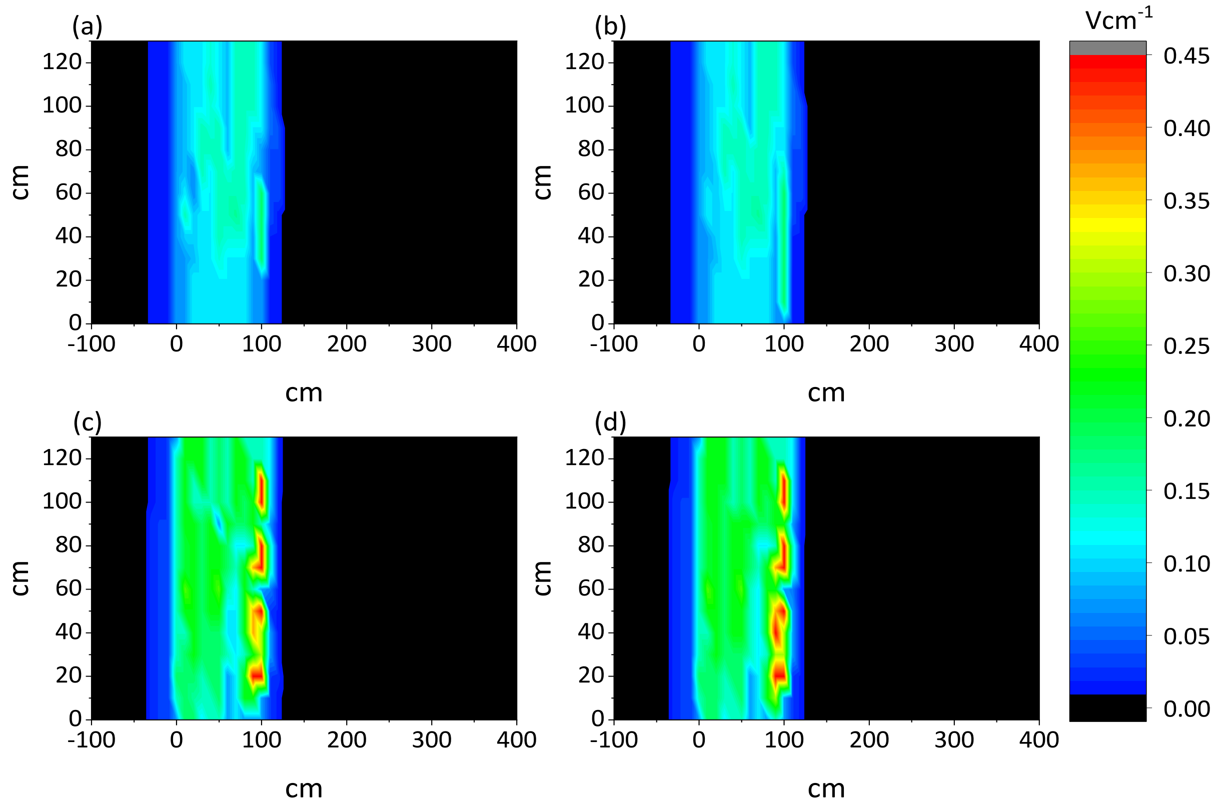


Figure 4.4. Electric field (Vcm^{-1}) generated during the flowing water tests. (a) and (b) represent mean *twitch* condition and (c) and (d) represent mean *tetany* condition. Flow direction is from left to right. The x axis represent the longitudinal distance along the flume; 1 m upstream (x = −100) and 4 m downstream of the first 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.

4.3.2 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 4.1). 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 [± SD] (Experiment 1) = 12.8 [± 1.23] °C, (Experiment 2) = 9.96 [± 1.55] °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 4.1. Collection date and numbers of adult (silver-phase) 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 [± SD] (°C)	Mean experimental temperature [± SD] (°C)
26 October 2017	40	1	2 - 8 November	13.20 [± 0.89]°C	13.40 ± [0.62]°C
24 November 2017	60	1 + 2	28 November - 6 December	Experiment 1: 10.7°C Experiment 2: 10.87 [± 0.79]°C	Experiment 1: 10.7 [± 0.07]°C Experiment 2: 11.72 [± 0.93]°C
15 December 2017	55	2	18 - 20 December	9.13 [± 1.62]°C	9.81 [± 1.61]°C

4.3.3 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 (Precision Gold N76CC).

4.3.3.1 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) (Figure 4.5). For the double pulse-2 Hz waveform the time between the pulses in the set of two (i.e. pulse break) was 50 ms. Square PDC waveforms have been used in previous research (Dawson *et al.,* 2006) and allow parameters (i.e. pulse frequency, 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). To generate the correct field strength, the input voltage on the pulse generator was divided by the distance between the electroplates and then verified using a custom-built probe connected to the oscilloscope.

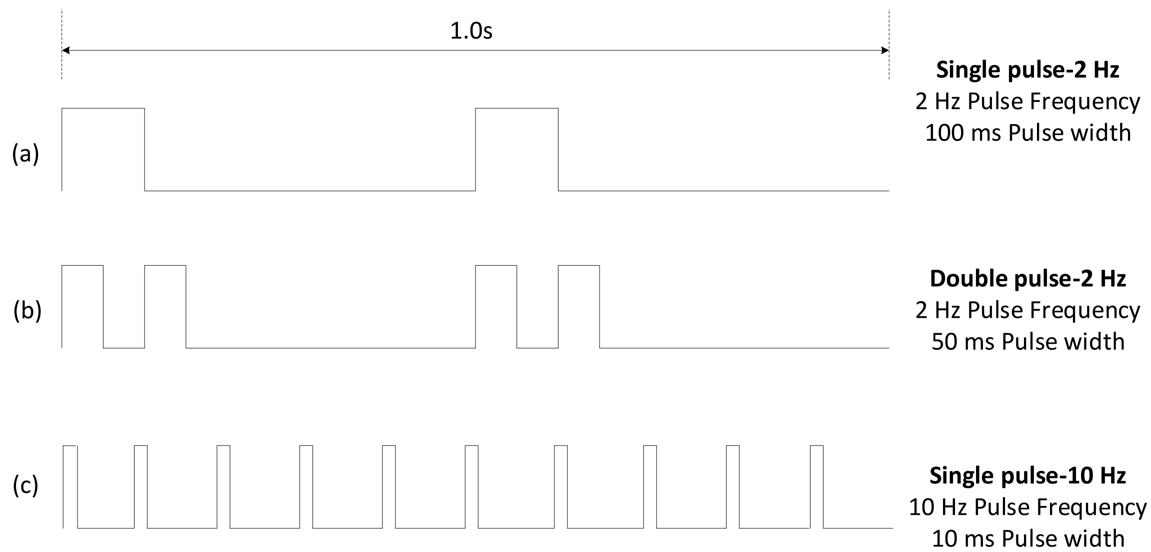


Figure 4.5. Three PDC waveforms: (a) single pulse- 2 Hz, (b) double pulse- 2 Hz, and (c) single pulse- 10 Hz waveforms used to investigate European eel (silver-phase) response to electric fields under static water conditions (Experiment 1).

One eel was placed in the experimental area between the mesh screens (Figure 4.1) and left for 10 minutes to acclimatise. 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 minute recovery. The 10 s – 10 s control – treatment cycle was repeated with field strength increased in increments of 0.05 Vcm^{-1} for every cycle until *tetany* was observed. The physiological 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 [± SD] = 13.0 [± 1.12]°C; mean end temperature = 13.0 [± 1.14]°C). At the end of each trial fish (n = 40) were weighed (mean mass [± SD] = 339.9 [± 89.5] g) and measured (mean total length [± SD] = 560.1 [± 49.7] mm).

4.2.2.2 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 (Figure 4.3b) for five minutes before released from that point. 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 [± SD] = 10.7 [± 1.63]°C; mean end temperature = 10.8 [± 1.63]°C) and water conductivity (HANNA HI98303 Conductivity Meter) (mean ambient water conductivity [± SD] = 631.3 [± 10.01] µS.cm^{-1}) were recorded at the start and end of each trial. Water depth (mean water depth downstream [± SD] = 37.4 [± 0.66] cm; mean water depth upstream = 31.0 [± 1.88] cm) and water velocity were recorded every five trials. At the end of each trial, fish (n = 98) were weighed (mean mass [± SD] = 338.3 [± 100.5] g) and measured (mean total length [± SD] = 566.2 [± 51.8] 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).

4.3.4 Fish behaviour and data analysis

4.3.4.1 Experiment 1- static water tests

The physiological metrics defined (Table 4.2) were based on experimental observations under the specified pulse frequencies and widths used.

Table 4.2. 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 fish 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, 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.

4.3.4.2 Experiment 2- flowing water testing

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 4.3). 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.

Table 4.3. Definitions of behavioural metrics; *total distance travelled*, *transit time* and *ground 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*

Within the flume, fish 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 4.4).

Table 4.4. 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 - 360^o turn in body position
Rejection	180^o 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 (Y/N) 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*, *ground speed and transit time* was analysed using Kruskal-Wallis Rank sum tests on pairs of treatments.

4.4 Results

4.4.1 Experiment 1- static water testing

4.4.1.1 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 (Figure 4.6). 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 pulse- 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.

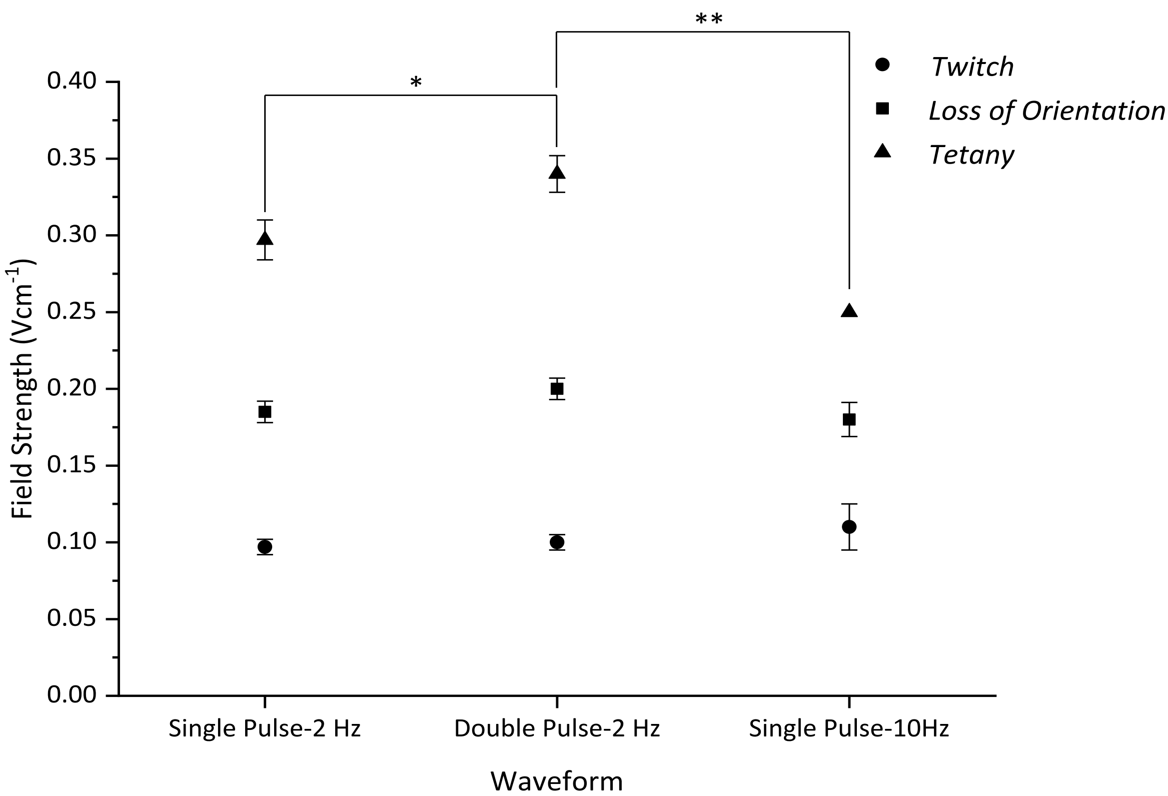


Figure 4.6. Mean threshold field strengths [± SE] for three physiological responses; *twitch*, *loss of orientation* and *tetany* exhibited by silver-phase European eel under three waveforms: single pulse-2 Hz, double pulse-2 Hz and single pulse-10 Hz. Note * denotes p < 0.05 and ** denotes p < 0.01.

4.4.2 Experiment 2- flowing water testing

4.4.2.1 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 (*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) (Figure 4.7). Field strength did not influence any of the tracking behavioural metrics (Table 4.5).

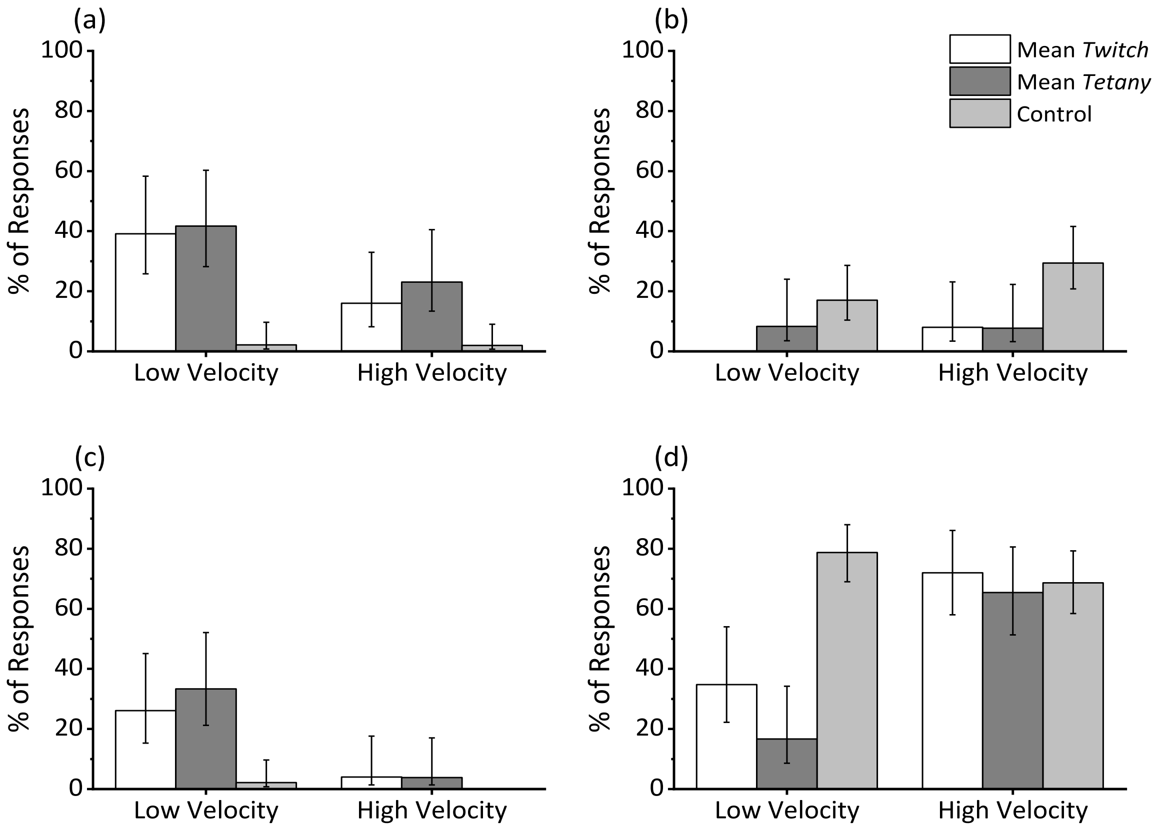


Figure 4.7. Mean percentage of all initial responses [± 95% CI] exhibited by European eel for the four behaviour metrics: (a) *acceleration*, (b) *change in orientation*, (c) *rejection* and (d) *no change* between the two treatment field strengths; mean *twitch* (≈ 0.15 Vcm^{-1}) and mean *tetany* (≈ 0.3 Vcm^{-1}) and control under the low and high water velocity.

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

Acceleration and *rejection* was more common under the low than high velocity treatment (*acceleration*: z = -2.22, p = 0.03, *rejection*: z = -2.83, p = 0.004), whereas *no change* was more frequent under the high than low velocity condition (z = 2.63, p = 0.009) (Figure 4.8). Water velocity had no effect on the occurrence of *change in 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%) (Figure 4.8). In contrast, under high velocity, *no change* was most common (68.6%), followed by *acceleration* (19.6%). A small proportion of eel exhibited *change in orientation* (7.84%) and *rejection* (3.92%).

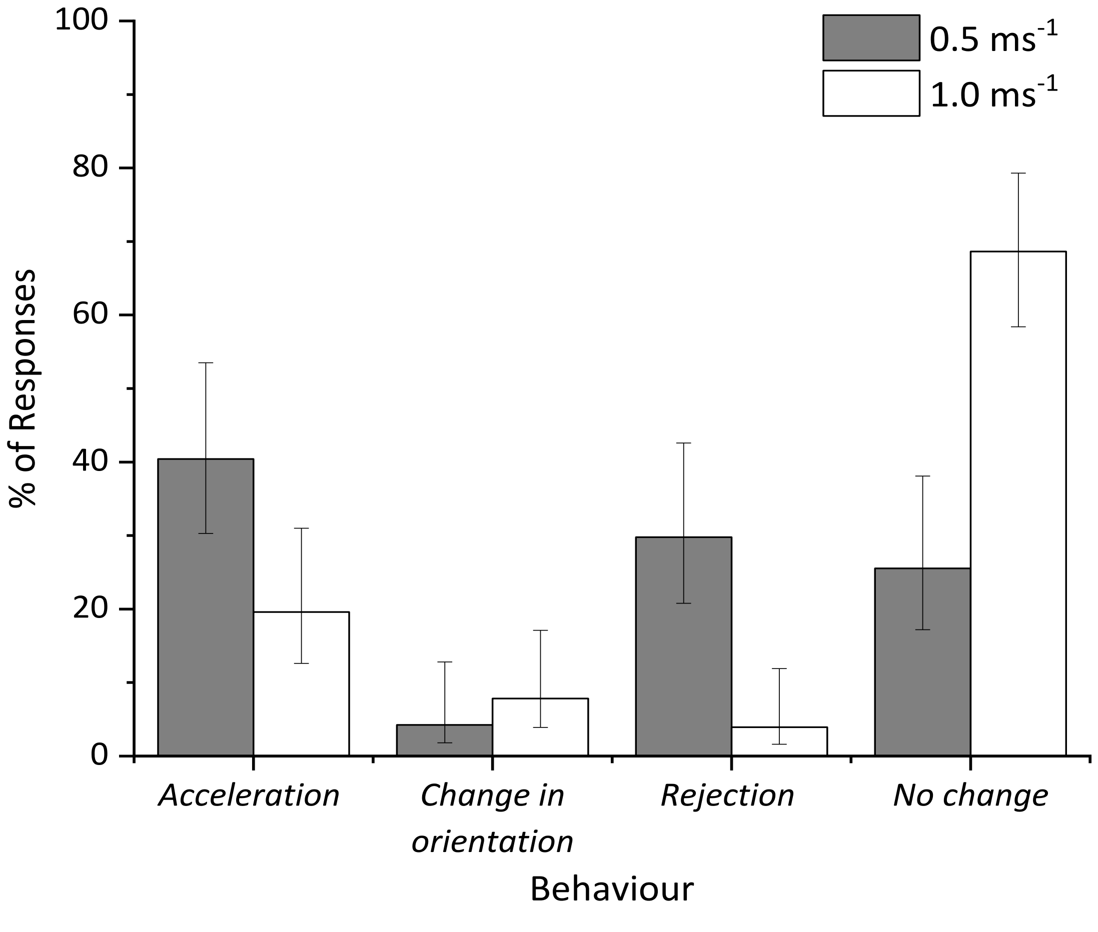


Figure 4.8. Mean percentage of initial responses [± 95% CI] exhibited by downstream migrating European eel observed for the four behavioural metrics; *acceleration*, *change in orientation*, *rejection* and *no change* under the two water velocities; 0.5 ms^{-1} and 1.0 ms^{-1}.

Both *total distance travelled* ($\chi^2(1) = 28.5$, $p < 0.0001$) and *transit time* was higher in the low velocity treatment ($\chi^2(1) = 43.9$, $p < 0.001$) (Table 4.5). In both high velocity treatments, the mean *ground speed* was higher than under the low velocity conditions ($\chi^2(1) = 24.7$, $p < 0.0001$).

Table 4.5. Mean [± SE] *total distance travelled*, *transit time* and *ground speed*, obtained from tracking analysis, across the six treatment groups.

Treatment	*Total distance travelled* (m), (Mean [± SE])	*Transit time* (s), (Mean [± SE])	*Ground speed* (ms^{-1}), (Mean [± SE])
Low Velocity, Mean *Twitch*	5.50 [± 0.88]	10.6 [± 2.26]	0.62 [± 0.05]
Low Velocity, Mean *Tetany*	7.41 [± 1.48]	16.4 [± 4.78]	0.61 [± 0.06]
High Velocity, Mean *Twitch*	3.15 [± 0.10]	4.25 [± 0.29]	0.80 [± 0.04]
High Velocity, Mean *Tetany*	3.68 [± 0.30]	4.65 [± 0.64]	0.86 [± 0.03]
Control (Low Velocity)	4.50 [± 0.55]	26.7 [± 8.07]	0.37 [± 0.02]
Control (High Velocity)	3.68 [± 0.18]	6.96 [± 0.96]	0.78 [± 0.06]

4.5 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 (e.g. Bearlin *et al.,* 2008 for Murray cod, *Maccullochella peelii peelii*), 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 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 for eel. 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 waveform. 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* is 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} (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.

Chapter 5 Response of upstream migrating juvenile European eel to electric fields: application of the marginal gains concept to fish screening

5.1 Summary

The decline in European eel (*Anguilla anguilla*) recruitment over the past half-century is partly due to river infrastructure that delays or blocks upstream migration to rearing habitat. Stimuli, such as electricity, can be used to modify the behaviour of downstream moving fish and guide them to preferred routes of passage at river infrastructure; but research on upstream migrating juvenile eel remains limited. The response of upstream migrating juvenile eel exposed to pulsed direct current (PDC) electric fields was investigated using a recirculatory flume. Eel were presented a choice of two routes upstream under either: (1) a treatment condition, in which the selection of one route resulted in exposure to High Electric Field (HEF) strength that was between 1.5 – 2 times stronger than the Low Electric Field (LEF) strength encountered in the alternative route; or (2) a control in which the electric field was absent in both routes. Under the treatment, five different mean HEF strengths (0.53, 0.77, 1.22, 2.17 and 3.74 Vcm^{-1}) were tested at one of two frequencies (2 and 10 Hz). Route choice, distance downstream of the first set of electrodes at which an initial response was observed and avoidance behaviours (*acceleration*, *retraction*, *switching* and *rejection*) were compared among treatments. For the 1.22, 2.17 and 3.74 Vcm^{-1} and under 2 Hz, eel preferred to pass the LEF route. Avoidance was greater in the HEF route and positively related to field strength. The distance of the initial response did not differ between routes, field strengths or frequency. Upstream migrating eel avoided electric fields indicating potential to develop this approach for fish guidance. Further work is needed to test prototypes in field settings, particularly in combination with traditional physical screens to water intakes as part of a process of applying the concept of marginal gains to advance environmental impact mitigation technology.

5.2 Introduction

The catadromous European eel has experienced substantial declines in escapement and recruitment since the 1970s (ICES, 2019). Juvenile (glass) eel recruitment has reduced by more than 90% in some catchments (e.g. River Thames; Gollock *et al.,* 2011), with this life-stage representing an important population bottleneck (Bult and Dekker, 2007; Gollock *et al.,* 2011). A decline in recruitment is translated to a reduction in eel density in freshwater habitats and ultimately lower spawning escapement of adults (Dekker, 2018). As both the juvenile and adult life-stages have historically maintained fisheries of high commercial importance (Moriarty and Dekker, 1997; Dekker, 2018), legislation has been enacted (e.g. Eel Regulation, European Council Regulation 1100/2007) to promote sustainable management and aid recovery across its range (Righton and Walker, 2013; Castonguay and Durif, 2016).

There are several potential causes for the decline of European eel, including pollution (Geeraerts *et al.,* 2011), habitat loss (Feunteun, 2002), overfishing (Briand *et al.*, 2003), and non-native parasites (Newbold *et al*., 2015; Currie *et al*., 2020). In the estuarine and freshwater environment, anthropogenic structures (e.g. barrages, dams, and weirs) can block or delay both the downstream adult (e.g. Piper *et al.*, 2013, 2017) and upstream juvenile migration (e.g. Piper *et al.,* 2012; Kerr *et al.,* 2015; Vowles *et al.*, 2015, 2017), representing a substantial challenge to escapement and recruitment (Feunteun, 2002). River infrastructure can also cause direct mortality of juvenile and adult eel entrained into water intakes, e.g. at hydroelectric or thermal power plants (Bryhn *et al.,* 2014; Dekker, 2018). As eel are entrained into water intakes to abstraction points, mortality can occur due to sharp changes in water temperature (e.g. in cooling water systems) and pressure, and mechanical damage caused by striking moving parts (Larinier, 2008; Calles *et al.*, 2010; Bryhn *et al.,* 2014; Kemp, 2015). Historically, research has been biased to the risks of infrastructure faced by downstream moving adults, while the threats to upstream migrating juvenile eel are less well understood (Åström and Dekker, 2007). Mitigating the impacts of river infrastructure on juvenile eel provides a feasible and important management option that can be adopted in the estuarine and freshwater domain.

Traditionally focusing on the adult life-stage, physical screens reduce or prevent the passage of eel into water intakes. However, these are not wholly effective and can incur high construction and maintenance costs (Hadderingh and Jager, 2002; Calles *et al*., 2010). Due to their small size, juvenile eel are unlikely to be blocked by existing screens designed for larger target species and life-stages and hence require expensive retrofits with very narrow-spaced designs (1-2 mm) (Sheridan *et al.*, 2014). Furthermore, eel may be impinged on poorly designed screens and suffocate if they are unable to escape because the velocities at the screen face exceed their burst swimming capabilities (Hadderingh and Jager, 2002; Calles *et al.*, 2010). Even if impinged eel can escape, like other species of fish (e.g. Swanson *et al.,* 2005 for delta smelt, *Hypomesus transpacificus*), they are likely to suffer physical injury due to the abrasion experienced when contacting the screen surface, resulting in secondary infection and delayed mortality.

Behavioural deterrents employed in fish guidance and exclusion, such as those based on acoustics (Sonny *et al*., 2006), bubbles (Patrick *et al.*, 1985; Flores Martin *et al.*, 2021), light (Ford *et al*., 2019) and electricity (Bajer *et al.*, 2022), have been developed as an alternative to traditional physical screens. They have the advantage of not requiring physical or mechanical elements, and thus lack the potential to cause impingement and abrasion. Unfortunately, they tend to be less effective than physical screens, resulting in being promoted by regulatory agencies only when physical exclusion screens are impractical (Turnpenny and O'Keeffe, 2005). However, behavioural deterrents may have an important role to play when used in conjunction with physical screens to reduce the negative impacts of the latter and improve overall system efficiency. For example, under experimental conditions acoustic stimuli have been used to enhance the effectiveness of physical screens in guiding downstream moving eel (Deleau *et al.*, 2020b). This approach is based on applying the concept of Marginal Gains to advance environmental impact mitigation technology. Originally developed in the field of performance sport (e.g. Hall *et al.,* 2012), the principle of Marginal Gains is that small incremental improvements in any process amount to a significant improvement when considering the system holistically. One of the main advantages of this approach in this context is that if the behavioural deterrents work then they can provide a cost-effective addition to physical and mechanical screening systems, with relatively low capital and maintenance expense compared to fine-screen retrofits (Turnpenny *et al.,* 1998; Turnpenny and O'Keeffe, 2005). For eel, acoustics (Sand *et al.*, 2000; Piper *et al.*, 2019; Deleau *et al.*, 2020b) and light (Hadderingh *et al.,* 1992; 1999) have garnered most interest, indicating variable efficacy, while electricity has received limited attention (e.g. McGrath *et al.*, 1969).

Designing a suitable electric deterrent for a target species requires testing of the most effective field characteristics (e.g. field strength and pulse frequency). For example, a field strength that is too weak would be ineffective, while one that is too strong may stun the fish, rendering it incapable of exhibiting the voluntary response needed, or even worse, injuring or killing it due to an excessive electric shock. The use of electric fields is likely to be more effective in the guidance of fish moving in the upstream, rather than downstream, direction. Should an individual be shocked and temporarily paralysed by an ill designed device, an upstream moving fish will be swept downstream away from the field where it should recover (Vibert, 1967). Conversely, an incapacitated downstream moving fish would be swept into the field and possibly into the dangerous area (e.g. turbine intake) that the device was designed to screen. Pulse frequency can also influence fish behaviour. For example, greater avoidance (i.e. failure to cross an electric field array) to an electric barrier was observed under a 3 Hz as opposed to 2 Hz pulse frequency for steelhead (*Oncorhynchus mykiss*) and Pacific lampreys (*Entosphenus tridentatus*) (Mesa and Copeland, 2009). However, while increasing frequency might be beneficial for effectively deterring fish movement, other studies suggest that more injuries can occur as frequency increases (e.g. silver carp; Culver and Chick, 2015).

This study investigated the response of upstream migrating juvenile (glass) eel to pulsed direct current (PDC) electric fields when offered a choice of route in an experimental flume. In the test section, the flume was divided longitudinally into two routes of equal dimension by a series of eight earthed vertical electrodes, presenting the upstream swimming eel with an opportunity to select a route: (1) of differing field strength (High or Low Electric Field Strength – HEF / LEF) under the treatment conditions; or (2) a control in which the electric field was absent in both routes. The influence of electric field strength and frequency on: (1) route selection, (2) distance from the electrodes at which an initial response was exhibited by upstream moving juvenile eel, and (3) nature (*acceleration, retraction, switching* and *rejection*) of avoidance response was investigated. We predicted that: (1) eel would prefer (deviation from the 50:50 route selection expected if choice was random) to pass the LEF route when offered a choice; and (2) distance of the initial response from the source of the EF and (3) occurrence of avoidance behaviour exhibited would be positively related to field strength, and that these relationships would be stronger under the high frequency (10 Hz) condition.

5.3 Methods

5.3.1 Experimental set-up

The experiment was conducted in an indoor open channel flume (12.0 m long, 0.3 m wide and 0.4 m deep) (Figure 5.1a). Within the flume a 2.04 m long section was isolated by a downstream flow straightener and upstream plastic mesh screen (mesh size: 0.28 x 0.79 mm) (Figure 5.1b). Note an upstream flow straightener was also installed outside the experimental area (3 m upstream of the upstream mesh screen). Eight earthed cylindrical steel electrodes (80 cm long x 1 cm diameter) were installed longitudinally down the centre of the flume at 12 cm intervals, dividing the channel into two routes that under the treatment conditions were defined as either High (HEF) or Low Electric Field (LEF) strength. In the HEF route, two positive and two negative earthed electrodes were installed laterally at 6 cm intervals (Figure 5.1b). The LEF route had two sets of two earthed electrodes (1^{st} and 2^{nd} dummy earthed electrodes, respectively) at the same longitudinal position as the positive and negative earthed electrodes in the HEF route. Earthed electrodes were arranged to best localise the electric field to the HEF route and prevent the field extending outside the experimental area. Each electrode was covered and secured with plastic mesh fabric to prevent direct contact by the eel.

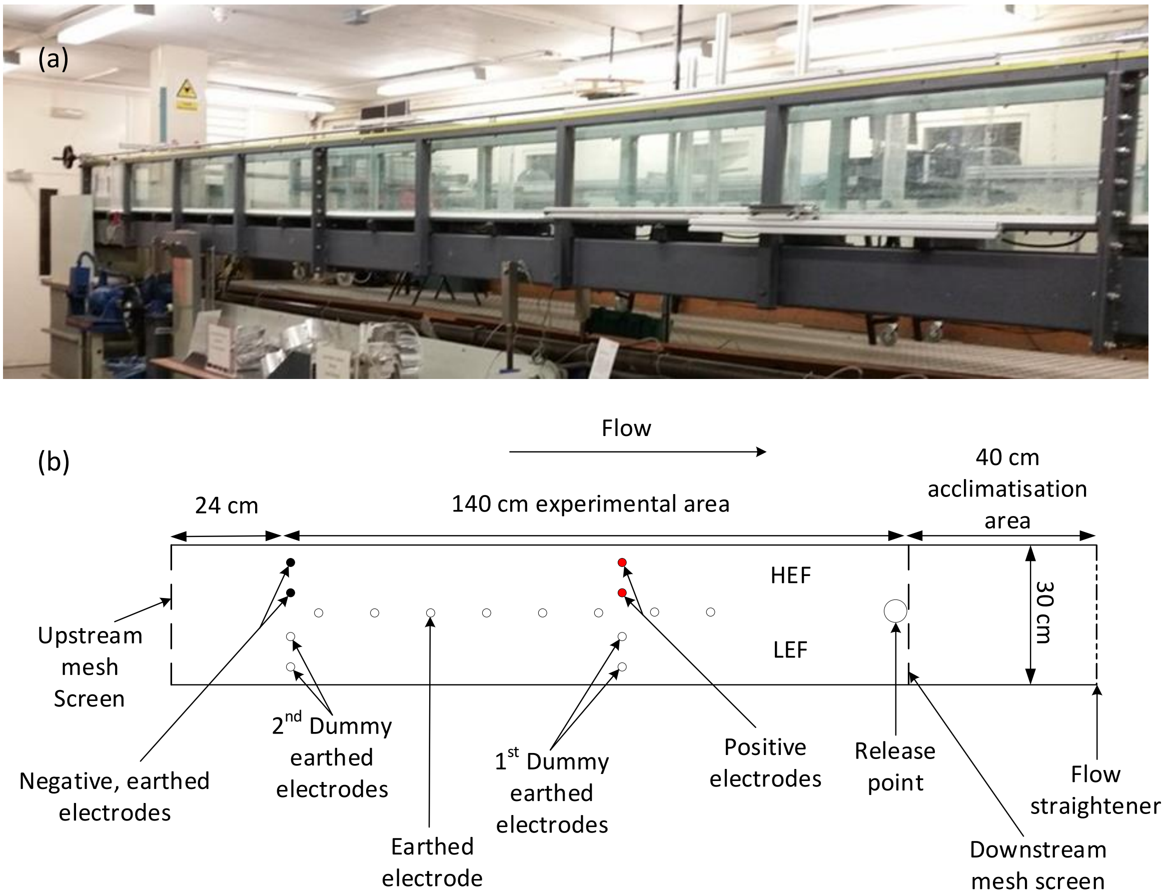


Figure 5.1. (a) Indoor 12 m recirculatory flume used for experimental trials and (b) Plan view of the experimental set-up used to investigate route choice of upstream moving juvenile European eel in response to encountering electric fields of differing strength. The flume was divided by eight centrally placed earthed electrodes separated 12 cm apart. Two positive and two negative earthed electrodes were installed to create a High Electric Field (HEF) strength route along one side of the channel. An adjacent Low EF (LEF) strength route was created by having two sets of two earthed electrodes (1st and 2nd dummy earthed electrodes, respectively) at the same longitudinal position as the positive and negative earthed electrodes in the HEF.

A black screen was placed alongside the flume to prevent disturbance to the fish by the observers. Six CCTV cameras (SWANN 1080p; 1920 X 1080 pixel resolution; 25 frames s^{-1}) were positioned above the experimental area (55 cm above the base of the flume) along the length of the flume. Two infrared lights (780 - 850 nm wavelength) were positioned at the downstream and upstream mesh to provide sufficient illumination for video capture under conditions of darkness.

Ambient light levels measured prior to the start of each trial were consistently less than 0.01 lux. Water depth and velocities were measured (Valeport Model 801) upstream of the last set of electrodes, within the electrode array (i.e. halfway longitudinally between the first and last set of electrodes), and downstream of the first set of electrodes after every five trials (Upstream: mean [± SD] = 18.5 [± 0.80] cm and 0.121 [± 0.008] ms^{-1}; Electrode Array: 18.4 [± 0.91] cm and 0.135 [± 0.009] ms^{-1}; Downstream: 17.8 [± 1.23] cm and 0.118 [± 0.009] ms^{-1}). The velocities were measured midway in the water column and at three lateral points across the flume. The test velocities were selected based on juvenile eel prolonged swimming capabilities of 0.2 - 0.4 ms^{-1} and maximum burst speeds of up to 0.5 ms^{-1} (Vezza *et al.*, 2020). This ensured that responses observed were a result of the electric field and not influenced by their swimming capabilities.

A Smith-Root Electrofishing pulse generator (BP-1.5 POW) was used to generate five different electric field strengths in the HEF route (Table 5.1) based on pilot testing of a subset of eel (n = 38). The mean electric field strength for either HEF or LEF was calculated over all the points measured in that route (HEF/LEF) throughout the experimental area. Two different pulse frequency PDC waveforms were implemented: (a) 2 Hz (100 ms pulse width) and (b) 10 Hz (20 ms pulse width) (Figure 5.2). PDC waveforms with these pulse frequencies were selected based on evidence that frequencies < 15 Hz reduce injuries in eel (Reynolds and Holliman, 2004) while providing an effective deterrent in other species (e.g. 2 Hz: white sturgeon, *Acipenser transmontanus*, Ostrand *et al.*, 2009; 10 Hz: fathead minnows, *Pimephales promelas*, Utz *et al.*, 2017). Pulse widths were generated by maintaining the same duty cycle (20%) between frequencies. Hence, in total there were 10 treatment conditions and one control (Table 5.1).

Table 5.1. The characteristics of the electric fields generated in adjacent High (HEF) and Low Electric Field (LEF) strength routes in an experimental flume under 10 treatments and a control. The experiment investigated the influence of electric field strength on route choice of upstream moving juvenile European eel. The number of replicates (n) for each treatment is provided. Note the High/ Low Electric field strengths were equivalent under both 2 and 10 Hz conditions.

Pulse Generator Output (V)	High Electric Field (HEF) Strength (Vcm^{-1})		Low Electric Field (LEF) Strength (Vcm^{-1})		Replicates (n)
	Mean [± SE]	Range	Mean [± SE]	Range	
0 (Control)	0	0	0	0	21
10	0.53 [± 0.06]	0 - 1.48	0.27 [± 0.03]	0 – 1.11	2 Hz: 25 10 Hz: 25
15	0.77 [± 0.08]	0 - 2.22	0.44 [± 0.04]	0 – 1.48	2 Hz: 23 10 Hz: 25
20	1.22 [± 0.13]	0 - 3.70	0.71 [± 0.06]	0 – 2.59	2 Hz: 23 10 Hz: 25
25	2.17 [± 0.22]	0 - 5.56	1.28 [± 0.14]	0 – 4.44	2 Hz: 24 10 Hz: 22
30	3.74 [± 0.34]	0 - 9.26	2.42 [± 0.22]	0 – 7.41	2 Hz: 26 10 Hz: 24

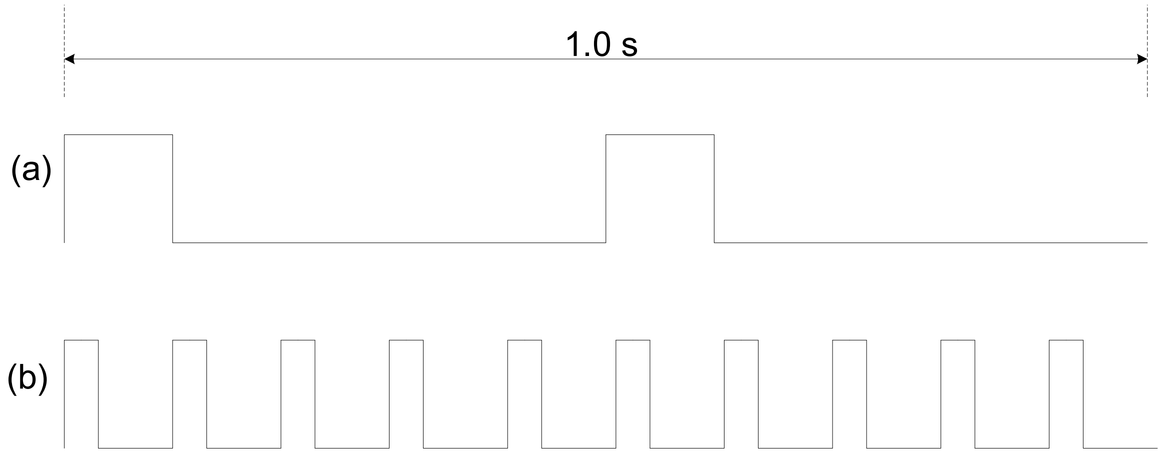


Figure 5.2. PDC frequencies (a: 2 Hz; b: 10 Hz) used to investigate juvenile eel response to electric fields in flowing water.

The electric field was mapped using a potential probe comprising two-point conductors 27 mm apart connected to an oscilloscope (Gwinstek GDS-1052-U) via a differential probe module (Probemaster 4232). Measurements were taken in a grid at a spacing of 10 cm in the x and 5 cm in the y directions at a water depth of 10 cm (from the surface) to record peak-to-peak voltage (Figure 5.3). Field strength was calculated as the quotient of the peak-to-peak voltage and the distance between the two-point conductors. Maps of the electric field were created for all five HEF strengths, under both the 2 and 10 Hz pulse frequencies (Figure 5.3). Ambient water conductivity was 580 µS.cm^{-1}.

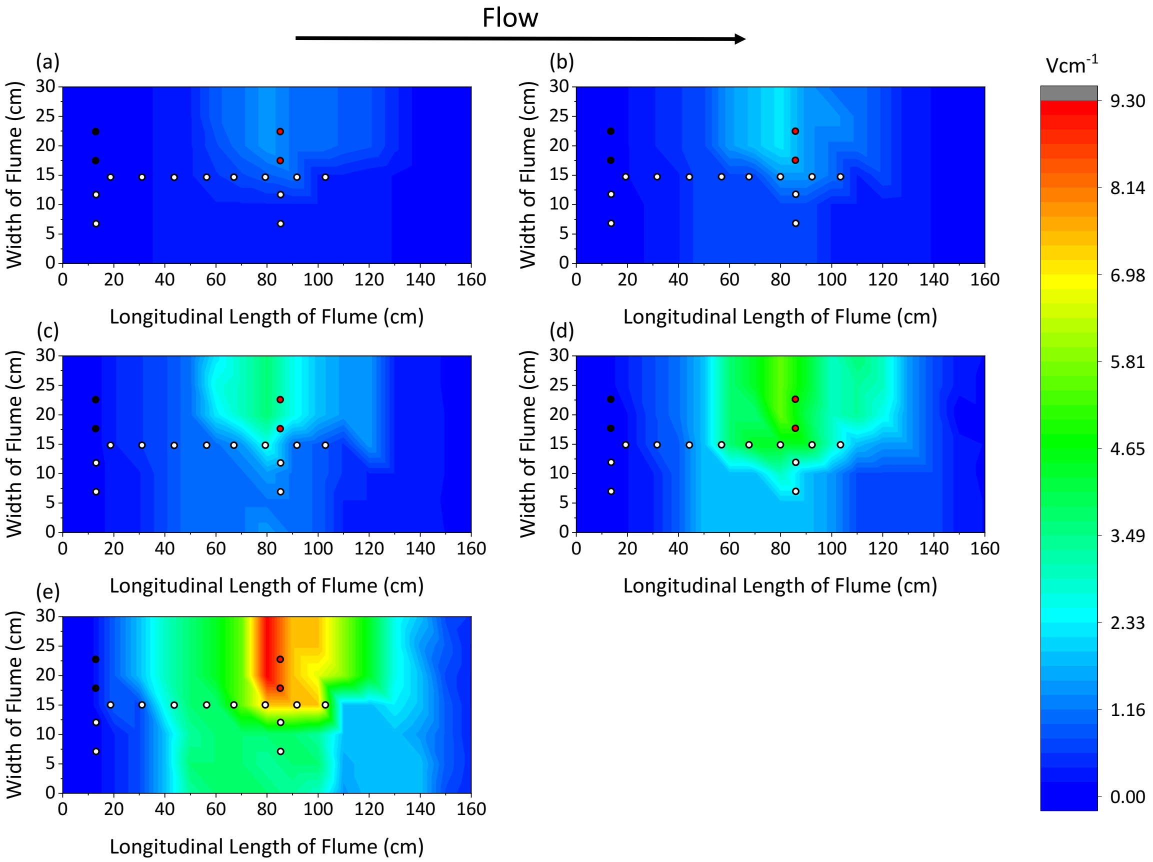


Figure 5.3. Electric field (Vcm^{-1}) generated by the pulse generator output of (maps represent both 2 and 10 Hz frequencies as field distribution was the same): (a) 10 V (Mean HEF Strength: 0.53 Vcm^{-1}), (b) 15 V (Mean HEF Strength: 0.77 Vcm^{-1}), (c) 20 V (Mean HEF Strength: 1.22 Vcm^{-1}), (d) 25 V (Mean HEF Strength: 2.17 Vcm^{-1}) and (e) 30 V (Mean HEF Strength: 3.74 Vcm^{-1}). The x axis represent the longitudinal distance along the flume and the y axis the width of the flume. Centrally earthed electrodes (white dots) were positioned at x = 18, 30, 42, 54, 66, 78, 90, and 102 cm and at y = 15 cm. Positive electrodes (red dots) were positioned at x = 84 cm and y = 18 and 24 cm. Negative earthed electrodes (black dots) were positioned at x = 12 cm and y = 18 and 24 cm. Dummy earthed electrodes (white dots) were at (84, 6) and (84, 12) and (12, 6) and (12, 12). Measurements were taken at 10 cm water depth from the surface.

5.3.2 Fish husbandry

Glass eel (batch of 200 g) were captured from the River Severn by UK Glass Eel Ltd on 25 February 2019 and transported in chilled river water (8°C) to the International Centre for Ecohydraulics Research laboratory at the University of Southampton. Fish were held in a porous container in the sump of the flume where the water was chilled to 8°C at the time of their arrival and increased gradually by 2°C daily until a target temperature of 12°C was reached. Daily sump temperatures were recorded manually and with submersible temperature loggers (mean holding sump acclimation temperature [± SD] = 12.5 [± 0.59]°C). Two aquarium air pumps were used to provide aeration. Fish health and water quality was monitored daily to ensure consistent conditions (pH: 7.8 - 8.4, Ammonia: 0 ppm, Nitrite: 0 ppm, Nitrate: < 40 ppm).

5.3.3 Experimental procedure

Trials were conducted during hours of darkness (18:00 - 02:00 hr), to replicate the natural nocturnal migration of glass eel (Tesch, 2003), between 27 February and 8 March, 2019.

For each trial a single eel was removed from the holding tank and placed in a plastic tube secured at both ends with mesh coverings before being placed in a 0.4 m long acclimatisation zone located at the downstream end of the flume section (Figure 5.1b). Eel were allowed a minimum of 60 minutes to acclimatise, before being released centrally immediately upstream of the downstream mesh that separated the acclimatisation zone from the experimental area (release point, Figure 5.1b). After acclimation each trial lasted a maximum of 60 minutes or until the eel had passed through the final (most upstream) set of electrodes. Each eel was used once only. Treatment electric field strengths and pulse frequencies were alternated across trials and the side of the flume assigned HEF / LEF was switched daily to prevent side bias.

Flume temperature was maintained close to the target of 12°C (mean [± SD] = 12.6 [± 0.17]°C), as the migratory behaviour of glass eel is reported to decline below a threshold temperature range of around 11 – 12°C (Gascuel, 1986; McGovern and McCarthy, 1992; Jessop, 2003), and trials were terminated if the temperature exceeded 13°C. Ambient water conductivity (HANNA HI98303 Conductivity Meter; mean [± SD] = 582.8 [± 5.43] $\mu S.cm^{-1}$) and eel length (mean total length [± SD] = 7.04 [± 0.3] cm) and mass (mean body mass [± SD] = 0.42 [± 0.1] g) was measured at the start and end of each trial, respectively.

5.3.4 Fish behaviour

Analysis of video recordings allowed the characterisation and quantification of route choice and avoidance exhibited (Table 5.2) as eel passed through the experimental area (Figure 5.1b). Behaviour was recorded during the entire trial, and in the event that an eel exhibited more than one response type it was assigned that of the highest magnitude (1 - 5) (hierarchy of response adapted from Vowles *et al.*, 2014, Table 5.2).

Table 5.2. Definitions of different categories of avoidance behaviours exhibited by upstream migrating juvenile eel on encountering an electric field in a flume. The response is ranked in a hierarchy of magnitude from 1 (lowest) to 5 (highest) (Adapted from Vowles *et al.,* 2014).

Metric	Definition
(5) Rejection	180^{o} turn in body position and downstream movement for at least one body length
(4) Switching	Movement from one route (HEF/LEF) to the other
(3) Retraction	Recoil of body in direction of travel of at least half body length
(2) Acceleration	Increase in swimming speed
(1) No change	No change in swimming speed or body orientation

Image analysis software (Logger Pro v. 3.8.2, Vernier Software) was used to obtain x and y spatial coordinates for the downstream distance (cm) from the positive electrodes in the HEF and the first dummy earthed electrodes in the LEF at which the initial response (any of the defined behaviours in Table 5.2 observed in the experimental area) occurred.

5.3.5 Statistical analyses

Statistical analyses were conducted using R 4.0.2 (R Core Team, 2020). Normality was assessed using the Shapiro-Wilk test. Attempts were made to transform data to achieve normal distributions, and if unsuccessful, non-parametric tests were performed. A goodness-of-fit (χ^2) test determined whether the route choice (HEF or LEF) deviated from the 50:50 ratio expected if the selection was random (null hypothesis – equal probability of selecting either channel under both control and treatment conditions). For statistical purposes the route that was assigned the HEF during the treatment conditions was also designated as the HEF for the control, even though the electric field was absent. Due to the low number of observations of some of the behaviours (i.e. *rejection*), all defined responses (*acceleration*, *switching*, *retraction* and *rejection*) were combined as a single avoidance response. Differences between the routes, field strength and frequency for distance of initial response were analysed using separate Kruskal-Wallis tests. A generalised linear mixed model (GZLMM) with a binomial distribution was used to determine whether route choice (HEF or LEF), field strength or frequency influenced avoidance behaviour. Eel-ID was included as a random effect as some individuals sampled both routes (HEF and LEF) and so have two responses.

5.4 Results

5.4.1 Route choice

The percentage of eel that passed through the LEF route did not differ from 50% under the 0 Vcm^{-1} control, 0.53 Vcm^{-1} and 0.77 Vcm^{-1} treatments ($p > 0.05$) (Figure 5.4). There was also no significant deviation from 50% LEF passage in the 10 Hz treatment for 1.22, 2.17 and 3.74 Vcm^{-1} ($p > 0.05$) (Figure 5.4). Conversely, more eel passed through the LEF route in the 2 Hz treatment for 1.22, 2.17 and 3.74 Vcm^{-1} with a significant deviation from 50% (1.22 Vcm^{-1}: $\chi^2(1) = 7.35$, $p = 0.007$, 2.17 Vcm^{-1}: $\chi^2(1) = 5.26$, $p = 0.02$ and 3.74 Vcm^{-1}: $\chi^2(1) = 6.76$, $p = 0.009$) (Figure 5.4).

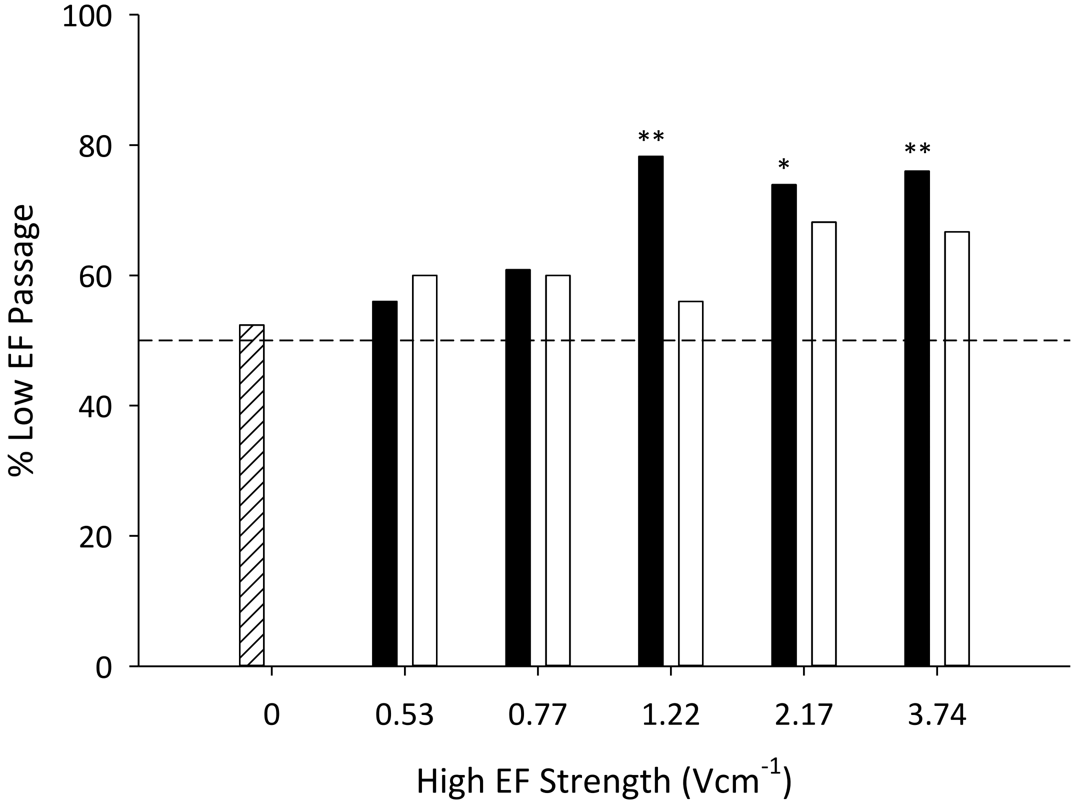


Figure 5.4. Percentage of upstream migrating juvenile eel that passed the Low Electric Field (LEF) route under the five High EF Strengths (0.53, 0.77, 1.22, 2.17 and 3.74 Vcm^{-1}) for both 2 Hz (solid bars) and 10 Hz (clear bars) treatments. Control (0 Vcm^{-1}) is shown as white hatched bar. The dashed line indicates the expected (50% frequency) random selection if electric field strength has no influence on route choice. Note * denotes $p < 0.05$ and ** $p < 0.01$.

5.4.2 Distance of initial response

Distance of initial response was assessed only for those that occurred downstream of the positive electrodes, any response that occurred upstream was omitted (n = 7). Route had no effect on the distance of initial response ($\chi^2(1) = 0.39$, $p = 0.53$). Consequently, data was aggregated for comparison between field strength and frequency. There was no effect of field strength ($\chi^2(4) = 1.1$, $p = 0.89$) or frequency ($\chi^2(1) = 0.61$, $p = 0.44$) on the distance of initial response (Figure 5.5).

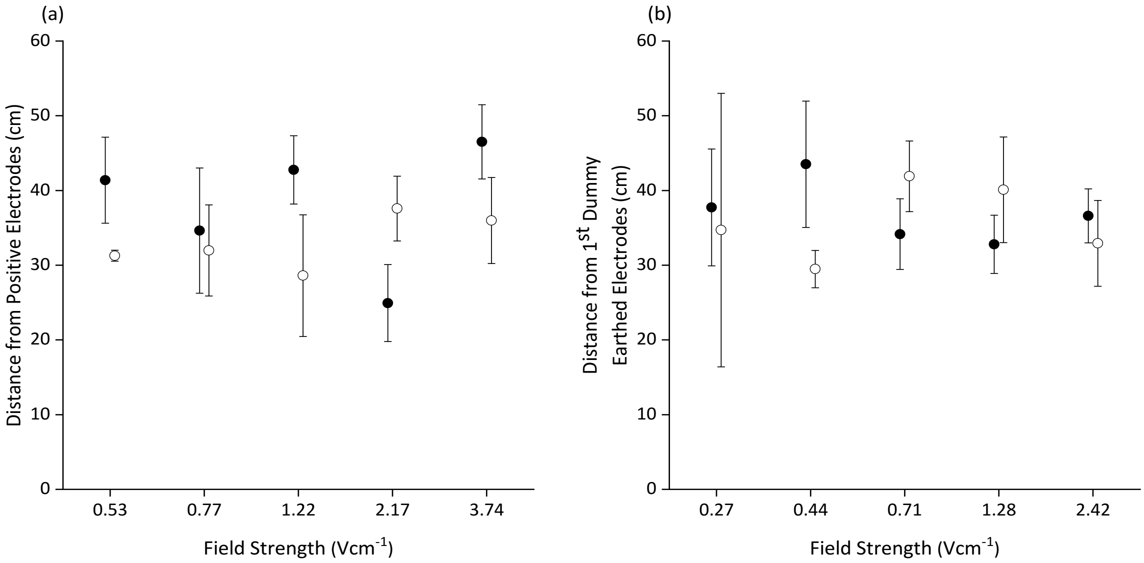


Figure 5.5. Distance (cm) of initial response [± SE] from positive and 1st dummy earthed electrodes in both (a) HEF and (b) LEF route, respectively, for upstream migrating juvenile eel in the 2 Hz (solid circles) and 10 Hz (clear circles) treatment.

5.4.3 Avoidance behaviour

The exhibition of avoidance differed with route selected ($\chi^2(1) = 4.75$, $p = 0.03$) with more eel responding in the HEF (73.7%) than the LEF (63.0%) route (Figure 5.6). The most common behaviour exhibited in the HEF was *switching* (44.0%), whereas *no change* was more frequent in the LEF route (37.0%).

As avoidance differed between routes, the results in the HEF and LEF were analysed separately to enable comparisons between field strength and frequency. For the HEF, behaviour was influenced by field strength ($\chi^2(5) = 25.5$, $p < 0.001$), with eel more likely to exhibit avoidance under 2.17 Vcm^{-1} (93.1%, $z = 3.05$, $p = 0.03$) and 3.74 Vcm^{-1} (88.9%, $z = 2.99$, $p = 0.03$) than the control (46.7%). There was also greater avoidance in the 2.17 Vcm^{-1} ($z = 3.5$, $p = 0.006$) and 3.74 Vcm^{-1} ($z = 3.63$, $p = 0.004$) than the 0.53 Vcm^{-1} (43.3%) treatment. Avoidance was not affected by pulse frequency ($\chi^2(1) = 0.72$, $p = 0.4$). The percentage of eel exhibiting *rejection* in the HEF was < 10% for all field strengths except for 3.74 Vcm^{-1} (22.2%). Field strength was also influential in the LEF route, ($\chi^2(5) = 25.9$, $p < 0.001$), with eel more likely to exhibit avoidance under 2.42 Vcm^{-1} (95.2%, $z = 3.92$, $p = 0.001$) than the control (35.7%), 0.27 Vcm^{-1} (40.5%, $z = 4.23$, $p < 0.001$), 0.44 Vcm^{-1} (48.7%, $z = 3.85$, $p = 0.0015$) and 1.28 Vcm^{-1} (63.4%, $z = 3.08$, $p = 0.02$) treatments. For all the field strength treatments in the LEF the percentage of eel exhibiting *rejection* was < 10%. Avoidance was not influenced by pulse frequency ($\chi^2(1) = 0.004$, $p = 0.95$).

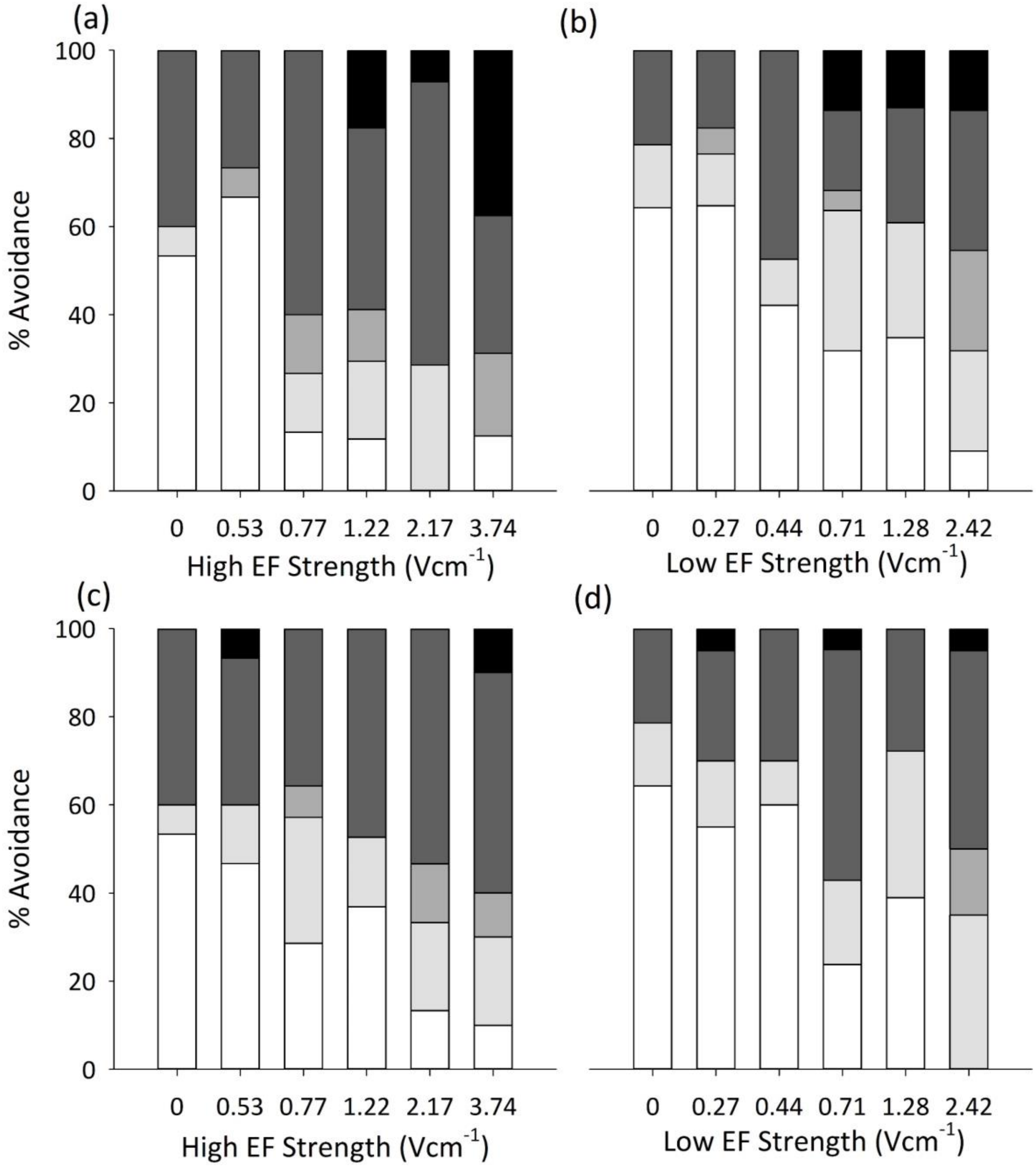


Figure 5.6. Influence of field strength and pulse frequency on the avoidance response exhibited by upstream moving juvenile eel in the HEF or LEF route. (a) HEF, 2 Hz, (b) LEF, 2 Hz, (c) HEF, 10 Hz and (d) LEF, 10 Hz. Clear, light grey, mid grey, dark grey and solid bars correspond to *no change*, *acceleration*, *retraction*, *switching* and *rejection*, respectively.

5.5 Discussion

Under the experimental conditions described, upstream migrating juvenile European eel were more likely to pass a route in which they encountered a weak electric field (LEF) than one with a strong field (HEF) when offered a choice, but only at the higher field strengths (1.22, 2.17 and 3.74 Vcm^{-1}) and under the 2 Hz frequency treatment. More eel exhibited avoidance in the HEF route, and avoidance was positively related to field strength. There was no relationship between distance of initial response and field strength or frequency. To the best of our knowledge, this is the first study to directly test guidance and avoidance in juvenile (glass) eel in relation to PDC electric fields. The results support the potential use of electric fields as a method for guiding juvenile European eel movements, perhaps in combination with traditional physical screens at intakes to abstraction points as part of the application of the marginal gains concept to advancing environmental impact mitigation technology (Deleau *et al.*, 2020b).

Eel were more likely to pass the LEF route under the higher field strengths (1.22, 2.17 and 3.74 Vcm^{-1}). Interestingly, this was the case only under 2 Hz treatment, contradicting the prediction greater avoidance occurs at high pulse frequencies (Mesa and Copeland, 2009). A possible explanation for the observations is that the longer pulse width (100 ms for the 2 Hz treatment compared to 20 ms for the 10 Hz waveform) may have resulted in a higher mean power transmitted to the fish due to an exponential rise in current under the lower frequency condition (Beaumont, 2016). In the 2 Hz waveform treatment the current has time to rise to a maximum and fall back to zero during each period; a process that is less likely to occur in the 10 Hz waveform treatment due to the higher density of pulses. If this was the case, eel would have experienced a greater variation in current when encountering a 2 Hz waveform, potentially explaining a greater influence on behaviour despite a higher frequency of pulses in the 10 Hz treatment. Furthermore, a longer 'off' period between pulses in the 2 Hz treatment may have limited the possibility of acquired insensitivity to the stimulus over time (e.g. due to increased tolerance or habituation that has been found for acoustic cues with shorter intervals between stimuli e.g. Knudsen *et al.,* 1992). Interestingly, our findings support the observations for different families of fish (e.g. juvenile and adult rainbow trout, *Oncorhynchus mykiss*) in that longer pulse widths can enhance the efficiency of experimental electric deterrents (Layhee *et al.*, 2016). These observations have important implications for the design of effective electrical deterrents that do not negatively impact fish welfare, as injury and mortality is positively related to pulse frequency (e.g., McMichael, 1993; Sharber *et al.*, 1994; Dalbey *et al.,* 1996; Dolan *et al.,* 2002; Culver and Chick, 2015; Pottier *et al.,* 2020).

Although the distance of the initial response did not differ between route, field strength or frequency, when given a choice eel avoidance was higher in the HEF route, and overall avoidance in both channels increased with the strength of the electric field. This is not unexpected considering that the voltage gradient across the fish (anterior to posterior if actively swimming upstream) is a strong predictor of fish response to electric fields (Fisher, 1950). When pulsed (i.e. PDC), the electric field alternates between an on and off phase, and if very high field strengths (i.e. higher than those used in this study) are used the rapid change in the voltage gradient across the fish body can elicit extreme responses, such as muscular convulsions and possible spinal injury (Snyder, 2003). In the HEF route and under the higher field strengths, the rate of change in voltage gradient across the body between the on and off periods was greater than for the alternative treatments, resulting in an elevated probability of avoidance. Studies that explored the relationship between injury and electric fishing (e.g. Dwyer and Erdahl, 1995 for Yellowstone cutthroat trout, *Oncorhynchus clarkii bouvieri*, and rainbow trout) and invasive species management (e.g. Gross *et al.*, 2015 for rainbow trout embryos), rather than guidance, also reported greater mortality at higher voltages.

While some avoidance behaviours, such as *acceleration*, *switching*, *retraction* were exhibited consistently in all treatments, higher field strengths were required to elicit *rejection* (i.e. a movement in the opposite direction). Moreover, relatively high rates of *rejection* (> 10% of eel) were observed in the HEF route under the 3.74 Vcm^{-1} only. This might be explained by the migratory phase juvenile eel used in this study being highly motivated to move upstream and unlikely to respond in a contrary fashion until the stimulus was sufficiently intense. We are unable to discount the possibility of different physiological mechanisms underpinning the behaviours observed (Bearlin *et al.,* 2008), and it is unclear whether some *rejections* may have been an unconditioned reflex stimulated at higher field strengths, rather than being a volitional avoidance behaviour. Nevertheless, aside from the mechanisms a deterrent/guidance system will only be effective if it elicits the desired response (e.g. lateral movement or *rejection*) from the management perspective, and this is likely to change with species, site and application (e.g. barrier versus guidance). Hence, further work is needed to understand the mechanisms which underpin this behavioural variability to improve design criteria.

From the perspective of developing behavioural guidance systems for eel, this study demonstrates that under certain field strengths and pulse frequencies the upstream migrating juvenile life-stage exhibits avoidance to electric fields. Enhanced guidance towards areas with a weaker electric field was achieved at higher field strengths and the lower frequency waveform (e.g. 2 Hz rather than 10 Hz), the latter providing the additional benefit of lower risk of injury and power consumption costs. We recommend further investigation to optimise electric field parameters (e.g. pulse frequencies) and electrode orientation (e.g. 45° to the flow) to continue to improve guidance for juveniles, other life-stages of eel (e.g. downstream migrating silver-phase and yellow-phase eel) and species, under different site conditions (e.g. water conductivities in tidal estuaries) and management strategies (e.g. upstream passage solutions). In particular, we suggest that future research should investigate further an approach based on the marginal gains concept to enhance the effectiveness of existing environmental impact mitigation measures, such as eel passes and physical screens, to provide more efficient and cost-effective hybrid behavioural guidance systems.

Chapter 6 Response of yellow- and silver-phase European eel to a two-choice electric field test

6.1 Summary

The European eel (*Anguilla anguilla*) has suffered substantial declines over the past half century. River infrastructure can impede migration and cause direct mortality if eel become entrained at water intakes. Behavioural stimuli, such as electric fields, offer the potential to guide eel away from water intakes and/or towards safer routes of passage, such as bypasses. In this study, the response of two life-stages of European eel, (1) yellow- and (2) silver-phase (experiment 1 and 2, respectively), exposed to pulsed direct current (PDC) electric fields was investigated using a recirculatory flume. In both experiments, eel were offered a choice of two channels through which to pass under either: (1) a treatment condition, in which the selection of one channel resulted in exposure to an electric field (Electrified Channel - EC) and the other a negligible electric field (Non-Electrified Channel - NEC), or (2) a control in which the electric field was absent in both routes. In experiment 1, the influence of the EC field strength (0.28, 0.37 and 0.66 Vcm^{-1}) and direction of approach (upstream or downstream) on both *initial* and *total channel passage* and *initial* and *total avoidance* (*reaction*, *route change* and *rejection*) in yellow-phase eel was assessed. In experiment 2, the influence of EC field strength (0.18 and 0.30 Vcm^{-1}) and pulse frequency (2 and 10 Hz) on *initial channel passage* and *avoidance* for silver-phase eel was investigated. The percentage that passed the NEC did not differ from that of the control for either yellow- or silver-phase eel. In experiment 1, yellow-phase eel exhibited greater *total avoidance* (*reaction* and *rejection*) in the EC than NEC and lower levels of *no change* when travelling upstream in the EC, but field strength had no effect. In experiment 2, silver-phase eel exhibited more *initial avoidance* in the EC than the NEC, but neither field strength nor frequency had any effect. Future research should focus on optimising parameters to achieve effective guidance using electricity for both yellow- and silver-phase European eel, perhaps in combination with other cues or traditional physical screening devices.

6.2 Introduction

The critically endangered European eel population has declined by more than 90% over the past half-century (Pike *et al.,* 2020; ICES, 2021), impacted by multiple stressors that include overfishing (Aalto *et al.,* 2016), habitat loss (Bevacqua *et al.,* 2015), pollution (Belpaire *et al.,* 2016), shifts in oceanic currents (Baltazar-Soares *et al.,* 2014), non-native parasites (Sjöberg *et al.,* 2009) and river infrastructure (Besson *et al.,* 2016). River infrastructure (e.g. dams, weirs) can impede migration and entrain fish at water intakes (e.g. at hydropower and pumping stations) (Noonan *et al.,* 2012; Piper *et al.,* 2013; Fuller *et al.,* 2015). Furthermore, compared to other species of fish, the elongated body morphology of eel puts them at greater risk of injury and mortality (e.g. blade strike, cavitation, grinding) during passage through turbines and pumps (Russon *et al.,* 2010; Kemp, 2015) and in some cases 100% mortality has been reported (Dainys *et al.,* 2018).

Concerns related to mortality and impeded movement (migratory delay) of eel at river infrastructure has led to the development of environmental impact mitigation technologies, such as fish passes (Kerr *et al.,* 2015; Vowles *et al.,* 2015, 2017) and screens (Calles *et al.,* 2013). These have largely focused on the two migratory life-stages, the upstream migrating juveniles (glass eel and elver) (e.g. Podgorniak *et al.,* 2015; Watz *et al.,* 2019) and downstream moving adults (silver-phase eel) (e.g. Gosset *et al.,* 2005; Meister *et al.,* 2022). Less attention has been directed at the non-migratory freshwater resident life-stage (yellow-phase eel) (see Santos *et al.,* 2016) and knowledge gaps on movement behaviour remain (Verhelst *et al.,* 2018c). Nevertheless, yellow-phase eel are known to embark on upstream and downstream exploratory movements during which they encounter infrastructure (Riley *et al.,* 2011). Hence, while the migratory life-stages are of high importance, the whole life-cycle should be considered when developing mitigation strategies to minimise the negative impact of river infrastructure on eel populations.

Physical and mechanical screens are traditionally used to protect fish at water intakes (Kemp, 2015). However, these can themselves have negative environmental impacts. For example, eel can become impinged and suffocate on the screen surface if the velocities exceed burst swimming capabilities (e.g. Calles *et al.,* 2010 for silver-phase European eel), while efficiency of screens designed to guide them to bypass routes can be as low as 0% (e.g. Calles *et al.,* 2012 for silver-phase European eel), resulting in increased energetic costs and predation risks associated with delayed migration (Lennox *et al.,* 2018; Verhelst *et al.,* 2018a). Some suggest that behavioural stimuli (e.g. light, bubbles, and acoustics) that elicit avoidance may be used to enhance fish guidance and the effectiveness of physical screens (e.g. Nestler *et al.,* 1995; Ploskey *et al.,* 1995; Deleau *et al.*, 2020b), although further research is needed to identify the most appropriate cue(s) for eel.

Multiple stimuli have been investigated to select those most appropriate for eel guidance. In particular, light (Hadderingh *et al.,* 1992, 1999) and acoustics (Piper *et al.,* 2019; Deleau *et al.,* 2020a, 2020b) have received much attention with mixed effectiveness reported. For example, up to 85% of downstream migrating silver-phase eel were deflected using underwater light in one study (Hadderingh *et al.,* 1992), while another reported a lower deflection rate of 50 - 65% when using the same stimuli (Hadderingh *et al.*, 1999). Similarly, in relation to acoustics one field study found infrasound effectively diverted adult eel (Sand *et al.,* 2000) whereas others have found limited (Piper *et al.,* 2019) or even no response (Bau *et al.,* 2011). Other stimuli have received less attention, leading to a lack of understanding and agreement on the most applicable stimuli to deter and guide different life-stages of European eel. Thus, there is a need to develop, test and validate the effectiveness of a range of stimuli so that the most appropriate cues (or combination of technologies) might be employed.

Electric fields offer potential for fish guidance as it is thought they produce a more consistent response compared to other behavioural stimuli (Bajer *et al.,* 2018). While electricity has previously been used to deter fish, primarily to control the upstream movements of invasive species (e.g., Maceina *et al.,* 1999 for grass carp, *Ctenopharyngodon idella*; Swink, 1999, for sea lamprey, *Petromyzon marinus;* Dawson *et al.,* 2006, for Eurasian Ruffe, *Gymnocephalus cernuus* and Bajer *et al.,* 2022 for common carp, *Cyprinus carpio*), application to eel guidance has been limited (see Mcgrath *et al.,* 1969). In the case of fish conservation it has been suggested that electric fields, and particularly those that are graduated, have potential value for upstream moving species that are likely to encounter hazardous areas (e.g. tail races of hydropower stations) (Burger *et al.,* 2015). In such instances, and if the deterrent has been poorly designed so that the target fish is stunned by the field, then it will simply be swept with the direction of flow and out of danger (Beaumont, 2016). Conversely, should the same scenario occur for downstream moving fish (e.g. as they approach intakes to hydropower turbines at a dam forebay), incapacitation will result in the fish being involuntarily entrained with no means of escape (Weber *et al.,* 2016). To improve the potential of electric fish guidance systems, further research is needed to optimise field distribution and other parameters that are known to influence fish behaviour, such as pulse frequency (Mesa and Copeland, 2009 for steelhead, *Oncorhynchus* *mykiss* and Pacific lamprey, *Entoshpenus tridentatus*) and field strength (Holliman *et al.,* 2015 for silver carp, *Hypophthalmichthys molitrix*). Provided that electric fields can achieve effective guidance to meet management needs, they present an attractive solution to the challenge of protecting fish while also enabling the use of important infrastructure.

This study investigated the response of yellow- (experiment 1) and silver-phase (experiment 2) European eel to pulsed direct current (PDC) electric fields when offered a choice of route of passage via two channels of equal dimension in an experimental flume. The two channels provided an opportunity to select a route: (1) with either an electric field (Electrified channel - EC) or where the influence of electricity was negligible (Non-Electrified Channel - NEC) under treatment conditions; or (2) a control in which the electric field was absent in both channels. In experiment 1, the influence of electric field strength and direction of approach on *initial* and *total*: (1) *channel passage* and (2) *avoidance* was investigated. In experiment 2, the influence of electric field strength and frequency on *initial*: (1) *channel passage* and (2) *avoidance* was tested. Assuming that fish exhibit aversion to electricity, we predicted that eel avoidance would be: (1) associated with the EC when offered a choice (experiments 1 and 2, Hypothesis 1 [H1]); (2) positively related to field strength (experiment 1 and 2, Hypothesis 2 [H2]), as would *passage* through NEC; (3) more likely during upstream approach (experiment 1, Hypothesis 3 [H3]); and (4) greater under the higher frequency (10 Hz) condition (experiment 2, Hypothesis 4 [H4]).

6.3 Methods

6.3.1 Experimental set-up

Experiments 1 and 2 were conducted in an indoor open channel flume (21.4 m long, 1.4 m wide and 0.6 m deep) at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton (Figure 4.3a). A negative earthed aluminium sheet (200 cm long x 76.3 cm wide x 0.5 cm deep) was used to divide the flume longitudinally into two channels of equal dimension that under the treatment conditions were defined as either the Electrified (EC) or Non-Electrified Channel (NEC) (Figure 6.1). In the EC, two sets of two positive electrodes (80 cm long x 1 cm diameter) were installed across the channel width at 27.6 cm intervals. In the NEC two sets of two dummy earthed electrodes were positioned at the same positions as the positive electrodes in the

EC. Earthed electrodes and the aluminium sheet were arranged to improve the localisation of the electric field, from Chapter 5, within the EC and prevent it extending outside the experimental area. Each 80 cm long electrode was maintained 1 cm above the flume floor and covered with electrically insulated mesh fabric (mesh size: 0.28 x 0.79 mm) to prevent direct contact between the eel and live electrodes. In experiment 2 due to the strong negative rheotaxis of silver-phase eel the distance between release point and experimental area was 1 m less than for the yellow-phase trials (experiment 1) to better ensure a central approach.

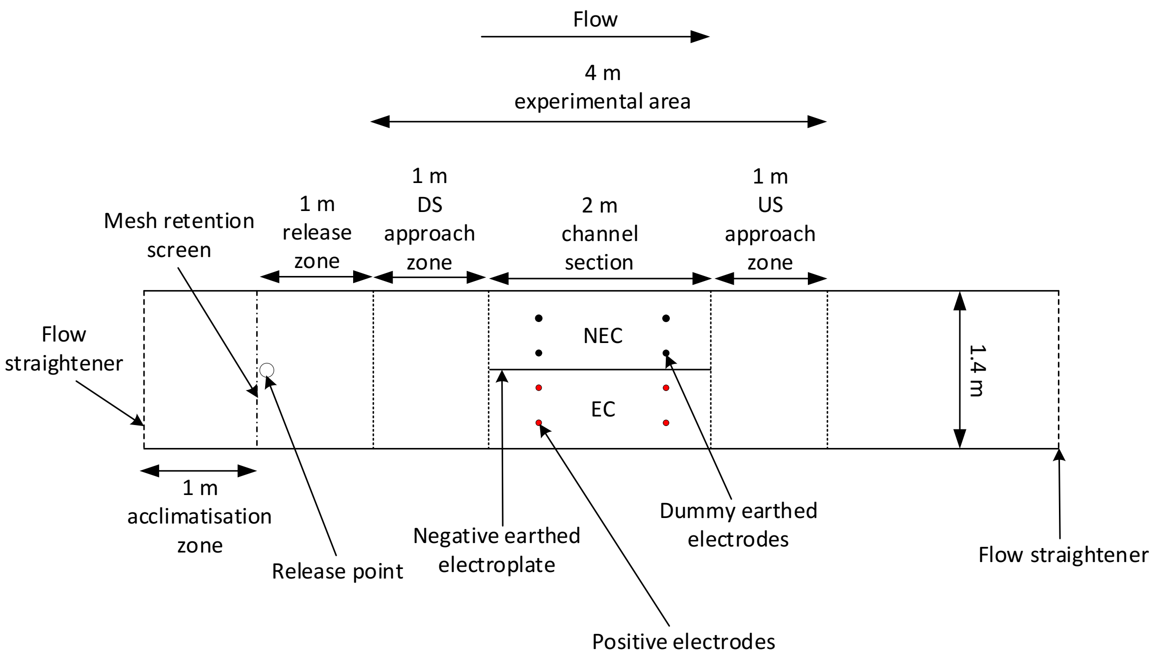


Figure 6.1. Plan of the set-up of an experiment to investigate European eel response to electric fields and subsequent channel passage in an open channel flume. The flume was divided longitudinally down the centre of a 2 m section of the channel by a negative earthed aluminium sheet (electroplate). Two sets of two positive electrodes were installed to create the Electrified Channel (EC). An adjacent Non-Electrified Channel (NEC) was created by installing two sets of two earthed electrodes (dummy) at the same longitudinal position as the positive electrodes in the EC. N.B. the yellow-phase eel trials (experiment 1) had an additional 1 m between the release point and experimental area than the silver-phase trials (experiment 2).

A black screen was placed alongside the flume to prevent disturbance to the fish by the observer. Overhead cameras (experiment 1: 8 SWANN CCTV 720p and experiment 2: 6 SWANN 780 and 1080p) and infrared lights (780 – 850 nm wavelength, experiment 1: 9 and experiment 2: 4 units) were used to provide sufficient illumination for video capture under conditions of darkness.

Treatment field strengths (Table 6.1) were generated using a Smith-Root Electrofishing pulse generator (BP-1.5 POW) and selected accounting for the results of a previous study in which silver-phase eel exhibited avoidance under field strengths of 0.15 - 0.3 Vcm^{-1} in flowing water (see Chapter 4). The slightly higher field strengths tested in experiment 1 were based on the shorter body length of yellow-phase eel (yellow: 24 – 55.5 cm; silver: 31 - 67 cm) as this is a predictor of electrosensitivity (Dolan and Miranda, 2003). Although a weak electric field was present in the NEC due to leakage (mean field strength ≤ 0.081 Vcm^{-1}) it was deemed as negligible for the purpose of this study as previous research on adult silver-phase eel indicated that the mean threshold field strength required to elicit a response was 0.10 Vcm^{-1} (2 Hz, 100 ms waveform) and 0.11 Vcm^{-1} (10 Hz, 10 ms waveform) (see Chapter 4).

Waveforms were selected accounting for ethical considerations as PDC frequencies < 15 Hz reduce the probability of injury in eel (Reynolds and Holliman, 2004). Both 2 and 10 Hz pulse frequencies have been observed to be effective at guiding fish (e.g. 2 Hz: for juvenile European eel, see Chapter 5; 10 Hz: sea lamprey, Swink *et al.,* 1999). Hence, in experiment 1 (yellow-phase eel), a PDC waveform with a frequency of 10 Hz and 20 ms pulse width was used (Figure 6.2a). For experiment 2 (silver-phase eel), 2 Hz (100 ms pulse width) and 10 Hz (20 ms pulse width) waveforms were employed (Figure 6.2).

Table 6.1. The characteristics of the electric field generated in an Electrified Channel (EC) and adjacent Non-Electrified Channel (NEC) in an experimental flume study to investigate yellow- and silver-phase European eel response to electricity (Experiments 1 and 2, respectively). The mean [± SE] and range field strengths were calculated throughout the experimental area. The number of replicates (n) for each treatment is provided. Note the field strengths (for either EC or NEC) were equivalent under 2 or 10 Hz (experiment 2).

Pulse Generator Output (V)	Electrified Channel (EC) Field Strength (Vcm^{-1})		Non-Electrified Channel (NEC) Field Strength (Vcm^{-1})		Sample Size (n)	Experiment
	Mean [± SE]	Range	Mean [± SE]	Range		
0 (Control)	0	0	0	0	13	1
10	0.28 [± 0.014]	0 - 0.74	0.02 [± 0.002]	0 - 0.11	14	1
12.5	0.37 [± 0.02]	0 - 1.48	0.035 [± 0.004]	0 - 0.30	15	1
15	0.66 [± 0.03]	0 - 2.04	0.081 [± 0.008]	0 - 0.93	14	1
0 (Control)	0	0	0	0	20	2
5	0.18 [± 0.011]	0 - 0.52	0.0012 [± 0.0004]	0 - 0.07	2 Hz: 20 10 Hz: 19	2
10	0.30 [± 0.014]	0 - 0.74	0.006 [± 0.001]	0 - 0.09	2 Hz: 20 10 Hz: 20	2

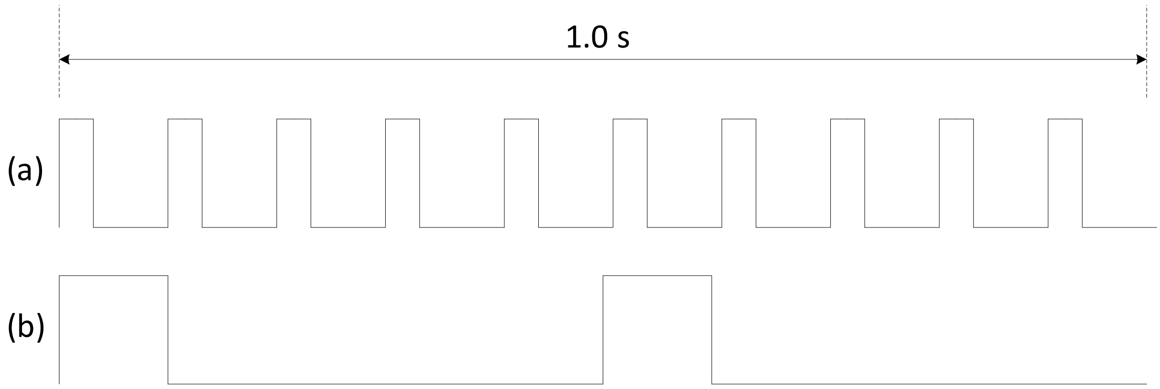


Figure 6.2. PDC frequencies: (a: 10 Hz; b: 2 Hz) used to investigate European eel response to two-choice test electric field. The 10 Hz frequency was used for yellow-phase eel (experiment 1) and both frequencies were tested in silver-phase eel trials (experiment 2).

The electric field was mapped using a potential probe comprising of two-point conductors 27 mm apart connected to an oscilloscope (Gwinstek GDS-1052-U) via a differential probe module (Probemaster 4232). Measurements were taken in a grid at a spacing of 10 cm in the x and y directions at a water depth of 15 cm (from the water surface) to record peak-to-peak voltage (Figure 6.3). Field strength was calculated as the quotient of the peak-to-peak voltage and the distance between the two-point conductors. Maps of the electric field were created for all EC treatment field strengths, under both the 2 and 10 Hz pulse frequencies (experiment 2 only) (Figure 6.3). Ambient water conductivity was 630 µS.cm^{-1}.

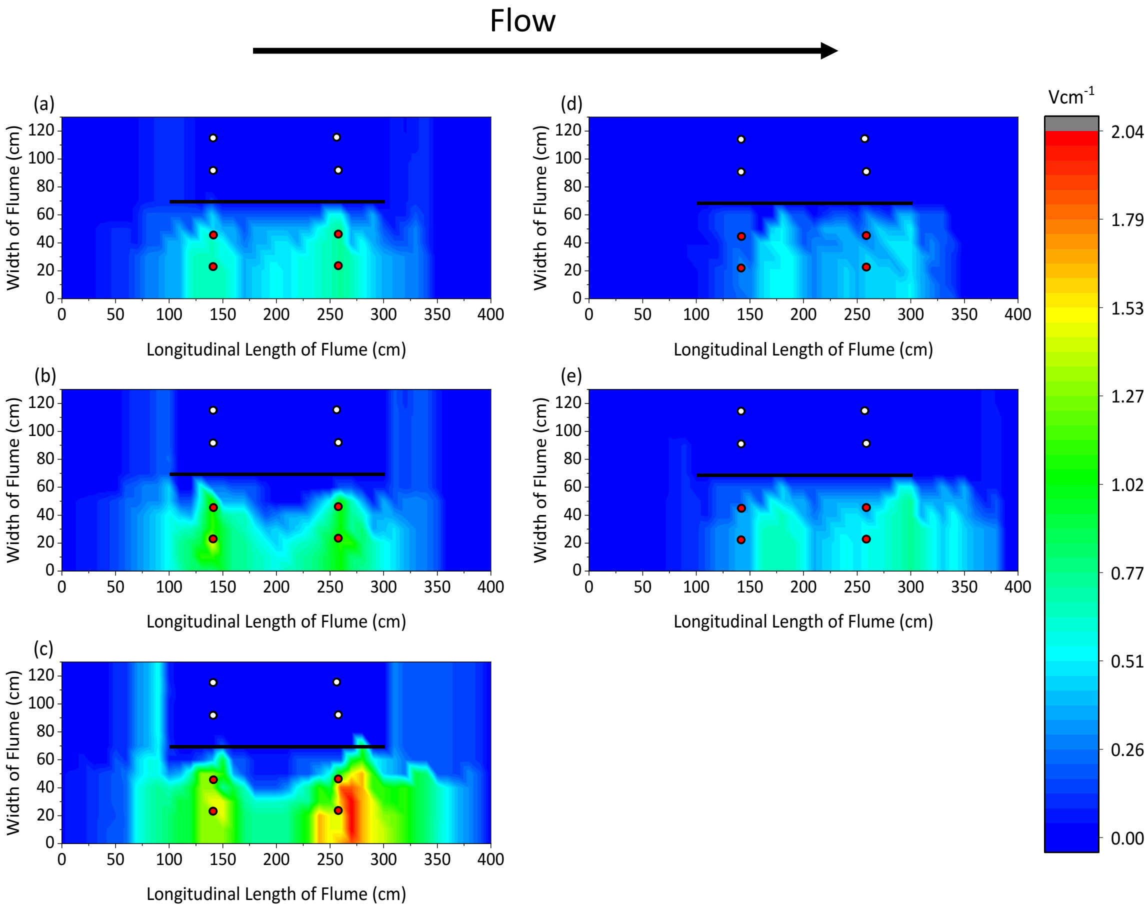


Figure 6.3. Electric field (Vcm^{-1}) generated by the pulse generator output for experiment 1: yellow-phase eel (a - c) of (a) 10 V (Mean EC Field Strength: 0.28 Vcm^{-1}), (b) 12.5 V (Mean EC Field Strength: 0.37 Vcm^{-1}) and (c) 15 V (Mean EC Field Strength: 0.66 Vcm^{-1}), and for Experiment 2: silver-phase eel (d - e) under (d) 5 V (Mean EC Field Strength: 0.18 Vcm^{-1}) and (e) 10 V (Mean EC Field Strength: 0.30 Vcm^{-1}). For experiment 2, field distribution was the same for both 2 and 10 Hz so only one map is depicted. The x axes represent the longitudinal distance along the flume and the y axes the width of the flume. The negative earthed sheet (black line) extended from x = 100 to 300 cm and y = 69 cm. Positive electrodes (red dots) were positioned at x = 140 cm and y = 23 and 46 cm. The second set of positive electrodes were positioned at x = 260 cm and y = 23 and 46 cm with dummy earthed electrodes (white dots) at x = 140 and 260 cm and y = 92 and 115 cm. Measurements were taken at 15 cm water depth from the surface.

6.3.2 Fish husbandry

European yellow-phase eel (n = 76) were obtained by electric fishing at Bosham stream (50°50'44.1"N, 0°50'48.3"W), which flows into Chichester Harbour, West Sussex (UK), on 20 August 2019. Adult European silver-phase eel (n = 106) were caught by a commercial fisherman using fyke nets installed in a drainage channel in the Lincolnshire Fens (UK) (7 and 20 November 2019). Eel were transported to the ICER facility at the University of Southampton in transportation tanks containing aerated river water. The fish were sorted into four 3000 litre outdoor holding tanks and three 1500 litre indoor holding tanks to ensure equal densities. The tanks were fitted with gravity fed external filters and UV filtration systems. A venturi pump on the filter outlets provided additional aeration to supplement that provided by large capacity air pumps. Fish health and water quality were monitored daily, the latter ensuring high quality was maintained (pH: 7.8 - 8.4, Ammonia: 0 ppm, Nitrite: 0 ppm, Nitrate: < 40 ppm). Furthermore, daily tank temperatures were recorded (Mean Holding Tank Temperature [± SD]: Experiment 1 = 20.7 [± 1.18] °C, Experiment 2 = 13.3 [± 0.79] °C). Differences in tank temperature between experiments reflect time of year trials were conducted (i.e. summer and winter, respectively).

6.3.3 Experimental procedure

Due to the natural life-cycle and availability of eel, experiments using yellow-phase (experiment 1) and silver-phase (experiment 2) eel were performed between 21 - 31 August 2019 and 25 - 29 November 2019, respectively. Trials were conducted between 18:00 - 06:00 hr to replicate natural nocturnal behaviour (Tesch, 2003). Treatments were alternated between trials and the channel of the flume assigned EC / NEC was switched daily to prevent side bias. Ambient light intensities during tests were less than 0.01 lux.

For each trial a single eel was removed from the holding tank and placed in a plastic tube secured at both ends with mesh coverings before being positioned within the 1 m long acclimatisation zone, located upstream of the experimental area (Figure 6.1). Eel were allowed a minimum of 60 minutes to acclimatise before being released centrally immediately downstream of the mesh retention screen (release point, Figure 6.1). For experiment 1 (yellow-phase eel), trials lasted 60 minutes allowing for both upstream and downstream approaches. For experiment 2, due to the strong negative rheotaxis of silver-phase eel (Tesch, 2003), trials lasted a maximum of 60 minutes or until eel had passed downstream through the experimental area. At the end of each trial the eel were weighed and measured (Table 6.2). Each eel was used once only.

Water depth and velocities were measured (Valeport Model 801) upstream and downstream of the channel section (Figure 6.1) every five trials (Table 6.2). The velocities were measured midway in the water column and at three lateral points across the flume width. Flume temperature and conductivity were measured at the start of each trial.

Table 6.2. Mean [± SD] measured variables during experimental trials of both yellow- and silver-phase European eel, *Anguilla anguilla* on encountering a two-choice electric field test in a flume.

Experiment	Mean Water Velocity [± SD] (ms^{-1})	Mean Water Depth [± SD] (cm)	Mean Flume Temperature [± SD] (°C)	Mean Ambient Water Conductivity [± SD] ($\mu S.cm^{-1}$)	Mean Mass [± SD] (g)	Mean Total Length [± SD] (cm)
(1) Yellow-phase	Upstream: 0.203 [± 0.015] Downstream: 0.215 [± 0.013]	Upstream: 27.7 [± 1.1] Downstream: 26.2 [± 1.2]	21.6 [± 1.59]	646.8 [± 6.36]	136.4 [± 63.1]	42.1 [± 7.77]
(2) Silver-phase	Upstream: 0.252 [± 0.005] Downstream: 0.260 [± 0.006]	Upstream: 30.4 [± 0.42] Downstream: 29.2 [± 0.61]	12.09 [± 0.55]	647.5 [± 4.81]	263.3 [± 125.6]	49.8 [± 9.60]

6.3.4 Fish behaviour

Analysis of video recordings allowed the characterisation and quantification of channel passage and avoidance behaviour (Table 6.3) as eel passed through the experimental area (Figure 6.1). Behaviour was recorded throughout the trial, and for eel that exhibited more than one response type on any given approach (experiment 1: n = 29, experiment 2: n = 3), that of the highest magnitude (1 – 4) was assigned (hierarchy of response adapted from Vowles *et al.,* 2014, Table 6.3).

Table 6.3. Definitions of different categories of avoidance behaviours and metrics obtained for yellow- and silver-phase eel (experiment 1 and 2, respectively) on encountering a two-choice electric field test in a flume. Behaviours are ranked in a hierarchy of magnitude from 1 (lowest) to 4 (highest) (Adapted from Vowles *et al.,* 2014).

Behaviour/Metric	Definition	Experiment
	Behaviour	
(4) *Rejection*	180^{o} turn in body position and movement for at least one body length	1 and 2
(3) *Route change*	Switching from one channel to the other (Electrified/Non-Electrified)	1 and 2
(2) *Reaction*	Change in behaviour such as increase in swimming speed, recoil or contraction of the body	1 and 2
(1) *No change*	No change in swimming speed or body orientation	1 and 2
	Metric	
Initial channel passage	Channel (EC or NEC) passed on first approach	1 and 2
Total channel passage	Percentage of total approaches with passage	1
Initial avoidance	Behaviour exhibited on first approach	1 and 2
Total avoidance	Percentage of total approaches with behaviour	1

6.3.5 Statistical analyses

Two of the yellow-phase (experiment 1) and seven of the silver-phase (experiment 2) eel did not approach the experimental area during the 60 minute trial and were excluded from further analysis. Statistical analyses were conducted using R 4.0.2 (R Core Team, 2020). Normality was assessed using the Shapiro-Wilk test. Attempts were made to transform non-parametric data, and if unsuccessful, non-parametric tests were performed. Due to the low number of observations of some of the defined behaviours (*reaction, route change* and *rejection)* for *initial avoidance* in both experiments, they were combined as a single response. For statistical purposes the EC assigned during the treatment was also designated as such for the control.

In experiment 1, due to the small sample size of yellow-phase eel, a Fisher's Exact test was used to determine whether *initial channel passage* for any of the treatments deviated from the percentage obtained under the control condition. *Initial avoidance* (Y/N) was assessed using a general linear model with binomial distribution. Main effects included were channel and field strength. *Total channel passage* (Y/N) and *total avoidance* (Y/N) were assessed using a generalised linear mixed model (GZLMM) fitted with a binomial distribution with Eel-ID as a random effect to account for multiple approaches and passes by individual eel. Main effects included were channel, field strength and direction of approach (downstream vs. upstream).

In experiment 2, a goodness-of-fit (χ^2) test determined whether *initial channel passage* (EC or NEC) by silver-phase eel for any of the treatments deviated from the percentage obtained under the control. A general linear model with binomial distribution was used to assess *initial avoidance* (Y/N). Main effects included were channel, field strength and frequency.

6.4 Results

6.4.1 Experiment 1: Yellow-phase eel

6.4.1.1 Channel passage

There was no difference between the percentage *initial channel passage* through the NEC under the control and 0.28 Vcm^{-1} ($p = 0.69$), 0.37 Vcm^{-1} ($p = 0.25$) or 0.66 Vcm^{-1} ($p = 0.44$) treatments (rejecting H1) (Figure 6.4).

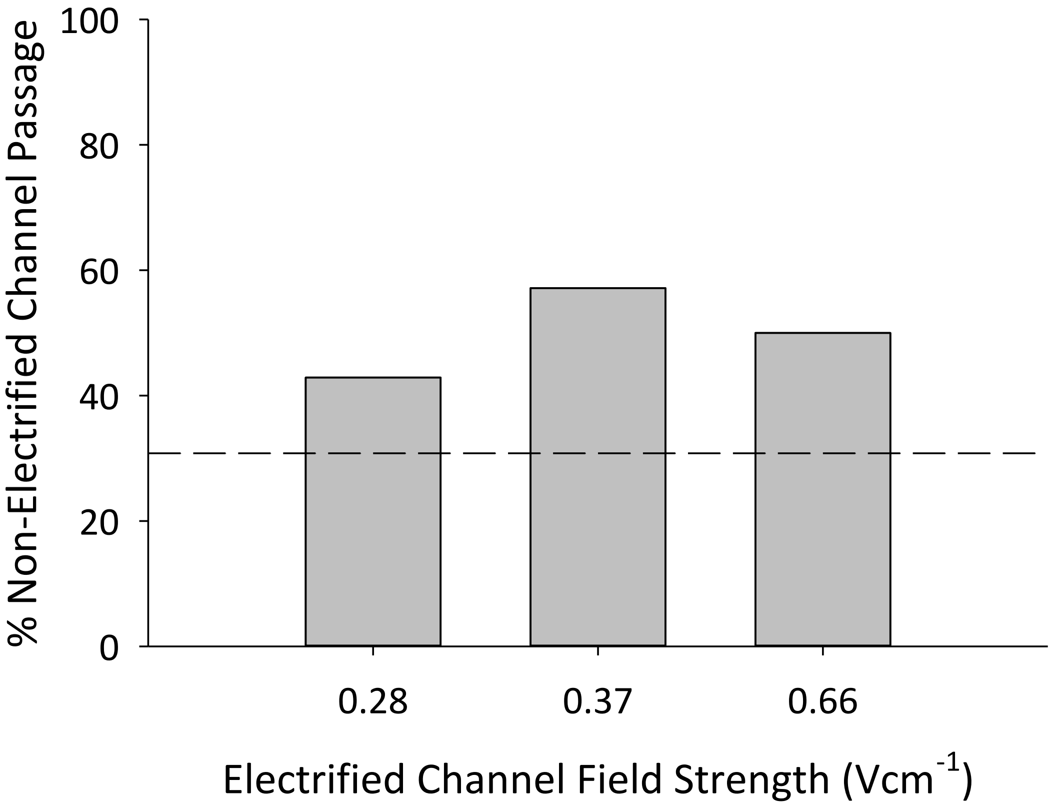


Figure 6.4. Percentage of yellow-phase European eel that initially passed the Non-Electrified Channel (NEC) under the three Electrified Channel (EC) Field Strengths (0.28, 0.37 and 0.66 Vcm^{-1}). Dashed line shows the percentage obtained under the control (0 Vcm^{-1}).

The probability of eel passing (*total channel passage*) was not influenced by channel ($\chi^2(1) = 3.37$, $p = 0.07$) (rejecting H1), field strength ($\chi^2(3) = 5.3$, $p = 0.15$) (rejecting H2) or direction of approach ($\chi^2(1) = 1.06$, $p = 0.3$) (rejecting H3) (Figure 6.5).

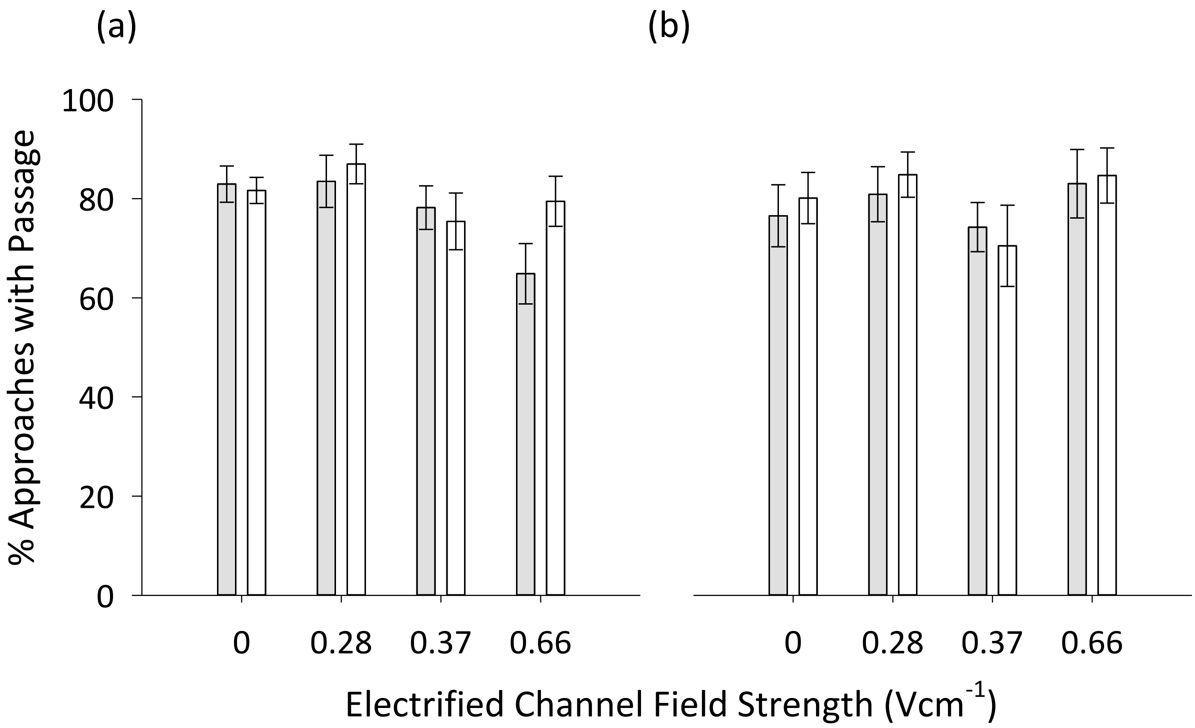


Figure 6.5. Mean [± SE] percentage *total channel passage* of (a) downstream and (b) upstream approaches by yellow-phase eel through the Electrified (EC) (grey bars) and Non-Electrified (NEC) (white bars) Channel under the control (0 Vcm^{-1}) and 0.28, 0.37 and 0.66 Vcm^{-1} treatments during the trial.

6.4.1.2 Avoidance behaviour

There was no difference in *initial avoidance* between the EC and NEC ($z = -1.76$, $p = 0.08$) (rejecting H2) (Figure 6.6). As a consequence, data was aggregated for comparison across field strengths. There was no difference in the occurrence of avoidance between field strengths ($\chi^2(3) = 2.84$, $p = 0.42$).

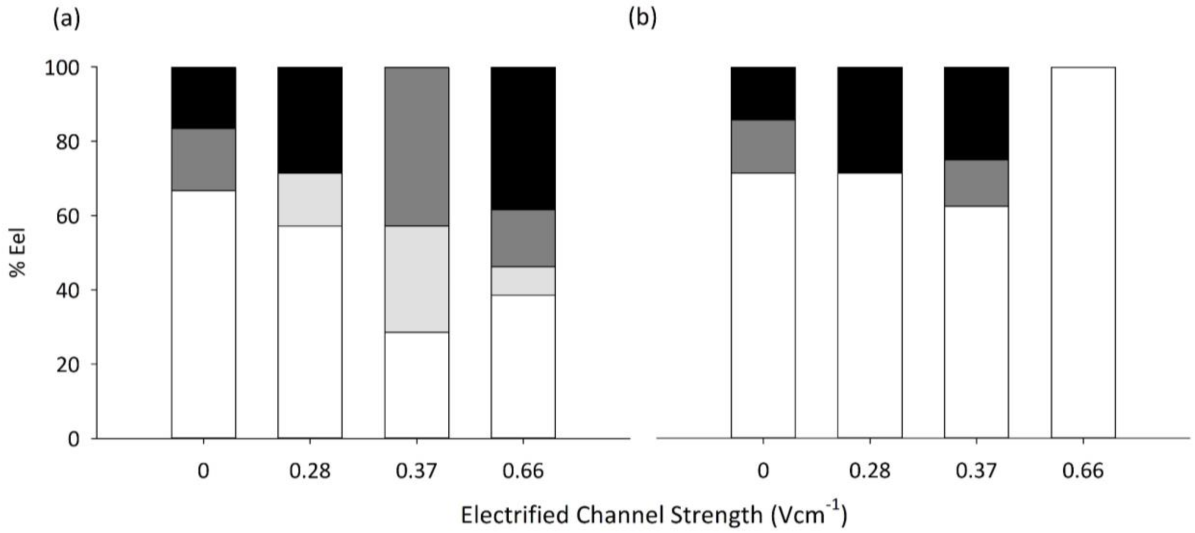


Figure 6.6. Percentage *initial avoidance* for yellow-phase European eel that exhibited *no change* (white), *reaction* (light grey), *route change* (dark grey) and *rejection* (black) as they encountered a choice of route through either (a) Electrified (EC) or (b) Non-Electrified (NEC) channel under the control (0 Vcm^{-1}), 0.28, 0.37 and 0.66 Vcm^{-1}.

In support of H2, *total avoidance* was influenced by channel with more *reaction*, *rejection* and less *no change* observed in the EC (*reaction*: $\chi^2(1) = 88.6$, $p < 0.001$, *rejection*: $\chi^2(1) = 6.02$, $p = 0.014$ and *no change*: $\chi^2(1) = 85.6$, $p < 0.001$) (Figure 6.7). In contrast, channel had no effect on the occurrence of *route change* throughout the trials ($\chi^2(1) = 0.014$, $p = 0.91$).

Due to differences in occurrence of behaviours between the channels, the effect of field strength and direction of approach was tested independently for each channel. In the EC, field strength effected the occurrence of *no change* ($\chi^2(3) = 30.4$, $p < 0.001$), *reaction* ($\chi^2(3) = 29.4$, $p < 0.001$) and *rejection* ($\chi^2(3) = 9.91$, $p = 0.02$), supporting H2 (Figure 6.7a, b). *Reaction* and *no change* were respectively more and less common under the treatments than the control (*no change*: 0.28 Vcm^{-1}: $z = -3.83$, $p < 0.001$, 0.37 Vcm^{-1}: $z = -4.31$, $p < 0.001$ and 0.66 Vcm^{-1}: $z = -5.23$, $p < 0.001$ and *reaction*: 0.28 Vcm^{-1}: $z = 4.75$, $p < 0.001$, 0.37 Vcm^{-1}: $z = 4.85$, $p < 0.001$ and 0.66 Vcm^{-1}: $z = 5.38$, $p < 0.0001$). *Rejection* occurred more frequently under the 0.66 Vcm^{-1} treatment than the control ($z = 3.13$, $p = 0.009$). In contrast, field strength did not influence the occurrence of *route change* ($\chi^2(3) = 7.33$, $p = 0.06$). In the NEC, none of the avoidance behaviours were influenced by field strength in the adjacent EC (*no change*: $\chi^2(3) = 2.06$, $p = 0.56$, *reaction*: $\chi^2(3) = 2.09$, $p = 0.55$, *route change*: $\chi^2(3) = 2.27$, $p = 0.52$ and *rejection*: $\chi^2(3) = 1.03$, $p = 0.79$) (Figure 6.7c, d).

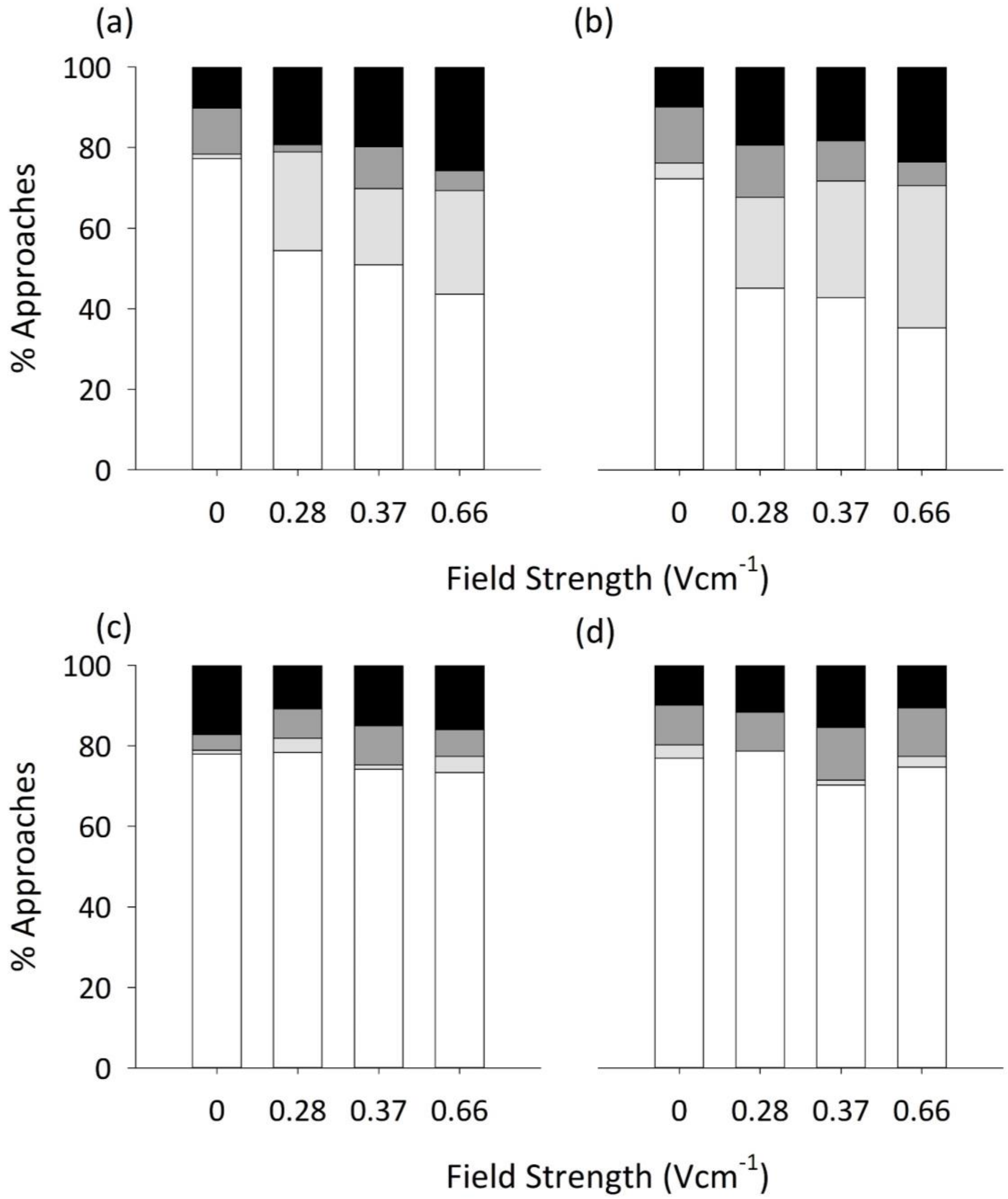


Figure 6.7. Percentage of *total avoidance* in (a,c) downstream and (b,d) upstream approaches of yellow-phase European eel in which either *no change* (white bars), *reaction* (light grey), *route change* (dark grey) or *rejection* (black) was exhibited for the (a,b) Electrified (EC) and (c,d) Non-Electrified Channel (NEC) under the control (0 Vcm^{-1}) or 0.28, 0.37 and 0.66 Vcm^{-1} treatments.

In support of H3, *no change* was observed less frequently for upstream approaches in the EC ($\chi^2(1) = 5.38$, p = 0.02) (Figure 6.8a). In contrast, *reaction*, *route change* and *rejection* were not affected by direction of approach (*reaction*: $\chi^2(1) = 3.63$, p = 0.06, *route change*: ($\chi^2(1) = 3.32$, p = 0.07 and *rejection*: $\chi^2(1) = 0.15$, p = 0.7). Direction of approach did not influence the occurrence of *total avoidance* in the NEC (*no change*: $\chi^2(1) = 0.02$, $p = 0.89$, *reaction*: $\chi^2(1) = 1.7$, $p = 0.19$, *route change*: $\chi^2(1) = 1.75$, $p = 0.19$ and *rejection*: $\chi^2(1) = 0.21$, $p = 0.64$) (Figure 6.8b).

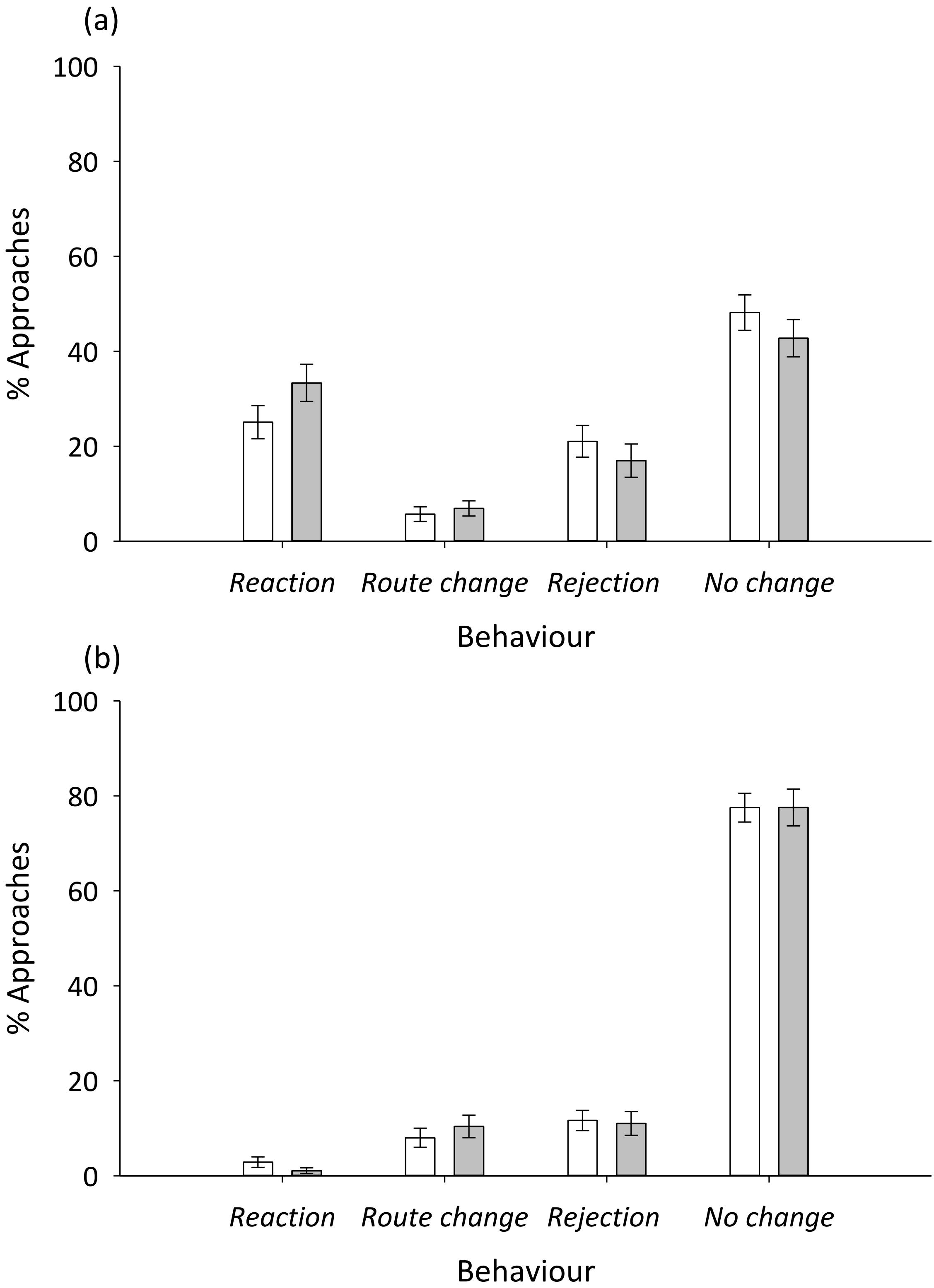


Figure 6.8. Mean percentage *total avoidance* [± SE] exhibited by yellow-phase European eel in an (a) Electrified (EC) and (b) Non-Electrified Channel (NEC) when moving downstream (white bars) or upstream (grey bars). Treatment data was aggregated for three field strengths (0.28, 0.37 and 0.66 Vcm^{-1}).

6.4.2 Experiment 2: Silver-phase eel

6.4.2.1 Channel passage

There was no difference between the percentage *initial channel passage* through the NEC under the control and any of the treatments (0.18 Vcm^{-1}, 2 Hz: $\chi^2(1) = 0.22$, $p = 0.64$, and 10 Hz: $\chi^2(1) = 0.42$, $p = 0.52$, 0.30 Vcm^{-1}, 2 Hz: $\chi^2(1) = 3.52$, $p = 0.06$ and 10 Hz: $\chi^2(1) = 0.22$, $p = 0.64$) (rejecting H1) (Figure 6.9).

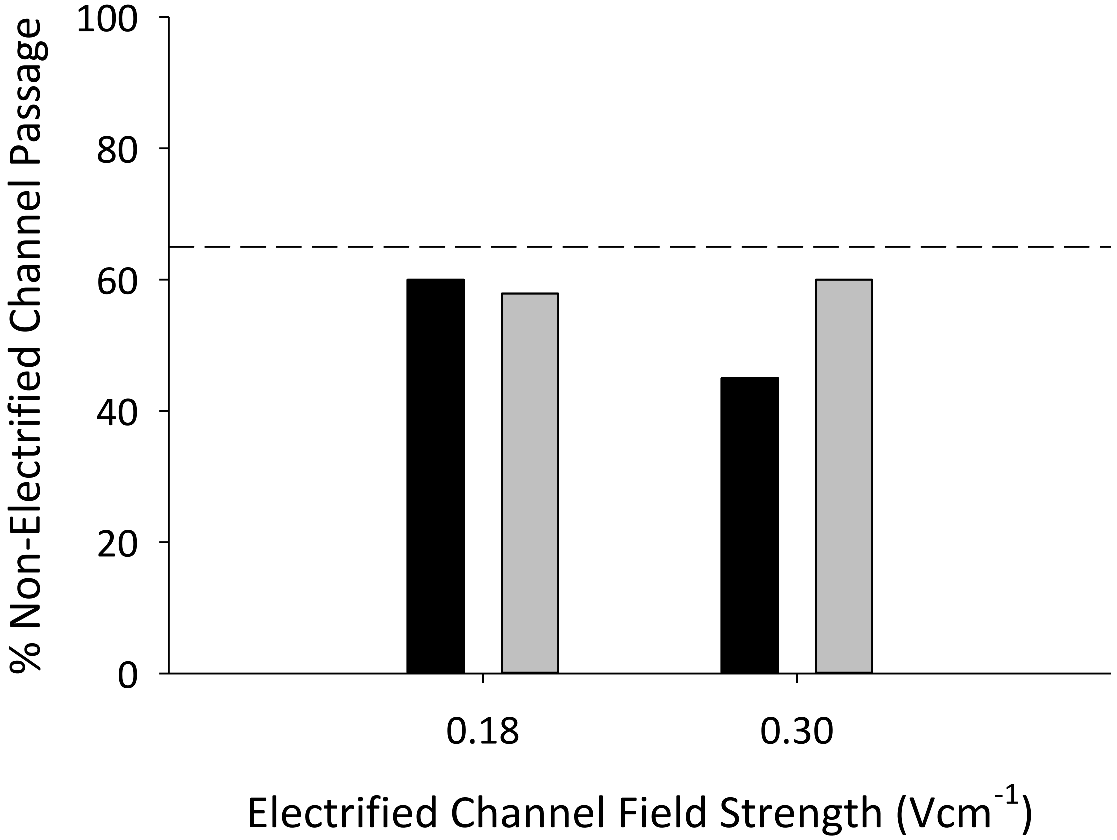


Figure 6.9. Percentage of silver-phase European eel that initially passed the Non-Electrified Channel (NEC) under the two Electrified Channel (EC) Field Strength treatments (0.18 and 0.30 Vcm^{-1}) under 2 Hz (black bars) and 10 Hz (grey bars). The dashed line indicates the percentage obtained under the control (0 Vcm^{-1}).

6.4.2.2 Avoidance behaviour

Under the treatments, 61.5% of eel exhibited *initial avoidance* having entered the EC and 12.5% in association with the NEC. In support of H2, channel influenced the occurrence of *initial avoidance* with more eel exhibiting a response in the EC ($z = - 4.39$, $p < 0.001$) (Figure 6.10).

Due to the differences in *initial avoidance* between channels, the data was separated for comparison between field strengths and frequency. In the EC, field strength influenced the occurrence of *initial avoidance* ($\chi^2(2) = 9.35$, $p = 0.009$) (Figure 6.10a,c) with greater avoidance under the 0.30 Vcm^{-1} than the control ($z = 2.4$, $p = 0.04$) (supporting H2). Frequency (2 vs. 10 Hz) did not affect the occurrence of *initial avoidance* ($\chi^2(1) = 1.89$, $p = 0.17$) (rejecting H4). In the NEC, neither field strength nor frequency influenced the occurrence of *initial avoidance* (field strength: $\chi^2(2) = 4.26$, $p = 0.12$ and frequency: $\chi^2(1) = 1.58$, $p = 0.21$) (Figure 6.10b, d).

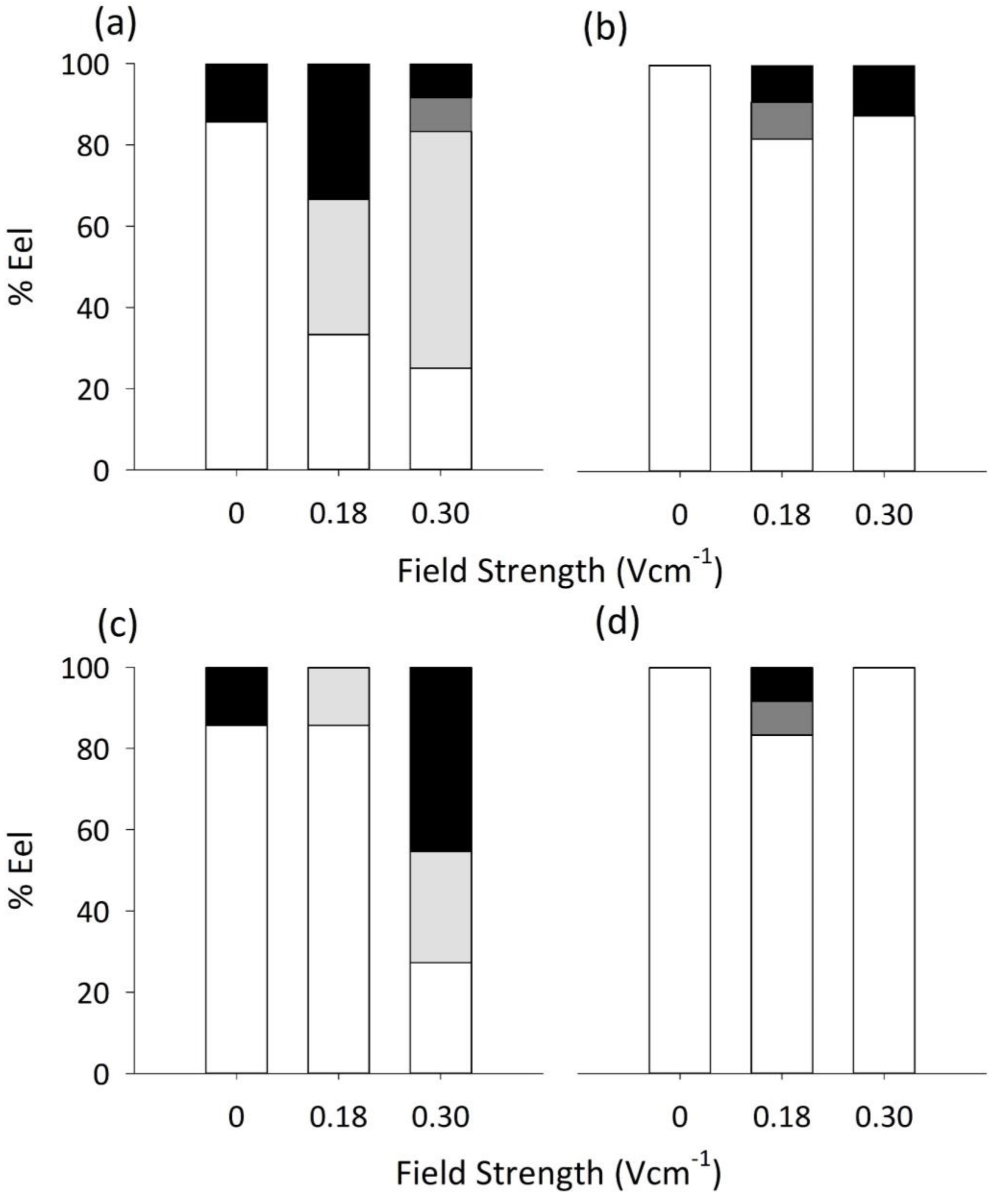


Figure 6.10. Percentage of *initial avoidance* of downstream migrating silver eel under either (a, b) 2 or (c,d) 10 Hz as they encountered a choice of channel through either an (a,c) Electrified (EC) or (b,d) Non-Electrified Channel (NEC) under two treatment field strengths (0.18 and 0.30 Vcm^{-1}) and a control (0 Vcm^{-1}). White, light grey, dark grey and black represent *no change*, *reaction*, *route change* and *rejection,* respectively.

6.5 Discussion

Both yellow- and silver-phase European eel exhibited avoidance when exposed to electric fields in this study. In contrast to our predictions, however, neither phase preferred to pass the NEC under any of the treatment conditions presented (experiments 1 and 2, respectively). In experiment 1, *total avoidance* was more often observed for yellow-phase eel in the EC and during upstream approaches, in accordance with our hypotheses. In experiment 2, also as predicted, silver-phase eel exhibited more frequent *initial avoidance* in the EC, although field strength and pulse frequency had no effect. The results of this study highlight the potential for the use of electric fields to elicit avoidance in both yellow and silver-phase European eel and further optimisation is now needed to achieve effective guidance.

In contrast to our first hypothesis, yellow-phase eel did not prefer to pass through the NEC under the treatments any more than the control (experiment 1). This may have been because the electric field strengths and/or frequencies used in this study were insufficient to elicit a consistent change in swimming trajectory (i.e. away from the EC) for this species under the conditions created. We selected field strengths based on previous experience of using silver-phase eel (see Chapter 4) and ethical considerations. However, the smaller yellow-phase eel could perhaps better tolerate the test fields to which they were exposed, and might require higher field strengths to achieve effective guidance. This relates to the relationship between body length and electrosensitivity, with shorter fish being less sensitive to electric fields due to the lower voltage gradient measured along their body (anterior to posterior) (Dolan and Miranda, 2003). Indeed, the effectiveness of electric fields for fish guidance has previously been linked to body size, with lower efficiencies observed for smaller fish (e.g. Kowalski *et al.,* 2022 for rainbow trout, *Oncorhynchus mykiss*).

In experiment 2, silver-phase eel did not prefer to pass through the NEC in contradiction to predictions. This may have been a consequence of the spatial variation in distribution of the electric field, with the greatest relative difference in field strengths between the two routes occurring between the channels themselves, rather than that encountered by eel on approach. If the relative difference in field strengths on approach was higher, eel may have been better able to differentiate between the two routes and exhibit a clearer choice prior to channel entry. Instead, eel tended to remain on the same trajectory once they had entered a channel, rather than exhibit *rejection* and swim back upstream to select the alternative route. Interestingly in neither experiment did eel exhibit an expected 50:50 channel passage (between EC and NEC) under the control. The exact reason for this is not known but perhaps it is due to another undetermined environmental factor.

Initial avoidance was more common in the electrified channel for silver-phase eel, in support of our second hypothesis, but not so for yellow-phase eel that also failed to exhibit a difference between treatment field strengths relative to the control. The difference between the life-stages may be explained by a difference in electric field characteristics between the two experiments, with a better localised field restricted to the EC in experiment 2. When considering *total avoidance*, however, yellow-phase eel appeared to discriminate between the two channels with more frequent *reaction* and *rejection* in the EC. Furthermore, yellow-phase eel exhibited more frequent *reaction* and less *no change* under treatment conditions than the control throughout the trial. In addition, compared to the control there was greater *rejection* under the highest field strength (0.66 Vcm^{-1}), although in contradiction to the second hypothesis there was no relationship between field strength and *total avoidance*. Similarly, while silver-phase eel exhibited more frequent *initial avoidance* in response to the highest field strength (0.30 Vcm^{-1}) in the EC compared to the control in the EC, there was no difference between treatments (i.e. 0.18 vs 0.30 Vcm^{-1}). Other studies have also observed a lack of influence of voltage on escape behaviour, possibly because fish exhibited a maximal avoidance response even at the lowest voltage setting tested, thus increased voltage resulted in no additional effect (e.g. Weber *et al.*, 2016 for walleye, *Sander vitreus*). More work is needed to investigate whether similar mechanisms may explain the response of eel in this study.

In support of hypothesis 3, the direction of approach (upstream or downstream) influenced *total avoidance* in yellow-phase eel with less avoidance (i.e. higher *no change*) when travelling downstream. The use of electric fields for behavioural guidance is thought to be more effective for upstream moving fish (Beaumont, 2016) because the direction of flow will ensure fish are displaced downstream with minimal effort if they detect the electrified zone and select to avoid it. In contrast, fish that are moving downstream may be more likely to be swept with the flow through the electrified area should the field be below some threshold at which the eel would exhibit clear avoidance.

Pulse frequency (2 and 10 Hz) had no effect on *initial channel passage* or *initial avoidance* for silver-phase eel (experiment 2) contradicting the fourth and final prediction. In the context of electric fishing, higher pulse frequencies can cause more adverse responses (i.e. myoclonic jerks) (Sharber *et al.,* 1994) and greater avoidance (e.g. Mesa and Copeland, 2009 for steelhead and Pacific lamprey). It is unclear why we observed a lack of response in this study although interspecific variation and our focus on a downstream moving fish may explain the apparent lack of sensitivity to differences in frequency.

This study provides insight into the future direction of electric field guidance for European eel. Both life-stages exhibited avoidance when exposed to electric fields, but this did not translate to an ability to manipulate route trajectory and guidance. Future research might focus on optimising electrode orientation and electric field parameters (i.e. field strength and pulse frequency) to enhance guidance for this species. Furthermore, the use of electric fields in combination with physical screens may enhance overall performance of guidance devices that attempt to manipulate behaviours of less sensitive species of fish.

Chapter 7 Developing electric deterrents for selective-fish guidance: interspecific variation in response to pulsed direct currents

7.1 Summary

In freshwater environments, electric fields have been used as barriers to reduce the range expansion of invasive fish, while in other cases protecting those of high conservation concern by guiding them away from dangerous areas. Behavioural barriers that block the spread of invasive fish are also likely to impede the movements of desirable species, thus decreasing connectivity and fragmenting habitat, resulting in a reduction in individual fitness and population viability. Furthermore, the effectiveness of electric barriers appears to be highly variable, influenced by context and possible interspecific differences, resulting in potential worst-case scenarios in which invasive species might remain unaffected while native fish are negatively impacted. To enhance the efficiency of electric barriers, and potentially advance selective-fish guidance technology to meet management objectives, there is a need to better define the electrosensitivity for multiple species. This experimental study quantified the electrosensitivity of two species of carp (grass carp, *Ctenopharyngodon idella*, and common carp, *Cyprinus carpio*) that are invasive outside of their natural range and compared the values with those previously obtained for adult European eel (*Anguilla anguilla*), a species of high conservation interest. Electric field strengths (Vcm^{-1}) required to elicit physiological responses (*twitch*, *loss of orientation* and *tetany*) were identified across four pulsed direct current (PDC) electric waveforms (single pulse-2 Hz, double pulse-2 Hz, single pulse-3 Hz and double pulse-3 Hz). Grass carp were sensitive to differences in waveform with *tetany* exhibited at lower field strengths under the single pulse-2 Hz. Both cyprinid species responded similarly and were less sensitive to PDC than adult European eel, although *loss of orientation* occurred at lower field strengths for grass than common carp under the single pulse-3 Hz waveform. The interspecific variation in electrosensitivity indicates the potential for electric fields to provide selective fish guidance system in areas where invasive and native species of high conservation concern occur in sympatry.

7.2 Introduction

With the global human population predicted to continue to grow, at least during the first half of the current century (Adam, 2021), fresh waters will be increasingly exploited, e.g. to generate energy and produce food. This will require the construction of large dams to supplement those that have already impacted nearly two-thirds of the world's longest rivers (> 1000 km) (Grill *et al.*, 2019) in the drive to further economic development of society (Shi *et al.*, 2019). The rapid development of freshwater resources will cause further environmental and social-economic shocks associated with the modification and degradation of ecosystems and the services they provide (Kemp *et al.*, 2022), for example, through the disruption of fluvial connectivity and fragmentation of habitat. From the perspective of freshwater fisheries, dams impede movements between critical habitats of fish that might also be injured or killed if they enter intakes (e.g. to hydropower turbines or irrigation systems) (Kemp, 2015; Birnie-Gauvin *et al.*, 2017; Mueller *et al.*, 2017). The development of effective strategies to mitigate the negative impacts of river infrastructure is critical if environmental degradation is to be halted and reversed as society strives to meet sustainability targets (e.g. UN Sustainable Development Goals).

As part of a programme to advance the sustainability of river engineering, fish passes and physical and mechanical screens are built and installed at impoundments to preserve or restore migration routes and thus improve habitat connectivity (Clay, 1995) and prevent fish entering associated water intakes (Kemp, 2015), respectively. Furthermore, behavioural stimuli such as acoustics (Jesus *et al.*, 2019), light (Ford *et al.*, 2018), bubbles (Leander *et al*., 2021) and electric fields (Parasiewicz *et al.*, 2016) have been tested as an alternative to (e.g. Noatch and Suski, 2012), or to enhance the effectiveness of (e.g. Mussen and Cech, 2019; Haug *et al.*, 2022), physical and mechanical screens designed to block passage and/or guide fish away from dangerous areas.

Current mitigation strategies often provide partial solutions only, referred to as "half-way" technologies (Brown *et al*., 2013). In some cases, the mitigation can even itself be damaging or have unforeseen consequences that are often overlooked or underappreciated (Mclaughlin *et al.*, 2013). For example, fish passes that partially reconnect habitat critical for the completion of the life-cycle of desirable native species, such as those with high commercial, cultural, and conservation significance, may also facilitate range expansion of Aquatic Invasive Species (AIS) (Kerr *et al.*, 2021). The introduction of AIS can have large negative consequences for recipient ecosystems, acting through predation (e.g. Weyl and Lewis, 2006 for largemouth bass, *Micropterus salmoides*), parasitism (e.g. Patrick *et al.,* 2009 for sea lamprey, *Petromyzon marinus*), resource competition (e.g. Baker and Levinton, 2003 for zebra mussel, *Dreissena polymorpha*), habitat modification (e.g. Brown and Moyle, 1991 for Sacramento squawfish, *Ptychocheilus grandis*), hybridisation (e.g. Ludwig *et al.*, 2009 for Siberian sturgeons, *Acipenser baerii*) and disease transmission (e.g. Alderman *et al.,* 1990 for signal crayfish, *Pacifastacus leniusculus*), as well as causing substantial economic impacts (Pimentel *et al.*, 2000). Hence, trade-offs arise when mitigation strategies employed to benefit native species conflict with management decisions to control the spread of AIS (Mclaughlin *et al.*, 2013), resulting in a “connectivity conundrum” (Zielinski *et al.*, 2020). Consequently, there is a need to enhance conservation efforts that benefit native species, while reducing the risks posed by AIS. Developing selective environmental impact mitigation technologies could reduce the tensions between AIS control and native fish passage objectives (Rahel and McLaughlin, 2018).

Previous research to develop environmental impact mitigation technology and AIS control based on selecting specific traits exhibited by the target species has tended to focus predominantly on the use of physical structures to facilitate passage rather than guidance. Perhaps some of the earliest examples relate to sea lamprey control in the Laurentian Great Lakes (Zielinski *et al.*, 2019). Multiple barrier designs, such as fixed-, seasonal- and adjustable-crest weirs and velocity barriers have been used to limit the movements of invasive sea lamprey during peak migration (McLaughlin *et al.*, 2007), while allowing desirable families (such as the salmonids) to gain access to spawning streams. In another case, selective fish passage has been developed with the purpose to conserve native Pacific lamprey (*Entosphenus tridentatus*) in the Pacific Northwest of the United States through the design and installation of lamprey passes that compensate for the lack of effectiveness of technical fishways designed for salmonids (Moser *et al.*, 2011).

Behavioural deterrents designed to selectively block and/or guide fish away from dangerous areas to more preferred routes provide a management option to protect desirable species while deterring AIS (Noatch and Suski, 2012), but appear to be less common than traditional fish passage structures. There are early examples of the use of low-voltage electric fields for sea lamprey control in the Great Lakes dating back to the 1950s (e.g. Applegate *et al.,* 1952; Erkkila *et al.,* 1956; McLain, 1957). More recent examples of electric barriers include that activated in the Chicago Sanitary and Ship Canal in 2002, the world’s largest such device, designed to prevent the interbasin transfer of AIS (particularly the Asian carp species: bighead carp, *Hypophthalmichthys nobilis*, and silver carp, *Hypophthalmichthys molitrix*) from the Mississippi to the Great Lake catchments, and vice versa (Parker *et al*., 2015). Unfortunately, electric barrier and guidance devices too can have negative unintended environmental impacts, dating back to the early studies in which alternating current was used to block sea lamprey but resulted in excessive mortality of non-target species (Applegate *et al.,* 1952; Erkkila *et al.,* 1956). Despite improvements in understanding and design, this problem can resurface over more recent times, as illustrated by one study that evaluated the effectiveness of a portable seasonal electric barrier installed in a tributary of the Great Lakes for sea lamprey control, but that also blocked and killed hundreds of non-target fish (Johnson *et al.*, 2021).

Even when electricity-based mitigation systems work, their efficiencies can be variable. Some demonstrate close to 100% barrier effectiveness (e.g. Swink, 1999 for invasive sea lamprey; Sparks *et al.*, 2010 for common carp); whereas others are much lower if designed for guidance (e.g. Gosset and Travade, 1999, 5 – 28% efficiency for native Atlantic salmon smolts *Salmo salar* guided to a bypass). To advance selective electrical barriers and guidance systems that respectively facilitate the control of AIS and conservation of native species, there is a need to develop fundamental knowledge of sensory capabilities (e.g. electrosensitivities) and behavioural response from a multi-species / fish community perspective. This includes investigating intra- and interspecific response to electric fields across different parameters, such as field strength, pulse frequency and width, that are known to influence the behaviour and physical condition (e.g. Larson *et al.,* 2014; Layhee *et al.*, 2016) of different life-stages (e.g. Nutile *et al.,* 2013 for embryos).

To inform the design of a selective electric barrier, this experimental study obtained threshold field strengths (Vcm^{-1}) for three physiological responses (*twitch*, *loss of orientation* and *tetany*) for two invasive cyprinid species, grass and common carp, and compared these with values previously obtained for a native species of high conservation concern, the critically endangered European eel (see Chapter 4). The influence of: pulsed direct current (PDC) waveforms (treatment n = 4, differing with respect to pulse width and frequency) (Objective 1); species (treatment n = 2, grass and common carp) (Objective 2); and family (treatment n = 2, cyprinid and anguillid) (Objective 3) on threshold field strengths for physiological responses (n = 3) was assessed.

7.3 Methods

7.3.1 Experimental set-up

Experiments were conducted at the International Centre for Ecohydraulics Research (ICER) facility, University of Southampton, UK, using a clear glass (10 mm thick) rectangular tank with dimensions (1.5 m long x 0.60 m wide x 0.23 m deep) (see Chapter 4, Figure 4.1). 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 and 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 to prevent contact with the fish. 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.

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) to record peak-to-peak voltage. Electric field maps were generated for all output voltages and waveforms. Electric field strength was uniform across the tank and proportional to output voltage (see Chapter 4, Figure 4.2) (i.e. for 7 V output voltage with 142 cm between electrodes: $\frac{7}{142} = 0.05$ Vcm $^{-1}$). Ambient water conductivity during mapping was 630 µS.cm^{-1}.

Four CCTV cameras (Swann 1080p; 1920 x 1080 pixel resolution; 25 frames s^{-1}) were used to monitor fish behaviour: 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.

Water (conditioned tap water) depth was maintained at 15 cm and obtained from the holding tank in which the experimental fish used that day were housed

7.3.2 Fish husbandry

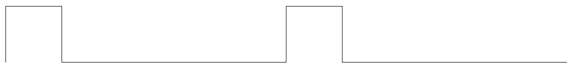
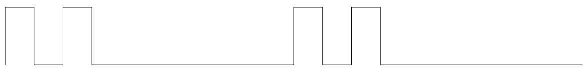
Forty grass carp and forty-five common carp were obtained from a supplier (Aquatics to your Door Ltd., 10 August 2018) and local hatchery (Hampshire Carp Hatcheries, 16 August 2018), respectively. Forty European eel were obtained from commercial fisherman using fyke nets on 26 October 2017 (see Chapter 4). The fish were split evenly over four 3000 litre outdoor holding tanks (mean holding tank temperature [± SD]: cyprinids = 17.9 [± 0.15]°C and anguillid = 13.2 [± 0.89]°C). The tanks were fitted with gravity fed external filters and UV filtration systems. A venturi system on the filter outlets provided aeration to supplement that provided by large capacity air pumps. Fish health and water quality was monitored daily, ensuring consistent conditions were maintained (pH: 7.8 - 8.4, Ammonia: 0 ppm, Nitrite: 0 ppm, Nitrate: < 40 ppm). Water temperature within the tanks was recorded using submersible temperature loggers and validated manually on a daily basis. Experimental trials were terminated if the difference in temperature between the holding and experimental tanks exceeded 2°C. Each fish was used once only to reduce potential for habituation or learnt behaviours.

7.3.3 Experimental procedure

Trials using cyprinids were conducted from 10 August - 4 September 2018. Grass carp are thought to have similar activity levels during the day and night (Mitzner, 1978), but common carp swimming activity is suggested to be higher at night (Rahman and Meyer, 2009), so trials were conducted between 17:00 - 06:00 hr to ensure direct comparison between species. Trials using adult European eel were conducted from 2 - 8 November 2017 between 17:00 - 02:00 hr (see Chapter 4) to replicate conditions experienced during the natural nocturnal downstream migration (Tesch, 2003). Ambient light levels during the trials were less than 0.01 lux.

The pulse generator was used to produce four different waveforms: (a) single pulse- 2 Hz, (b) double pulse- 2 Hz, (c) single pulse- 3 Hz and (d) double pulse- 3 Hz (Table 7.1). For the double pulse- 2 Hz and double pulse- 3 Hz waveforms, the time between the pulses in the set of two (i.e. pulse break) was 50 and 16.7 ms respectively. These waveforms were selected based on ethical considerations as PDC < 15 Hz is suggested to reduce injuries in fish (Snyder, 2003). Similar frequencies used in this study have also proved effective at guiding other species (2 Hz: white sturgeon, *Acipenser transmontanus*, Ostrand *et al.*, 2009; 3 Hz: Coho salmon, *Oncorhynchus kisutch*, Raymond, 1956) and enabled a direct comparison with eel (see Chapter 4). To generate the desired field strength the input voltage on the pulser was divided by the distance between the electrodes and then verified using a custom-built probe connected to an oscilloscope.

Table 7.1. Characteristics of waveforms used to test electrosensitivity of cyprinid (grass and common carp) and anguillid (European eel) fish with sample sizes provided.

Waveform	Pulse Width (ms)	Schematic (represents 1 s time frame)	Species Tested and sample size (n)
Single pulse- 2 Hz	100		Grass carp (n = 15), Common carp (n = 15) and European eel (n = 17)
Double pulse- 2 Hz	50		Grass carp (n = 15), Common carp (n = 15) and European eel (n = 17)
Single pulse- 3 Hz	33.3		Grass (n = 15) and Common carp (n = 15)
Double pulse- 3 Hz	16.7		Grass (n = 15) and Common carp (n = 15)

Prior to the start of each trial, a single individual fish was placed in the experimental area between the mesh screens and allowed to settle for 10 minutes (see Chapter 4, Figure 4.1). 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 minute recovery. The cycle of 10 s – 10 s control – treatment followed by recovery was repeated with increasing field strength in increments of 0.05 Vcm^{-1} until *tetany* was observed.

The response (*no response*, *twitch*, *loss of orientation*, *tetany*) was recorded for each treatment interval.

External light levels and experimental tank temperature were measured before (mean temperature start [± SD]°C: cyprinid = 19.4 [± 0.78]°C, anguillid = 13.35 [± 0.61]°C) and after each trial (mean temperature end [± SD]°C: cyprinid = 19.5 [± 0.78]°C, anguillid = 13.44 [± 0.63]°C) and fish were weighed (mean mass [± SD] g: grass carp = 17.4 [± 5.3] g, common carp = 26.3 [± 7.45] g and anguillid = 334.4 [± 94.4] g) and measured at the end of each trial (mean total length [± SD] mm: grass carp = 121.0 [± 10.8] mm, common carp = 118.4 [± 10.9] mm and anguillid = 558.7 [± 52.2] mm, mean fork length [± SD] mm: grass carp = 110.3 [± 10.9] mm and common carp = 105.3 [± 16.7] mm and mean standard length [± SD] mm: grass carp = 100.1 [± 10.3] mm and common carp = 95.5 [± 8.93] mm).

7.3.4 Fish physiology

Physiological responses (see Chapter 4, Table 4.2) were based on experimental observations under the specified pulse frequencies and widths used. The lowest electric field strength measured that elicited each behaviour was quantified as the threshold strength for that physiological response.

7.3.5 Statistical analyses

Statistical analyses were conducted using R 3.5.1 (R Core Team, 2018). Data was visually inspected for normality before conducting a Shapiro-Wilk test. In the case that the data was non-parametric efforts were first made to transform it to achieve normality, and if unsuccessful non-parametric tests were performed. For both grass and common carp, the field strengths for: *twitch, loss of orientation* and *tetany* were compared across waveforms with respect to pulse width and frequency using Kruskal-Wallis tests. Kruskal-Wallis tests were also performed to test for differences in field strengths between cyprinid species (grass and common carp) and families (cyprinid and anguillid). Post-hoc analyses were performed using the Dunn’s Test.

7.4 Results

7.4.1 Threshold field strengths for physiological responses for grass and common carp across waveforms (objective 1)

For grass carp there was no evidence that threshold field strengths for *twitch* and *loss of orientation* were affected by pulse width (*twitch*: $\chi^2(3) = 1.06$, $p = 0.79$, *loss of orientation*: $\chi^2(3) = 2.69$, $p = 0.44$) (Figure 7.1a). Conversely, *tetany* was affected by pulse width ($\chi^2(3) = 12.4$, $p = 0.006$). Post-hoc analyses revealed *tetany* was elicited at a lower field strength in the single pulse- 2 Hz waveform treatment than the double pulse- 3 Hz (Dunn's Test: $z = -3.21$, $p = 0.008$). Pulse frequency did not affect threshold field strengths for any of the responses (*twitch*: $\chi^2(1) = 0.22$, $p = 0.64$, *loss of orientation*: $\chi^2(1) = 0.15$, $p = 0.7$ and *tetany*: $\chi^2(1) = 1.57$, $p = 0.21$).

For common carp, threshold field strengths for *twitch*, *loss of orientation* and *tetany* were not affected by pulse width (*twitch*: $\chi^2(3) = 1.80$, $p = 0.62$, *loss of orientation*: $\chi^2(3) = 0.41$, $p = 0.94$, *tetany:* $\chi^2(3) = 4.55$, $p = 0.21$) (Figure 7.1b). Pulse frequency also had no effect on threshold field strengths for *twitch* ($\chi^2(1) = 0.19$, $p = 0.67$), *loss of orientation* ($\chi^2(1) = 0.07$, $p = 0.79$) or *tetany* ($\chi^2(1) = 0.05$, $p = 0.82$).

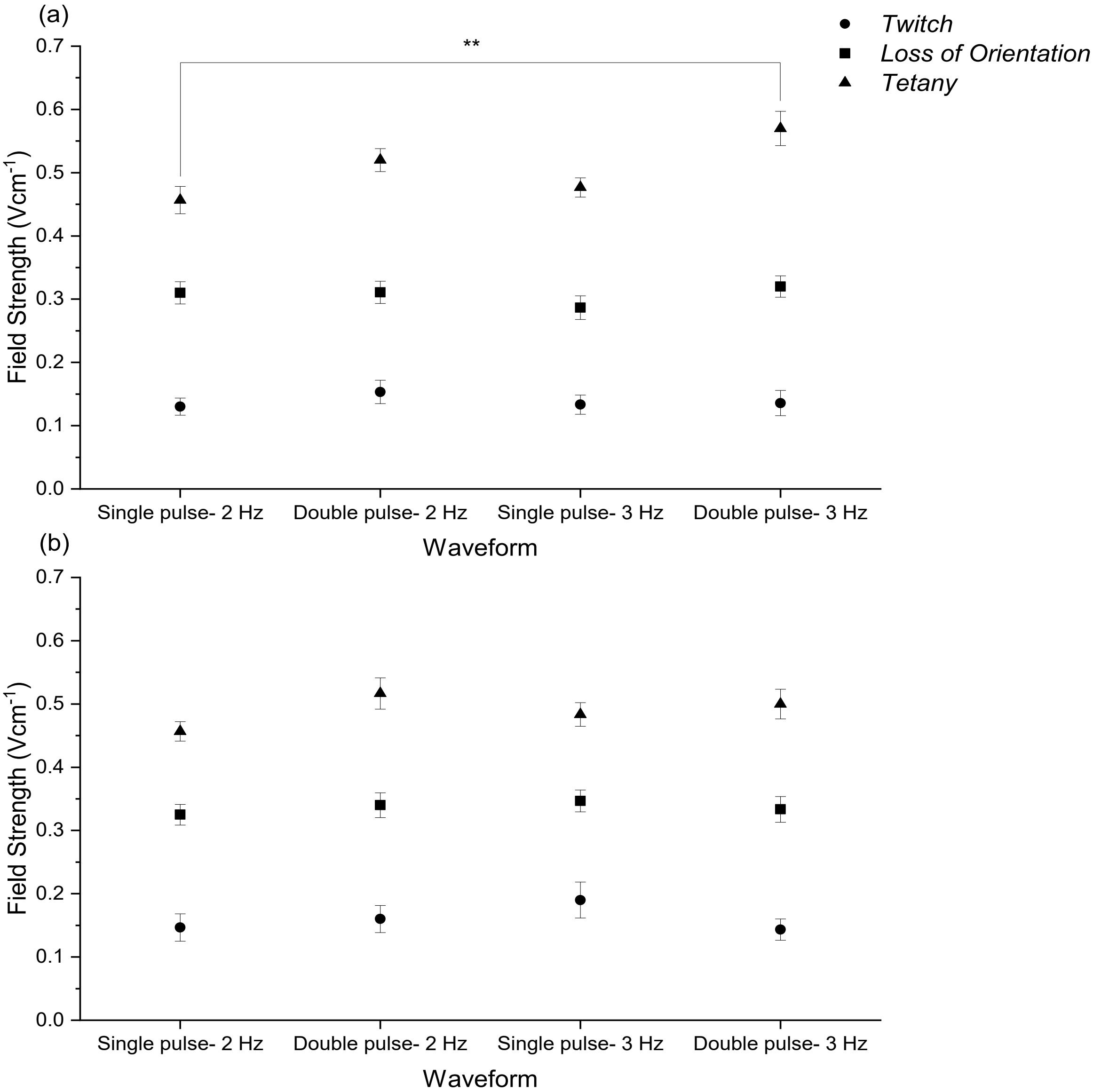


Figure 7.1. Mean threshold field strengths [± SE] for three physiological responses; *twitch*, *loss of orientation* and *tetany* exhibited by (a) grass carp and (b) common carp in four waveforms treatments (single pulse- 2 Hz, double pulse- 2 Hz, single pulse- 3 Hz and double pulse- 3 Hz). Note ** denotes $p < 0.01$.

7.4.2 Threshold field strengths for physiological responses between cyprinid species (objective 2)

In the single pulse- 2 Hz treatment there was no difference between grass and common carp for the threshold of *twitch* ($\chi^2(1) = 0.08$, $p = 0.78$), *loss of orientation* ($\chi^2(1) = 0.34$, $p = 0.56$) or *tetany* ($\chi^2(1) = 0.08$, $p = 0.78$) (Figure 7.2a). In the double pulse- 2 Hz there was no difference between grass and common carp for threshold of *twitch* ($\chi^2(1) = 0.002$, $p = 0.97$), *loss of orientation* ($\chi^2(1) = 1.30$, $p = 0.25$) and *tetany* ($\chi^2(1) = 0.007$, $p = 0.93$) (Figure 7.2b). In the single pulse- 3 Hz treatment there was no difference between grass and common carp for threshold of *twitch* ($\chi^2(1) = 1.96$, $p = 0.16$) and *tetany* ($\chi^2(1) = 0.10$, $p = 0.75$) (Figure 7.2c). Conversely, higher field strengths were required to ellict *loss of orientation* in common than grass carp ($\chi^2(1) = 5.51$, $p = 0.02$). In the double pulse-3 Hz there was no difference between grass and common carp for the threshold of *twitch* ($\chi^2(1) = 0.12$, $p = 0.73$), *loss of orientation* ($\chi^2(1) = 0.26$, $p = 0.61$) or *tetany* ($\chi^2(1) = 3.28$, $p = 0.07$) (Figure 7.2d).

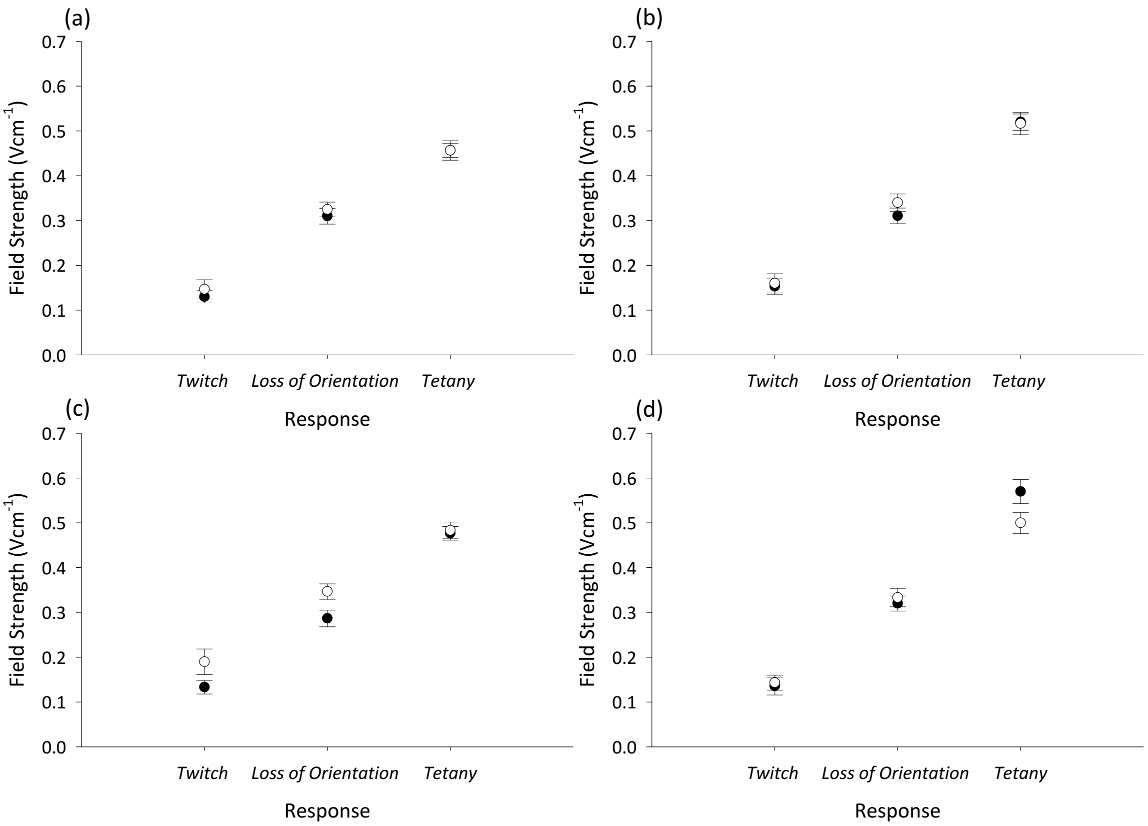


Figure 7.2. Mean [± SE] threshold field strengths of both grass (solid circles) and common (clear circles) carp for physiological responses (*twitch*, *loss of orientation* and *tetany*) across four waveforms tested (a) single pulse- 2 Hz, (b) double pulse- 2 Hz, (c) single pulse- 3 Hz and (d) double- 3 Hz.

7.4.3 Field strengths for physiological responses between cyprinids and anguillid species (objective 3)

As there were no differences for the single pulse- 2 Hz and double pulse- 2 Hz between grass and common carp for threshold responses (Figure 7.2a, b), data was aggregated (cyprinids) for comparison with European eel (anguillid) (Chapter 4).

For the single pulse- 2 Hz waveform each of the responses were elicited at a lower field strength for anguillid than cyprinids (*twitch*: $\chi^2(1) = 4.34$, $p = 0.04$, *loss of orientation*: $\chi^2(1) = 27.5$, $p < 0.0001$ and *tetany*: $\chi^2(1) = 28.9$, $p < 0.0001$) (Figure 7.3a). Similarly, for the double pulse- 2 Hz waveform all of the responses were elicited at a lower field strength for anguillid than cyprinids (*twitch*: $\chi^2(1) = 8.5$, $p = 0.004$, *loss of orientation*: $\chi^2(1) = 26.6$, $p < 0.0001$ and *tetany*: $\chi^2(1) = 28.1$, $p < 0.0001$) (Figure 7.3b).

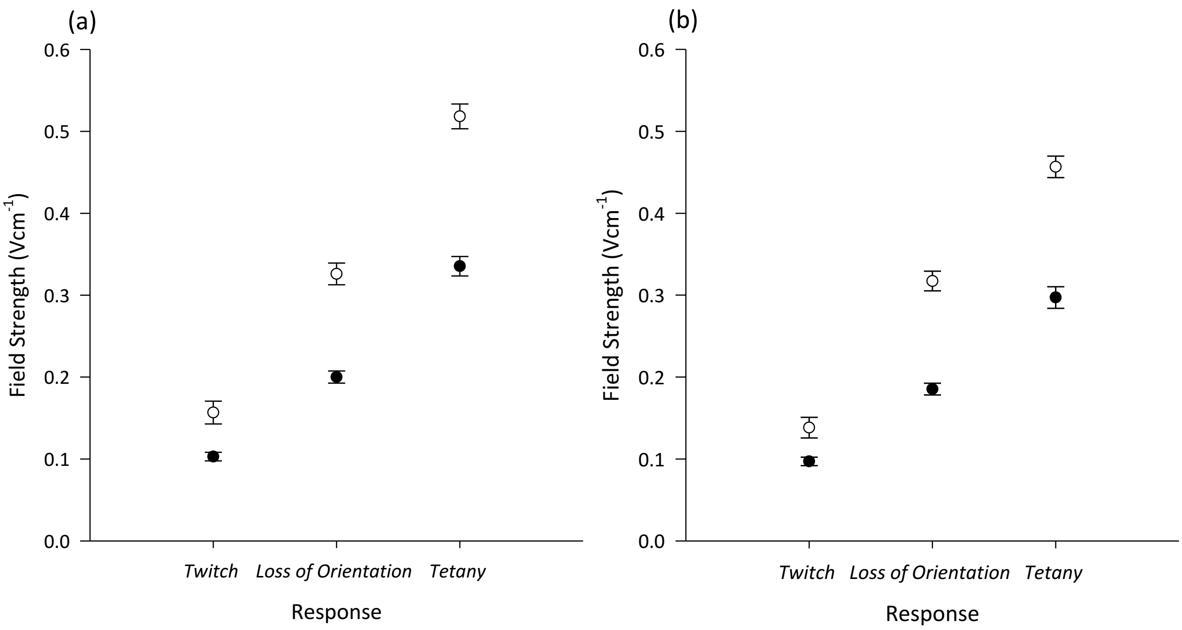


Figure 7.3. Mean [± SE] threshold field strengths in the (a) single pulse- 2 Hz and (b) double pulse- 2 Hz for three threshold physiological responses *twitch*, *loss of orientation* and *tetany* between cyprinid (clear circles) and anguillid (solid circles).

7.5 Discussion

To inform the development of selective fish guidance systems using electric fields, this study determined the electrosensitivity of two invasive cyprinids, grass and common carp, and compared the results with those obtained for an anguillid species of high conservation concern, the European eel (Chapter 4). For both cyprinids the threshold field strengths at which three key physiological responses (*twitch*, *loss of orientation* and *tetany*) were elicited were largely unaffected by the electric field parameters (pulse frequency and width), with one exception; grass carp exhibited *tetany* at lower field strengths under longer pulse widths. Electrosensitivity was similar between cyprinids except in the single pulse- 3 Hz waveform treatment where *loss of orientation* occurred at a slightly higher field strength for common than grass carp. The threshold field strengths for all physiological responses were higher for both cyprinid species (i.e. they exhibited lower electrosensitivity) than for adult European eel. This study provides the foundations for future research to further develop selective guidance / deterrent systems using electric fields.

At field strengths higher than 0.4 Vcm^{-1} both cyprinid species exhibited unvolitional *tetany*. At field strengths above this value effective guidance that requires the modification of a volitional response may be prohibited. Similar field strengths (0.2 – 0.4 Vcm^{-1}) are known to be effective at inhibiting common carp movement in the laboratory (Kim and Mandrak, 2017). Conversely, in the field higher field strengths (0.79 - 0.91 Vcm^{-1}) are employed to control Asian carp movement in the Chicago Sanitary Shipping Canal (Parker *et al.*, 2015), with the justification that no native species migrate through the canal (Moy *et al.,* 2011) and smaller silver carp are likely to have a lower electrosensitivity due to the voltage gradient measured across their body (anterior to posterior) (Dolan and Miranda, 2003; Parker *et al.*, 2015).

Minimal differences in threshold field strengths of responses were observed across the waveforms with respect to pulse width and frequency. However, for grass carp, *tetany* occurred at lower field strengths in the single pulse- 2 Hz treatment than for the double pulse- 3 Hz waveforms, presumably due to the longer pulse width in the former (100 ms compared to 16.7 ms). This observation might be explained by the fact that the current has more time to rise to a maximum and fall back to zero during each period when pulse widths are relatively long. Thus this would provide more time for voltage to rise across the capacitance of the fish, resulting in greater probability of eliciting *tetany* at lower field strengths. This suggestion makes sense when considering observations related to current applications. For example, higher peak voltages (power) are needed to immobilise fish when shorter pulse widths are used in electric fishing (Dolan and Miranda, 2003), while longer pulse widths reduce the probability of fish passing an electric barrier (Layhee *et al.*, 2016 for juvenile and adult rainbow trout, *Oncorhynchus mykiss*). Interestingly, pulse width did not have a similar and consistent effect for other responses, perhaps suggesting that the more extreme physiological responses, such as *tetany*, are more sensitive to differences in pulse width.

Pulse frequency did not influence any of the threshold field strengths of responses considered for either grass or common carp. The absence of an effect might be explained by the minimal difference in pulse frequency between the waveforms employed (2 vs. 3 Hz). We selected relatively low frequencies for use in this study because: (1) previous observations indicate they are effective at modifying fish movements (e.g. Mesa and Copeland, 2009 for steelhead, *Oncorhynchus mykiss* and Pacific lamprey, *Entosphenus tridentatus* at 3 Hz and 2 Hz; Savino *et al.,* 2001 for round Goby, *Neogobius melanostomus*, at 2 Hz); (2) the risk of injury is reduced compared to higher frequency waveforms (e.g. Miranda and Kidwell, 2010; Culver and Chick, 2015); and (3) low frequency waveforms can be generated using less power and thus would reduce economic costs and the carbon footprint compared to other systems (Beaumont, 2016). As already described, carp appear to have lower electrosensitivities than eel, and considering the information available this may be the case when compared with other species. Further research is needed to identify the electrosensitivities of other native fish that inhabit areas where an electric barrier might be deployed to control invasive carp.

Both cyprinid species exhibited similar electrosensitivities with no interspecific differences in the response to the single pulse- 2 Hz, double pulse- 2 Hz and double pulse- 3 Hz observed. However, the one exception was the *loss of orientation* exhibited by grass carp at lower field strengths than for common carp in the single pulse- 3 Hz waveform treatment. Previous work indicates that the threshold field strength for immobilisation is negatively related to the length of the fish (Briggs *et al.*, 2019). In this study, grass carp were longer than common carp, but the difference was slight (e.g. 5 mm in mean fork length). It may be possible that *loss of orientation* is more sensitive to differences in body length than the other physiological responses but further work is needed to confirm this. The alternative is that even among closely related species there is sufficient interspecific differences in physiological response to result in slight differences in the effectiveness of different electric field treatments and the potential to develop selective guidance systems that can separate closely related species within the same family.

European eel appear to be more electrosensitive than both cyprinid species, with lower threshold field strengths obtained for all physiological responses exhibited (see Chapter 4). The most likely explanation is the considerably longer body length of the adult eel resulting in a greater anterior-posterior voltage differential if parallel to field lines (Reynolds, 1996). The difference in electrosensitivity may also reflect physiological differences (e.g. fish conductivity, scale differences, muscle composition) between the two families, although further experimentation in which body length is controlled for is needed to test this.

This study quantified the threshold field strengths at which physiological responses are exhibited for two invasive carp species and compared these with previously collected data for European eel. Eel have a higher electrosensitivity than the invasive carp, while the carp largely responded to the electric field treatments in a similar way. The results have value in informing the development of selective multi-species barriers and guidance devices that employ electric fields. The differences in electrosensitivity exhibited between families indicates promise in adopting this approach as part of an integrated pest management programme in which there is also an interest in the conservation of native species at risk of river infrastructure. For instance, due to their higher electrosensitivity, such a device could employ a weak electric field to deflect eel towards preferred routes of passage while the less sensitive cyprinids might continue unaffected toward a trap. This study provides a fundamental first step in the design of future selective guidance systems that utilise field studies to validate the results obtained and optimise the parameters of the electric fields used.

Chapter 8 Thesis discussion

Globally, as human population continues to grow so too will the demands for energy, electricity, and water. Consequently, proposed plans for river infrastructure will increase and so place further pressure on freshwater ecosystems. Hence, there is a growing need to develop effective mitigation strategies to minimise the negative impacts on freshwater species. Historically, these strategies have focused on the use of physical devices such as screens and fish passes. However, screening can be costly and lead to injury and mortality (i.e. impingement) and fish passes can have low attraction efficiency and inadvertently facilitate the further spread of invasive species. Behavioural guidance systems have received attention as a potential alternative or enhancement to physical devices. These guidance systems could be used to divert fish from hazardous areas (e.g. water intakes) and/or towards safer routes (e.g. bypasses) (Coutant, 1999; Schilt, 2007) and block further spread of invasive species. Electric fields are one type of stimuli that could be adopted but to date limited research has been performed assessing both fundamental responses of fish to electricity and its potential as a guidance system. This thesis has provided initial insights into the use of electric fields for three key applications: (1) the guidance of critically endangered European eel (*Anguilla anguilla*), (2) controlling the spread of two invasive cyprinid species, grass carp (*Ctenopharyngodon idella*) and common carp (*Cyprinus carpio*) and (3) situations where both these applications are needed (i.e. selective guidance systems). This was achieved through laboratory (i.e. tank or flume) based experimental studies (Chapters 4 - 7). This chapter discusses the key findings of the research in terms of fundamental knowledge obtained, limitations, future directions and potential implications for management strategies using electric fields to successfully guide fish.

It is widely understood and accepted that fish react to electric fields, but many definitions of these responses exist (Lamarque, 1967). These definitions have also been largely documented in relation to evaluating and optimising electrofishing practices to minimise injury and mortality (e.g. Dalbey *et al.,* 1996; Pottier *et al.,* 2020) rather than within the context of fish guidance. The work presented throughout this thesis confirms that fish react to electric fields and responses were defined based on direct observations with respect to the experimental set-up and parameters used. Interestingly, the responses obtained under static water conditions were markedly different from those in flowing water. This is possibly due to the electric field distribution and the presence of flow enabling the fish to move out of the electrified area. Hence, these responses were broadly split into two categories: physiological (static water) and behavioural (flowing water).

The literature review revealed that fundamental research into the threshold field strengths eliciting physiological responses (i.e. electrosensitivity) is lacking for three species of management concern, European eel, grass and common carp. The results from Chapter 4 and 7 found all three species showed physiological responses when exposed to pulse direct current (PDC) waveforms in static water tests. Based on direct observations these physiological responses were defined as *twitch*, *loss of orientation* and *tetany* (Table 4.2). Each of these responses occurred at distinct field strengths which supports previous work on other species (e.g. Bearlin *et al.,* 2008 for Murray cod, *Maccullochella peelii peelii*). That is, for each physiological response a threshold intensity (i.e. field strength) must be met and if this is increased further to reach a new threshold, a different response will be elicited (Reynolds and Kolz, 2012). In Chapter 4 and 7 depending on waveform used, the mean threshold field strength for each of the responses occurred at a distinct intervals. For adult eel the mean threshold field strength was between 0.1 – 0.11 Vcm^{-1} for *twitch*, 0.18 – 0.2 Vcm^{-1} for *loss of orientation* and 0.25 – 0.34 Vcm^{-1} for *tetany*. To the best of our knowledge estimates for threshold field strengths for European eel have not been performed but flinching behaviour was observed for the majority of eel approaching an electric field of 0.1 – 0.15 Vcm^{-1} in a laboratory flume (Meister *et al.*, 2021). For grass carp the mean threshold field strength of *twitch* occurred between 0.13 – 0.15 Vcm^{-1}, *loss of orientation* between 0.29 – 0.31 Vcm^{-1}, and *tetany* between 0.46 – 0.57 Vcm^{-1}. A previous study found the immobilisation threshold for grass carp was within a comparable range of the field strengths found in Chapter 7, for example under 10 Hz this could be observed at 0.4 Vcm^{-1} (depending on water temperature and conductivity) (Briggs *et al.*, 2019). Finally for common carp the mean threshold field strength of *twitch* occurred between 0.14 – 0.19 Vcm^{-1}, *loss of orientation* between 0.33 – 0.35 Vcm^{-1} and *tetany* between 0.46 – 0.52 Vcm^{-1}. Another study found common carp respond to comparable field strengths (i.e. 0.2 – 0.4 Vcm^{-1}) (Kim and Mandrak, 2017). Other studies with cyprinids on silver carp (*Hypophthalmichthys molitrix*) have found thresholds for initial responses were seen at consistently 0.15 Vcm^{-1} (Holliman, 2015). However, care must be taken when comparing values as sometimes sufficient details of experimental set-up and parameters are not provided and differences in reported responses.

Studies on electrofishing have shown that parameters such as pulse frequency can affect injury and mortality rate of fish (e.g. Schreer *et al.,* 2004 for rainbow trout, *Oncorhynchus mykiss*). In Chapter 4 and 7 the effect of pulse frequency on threshold field strengths for physiological responses was assessed. The results showed that the relationships between field strengths and frequency was not consistent across species. However, for adult eel *tetany* was exhibited at lower field strengths under a higher pulse frequency (10 Hz) in Chapter 4. As frequency increases it is thought that myoclonic jerks due to muscle contractions become more severe (Sharber *et al.*, 1994) hence the likelihood of injuries grows (e.g. Culver and Chick, 2015 for silver carp). This could explain the lower field strengths required to elicit *tetany* under a higher pulse frequency for adult eel. Furthermore, in PDC the polarisation of the water occurs at rising and falling edges of each pulse and so under higher frequencies this will occur more often, increasing the likelihood of a response. In contrast, frequency had no effect on threshold field strengths for either cyprinid species in Chapter 7, but this could be due to the smaller relative difference in frequency tested in comparison to eel (1 Hz vs. 8 Hz respectively). Alternatively, the longer body length of eel might be more sensitive to changes in frequency and associated myoclonic jerks, as larger muscles are unable to relax between pulses (Halsband, 1967).

Pulse width is another variable thought to influence fish response but has received less attention than frequency. In Chapter 4 and 7, both adult eel and grass carp exhibited *tetany* at lower field strengths under longer pulse widths. Previous studies have found similar results for other species with lower field strengths required to elicit a response under longer pulse widths (e.g. Klima, 1974 for longspine porgy, *Stenotomus caprinus*, and scaled sardine, *Harengula jaguana*). Similarly, increasing pulse width lowered the voltage required to produce the same tension in muscle for plaice (*Pleuronectes platessa*) and Atlantic cod (*Gadus morhua*) (Stewart, 1990). One proposed explanation for these results is that during a longer pulse, the current has the ability to rise more. Hence, in Chapter 4 and 7, lower field strengths were sufficient to elicit *tetany* under longer pulse widths which are also reported to increase the mean electric power transferred to the fish (Beaumont, 2016). In contrast, a poor correlation was found between voltage gradients for responses and pulse width for rainbow trout and goldfish (*Carassius auratus*) (Bird and Cowx, 1993). In Chapter 4 and 7 only *tetany* was affected by pulse width for adult eel and grass carp and so perhaps more extreme responses (i.e. *tetany*) are more sensitive to changes in parameters. In this way, discrepancies in the effect of pulse width on fish responses between studies might be explained by differences in behaviours recorded. Whilst the results from the static water tests (Chapter 4 and 7) provide initial quantitative data, in order to assess the potential for electric fields as a fish guidance system, behavioural responses (both avoidance and guidance) need to be evaluated under more realistic conditions (i.e. flowing water). Hence, further experiments (Chapters 4, 5 and 6) were performed to assess avoidance and guidance behaviour.

The literature review (Chapter 2) revealed most of the research assessing the behavioural responses of fish in order to design electric guidance systems has focused on invasive species (e.g.

Dawson *et al.,* 2006 for Eurasian ruffe, *Gymnocephalus cernuus*) whereas studies with species of conservation concern such as European eel are very limited (e.g. McGrath *et al.*, 1969). Hence, the experiments in Chapter 4, 5 and 6 were performed to assess the behavioural responses of three key life-stages of European eel: glass, yellow- and silver-phase with respect to electric field parameters under flowing conditions.

In the same way as physiological responses, altering electric field parameters such as pulse frequency and field strength can all effect avoidance and guidance behaviour in fish (Mesa and Copeland, 2009; Holliman *et al.,* 2015; Layhee *et al*., 2016). Whilst frequency had no effect on avoidance in both adult and juvenile eel, a 2 Hz pulse frequency was more optimal at achieving guidance than 10 Hz for upstream migrating juvenile eel (Chapter 5). This was surprising as not only are higher pulse frequencies reported to increase injuries (e.g. Larson *et al.,* 2014 for Yellowstone cutthroat trout, *Oncorhynchus clarkii bouvieri*), but they have also been shown to reduce passage across an electric field array (e.g. Mesa and Copeland, 2009 for steelhead, *Oncorhynchus mykiss* and Pacific lampreys, *Entosphenus tridentatus*). The proposed explanation for the higher guidance efficiency under the lower pulse frequency for juvenile eel could be due to the longer pulse width of the 2 Hz waveform providing the current more time to rise to a maximum. Alternatively the higher pulse frequency (10 Hz) could have rendered the eel incapacitated and so be unable to exhibit voluntary movement but there was no evidence of this from the behavioural observations in flowing water conditions. If lower pulse frequencies are more effective at guidance this would be beneficial as this should reduce injury rate and potentially power consumption (Snyder, 2003; Beaumont, 2016). In contrast, guidance efficiency did not differ between frequencies (2 and 10 Hz) for downstream migrating (silver-phase) adult eel (Chapter 6). The difference between these two migratory life-stages could be due to their direction of travel (i.e. upstream vs. downstream) which might influence the sensitivity of individuals to alterations in pulse frequency. Alternatively, it could be due to differences in the set-up between experiments. That is, successful guidance for juveniles was defined as passage though the Low Electric Field Route (LEF), which eel could access at any point throughout the experimental area by lateral movements. Conversely, for adults, guidance was determined by passage through a Non-Electrified Channel which was separated from the Electrified Channel by a physical partition (aluminium sheet). Hence for successful guidance to be achieved for adults, eel either had to select the Non-Electrified Channel before the physical partition or exhibit *rejection* (within the Electrified Channel), re-approach and pass through the Non-Electrified Channel. It seems appropriate to suggest that the occurrence of *rejection*, particularly during the migratory life-stages (i.e. juvenile and adult eel), would be less common than lateral movements and so caution should be taken when directly comparing these two results.

Only juvenile eel appeared sensitive to changes in field strength for both avoidance and guidance behaviour (Chapter 5). Under the higher field strength treatments, guidance efficiency increased with more eel passing through the LEF and largely more avoidance observed. Conversely, no effect of field strength was found on avoidance or guidance (i.e. preference for Non-Electrified Channel) for yellow- or silver-phase eel (Chapter 4 & 6). This raises questions about the suitability of electric fields for fish guidance depending on life-stage and behaviour. There is limited information on the exact mechanism of how fish detect electric fields but it is possible that due to morphological, behavioural and/or physiological changes during the life-cycle of eel, the perception of electric fields may change. The results from these chapters more generally raise questions about how different life-stages perceive and detect differences in electric field parameters.

Overall, the findings from this research project suggest electric fields were more effective in terms of eliciting avoidance and guidance for upstream migrating juvenile eel and so electric barriers might be more suitable for this life-stage. For upstream moving fish, if electric fields elicit an adverse response, fish will turn and the natural flow direction will take them away from the area preventing further progression upstream. Hence, the applicability of electric fields for fish guidance is considered greater for upstream moving fish (Beaumont, 2016). In contrast, downstream moving fish are thought to be harder to guide as the electric field might render them incapacitated and so they could be swept through the barrier. The results from Chapter 6 also suggested yellow-phase eel were more likely to exhibit avoidance when moving upstream than downstream. Water velocity is often cited as a potential limitation to the effectiveness of an electric barrier for downstream migrating fish (see Pugh *et al.,* 1970; Miehls *et al.,* 2017). This might explain why more focus has been placed on implementing electric guidance systems for upstream migrating fish (e.g. Swink, 1999 for sea lamprey, *Petromyzon marinus*) whereas limited research has been placed on downstream moving fish and high effectiveness is often only observed under low water velocities (i.e. 0.03 - 0.05 ms^{-1} for round goby, *Neogobius melanostomus*; Savino *et al.,* 2001). This was supported by the results from Chapter 4 as downstream moving adult eel exhibited less avoidance under the higher water velocity (1.0 ms^{-1}). Additionally, even under a lower water velocity in Chapter 6 (approx. 0.26 ms^{-1}), successful guidance to the Non-Electrified Channel was still only observed for just over half (55.7%) of downstream migrating adult eel. Although the results suggest water velocity might limit the effectiveness of electric fields to guide downstream migrating fish, it is possible that this limitation could be alleviated or minimised using different parameters (i.e. field strength, frequency) and electrode orientation.

Research into fish responses to electric fields has tended to focus on one application, either blocking invasive species or guiding native fish away from hazardous routes (i.e. water intakes). Whilst this might be appropriate in areas where invasive and native species do not co-exist, often this is not the case. Hence, the next step in designing suitable guidance systems is accounting for site specific factors such as species assemblages with respect to management needs (i.e. invasive and/or native species) and assessing stimuli sensitivity to ensure species selectivity. Exploiting sensory differences to achieve selective fish guidance systems has been suggested (Rahel and McLaughlin, 2018) but specific research comparing electrosensitivities has not been explored. In this way, the final research chapter (Chapter 7) provided a direct comparison of electrosensitivities between the critically endangered adult European eel and two known invasive cyprinid species (grass and common carp). The results showed eel had a higher electrosensitivity than both cyprinid species, that is, all physiological responses (*twitch*, *loss of orientation* and *tetany*) occurred at lower field strengths for eel than both grass and common carp. This could be explained by the difference in body size as larger fish have been shown to have higher electrosensitivities due to the greater voltage gradient felt across their body (anterior to posterior) (Dolan and Miranda, 2003). Adult eel used in this study were almost five times the length of the cyprinid species and hence the voltage gradient felt along the body would be greater which could explain the higher electrosensitivity observed. It is also possible that other physiological differences, not explored in this research, between families could also influence electrosensitivity, such as muscle composition or scale differences (Stoot *et al.*, 2018) or metabolic variance and fish conductivity (Sternin *et al.,* 1976) but no exact values for these species exists. Consequently, the precise reason for the difference in electrosensitivity between cyprinids and anguillid is not known. However, ultimately the results from Chapter 7 are promising in terms of designing a selective fish guidance system as it might be possible to design an electric field in which native fish are guided to safer routes (e.g. bypasses) whilst invasive species are blocked or unaffected. Alternatively, an electric field could be set-up to deflect fish into a trap for either removal (i.e. invasive species) or release past the impoundment (i.e. native species). Further, utilising differences in electrosensitivity could be even more advantageous if the target and non-target species have different activity patterns as these systems can be completely switched off (Johnson *et al*., 2021). The results from this study provide a useful first step in the development of guidance systems to ascertain the electrosensitivity of species to inform future applied studies under more realistic flowing conditions.

8.1 Future research

The results presented throughout this thesis provided initial insights into the responses of fish to electric fields and directions for future research. Whilst some of the results suggest there might be potential limits to the use of electric fields for fish guidance, depending on what the management goal is (e.g. 100% effectiveness), these limitations may be alleviated or at least minimised through future research. This section will discuss some of the recommended future steps to achieve this.

Based on the findings from Chapter 4, 5 and 6 future research should investigate ways to translate avoidance behaviour more effectively into guidance for all life-stages of European eel. Moreover, whilst testing parameters that elicit avoidance is a useful first step, predicting movements after exposure (i.e. guidance) to the stimuli is crucial for management goals (Coutant, 1999). Further testing to optimise electric field distribution and parameters is one approach which could be used to improve effectiveness. For example, it might be possible to increase guidance efficiency through alternative electrode configurations (i.e. angled to the direction of water flow) and/or electric field parameters (i.e. frequency and field strength). One field study found electrodes orientated at 55° to the riverbank successfully guided 75% of upstream migrating sea lamprey into a trap (Johnson *et al.*, 2016). Different electrode orientations (30° and 45° to the direction of water flow) have also been tested in the laboratory for downstream migrating sea lamprey (Johnson and Miehls, 2014; Miehls *et al.,* 2017) but water velocity was a limiting factor to effectiveness. The limitation of higher water velocity on electric barriers was also found in Chapter 4 hence, future testing of parameters should also work to alleviate this.

Another possible strategy to improve the effectiveness of a guidance device would be to incorporate several stimuli into a multimodal system (Putland and Mensinger, 2019). Integrating multiple stimuli is thought to improve the effectiveness and minimise the chance of acclimatisation to a guidance system (Noatch and Suski, 2012). Moreover, if stimuli act on more than one sensory modality (i.e. auditory, visual) this could enhance detection and increase the probability of a response and consequently the efficiency of a guidance system (Deleau *et al.*, 2020b). Using electric fields in a multi-modal guidance system is relatively unexplored but one study found incorporating electricity into an acoustic barrier reduced the likelihood of acclimatisation for Atlantic salmon (*Salmo salar*) in field trials (Clegg, 1997). Other multimodal systems have also proved effective for example, bubbles and acoustics repelled 95% of Asian carp movements in the laboratory (Pegg and Chick, 2004). Similarly, when strobe lights were tested in combination with air bubbles, the avoidance response of Alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*) and American gizzard shad (*Dorosoma cepedianum*) increased from 38 – 73% to 90 – 98% (Patrick *et al*., 1985). Further, a barrier consisting of lights, bubbles and acoustics, termed the 'Bioacoustic Fish Fence', was effective at diverting a high proportion of juvenile Atlantic salmon from one river channel to the other (Welton *et al.,* 2002). Developing a multi-modal guidance system appears to be an attractive option to enhance effectiveness but it does also raise questions about how fish will perceive the interaction of the stimuli and whether desired behaviours will be elicited.

Management decisions on fish protection measures often poses a trade-off between physical devices which can incur large costs but offer high exclusion albeit with potential associated mortality, and behavioural devices which are more cost-effective but may not achieve 100% effectiveness. Hence, another future direction of research would be to explore a combination of both physical and behavioural devices. In this way, overall efficiency could improve and/or potentially mitigate against possible adverse effects (e.g. impingement). This has been shown in laboratory studies for example, light stimuli used in conjunction with physical louver rack achieved the highest rate of bypass usage (100%) for downstream moving white sturgeon (*Acipenser transmontanus*) (Ford *et al*., 2017). Similarly, in the field a fish protection system consisting of a physical barrier, light and acoustics proved effective in guiding fish at a dam on the Savannah River even though stimuli individually were not efficient (Nestler *et al*., 1995; Ploskey *et al*., 1995). Electric fields have also been integrated into physical devices by mounting electrodes onto vertical bar racks creating a hybrid barrier termed the 'Bar-Screen-FishProtector' (Haug *et al*., 2021) to prevent entrainment at hydropower water intakes. The mean fish protection rate from passage through the racks increased from 62% to 96% when the electrodes were activated (Haug *et al.*, 2022). Similarly, an electrified horizontal bar rack achieved 86% fish protection efficiency for eel although some injuries (e.g. haemorrhaging) were also reported (Meiste*r et al*., 2021). Another hybrid device termed the 'Electric Flexible Fish Fence' consisting of angled steel cables used both as a physical barrier and as electrodes found under all activated electric field setups the fish protection rates were > 97% (Tutzer *et al.*, 2021). A separate study using the electric fish fence at a pumping station showed less success in terms of fish avoiding the area (approx. 72%) (Egg *et al*., 2019). This mixed effectiveness could be due to the differing metrics recorded, environmental variables (e.g. temperature, water velocity) or experiment set-up (laboratory vs. field) hence further testing is needed.

This research project investigated the responses and use of electric fields for fish guidance under laboratory conditions. Whilst this is a crucial first step it cannot wholly replicate real-life situations. In the wild, variables such as water temperature or velocity could alter or even override behavioural responses (Popper and Carlson, 1998) and other factors such as substrate conductivity can affect the distribution and localisation of the electric field generated. Hence, whilst promising results may have been obtained within this research project these need to be tested and verified in the field. Moreover, differences have been found between laboratory and field studies for example, an electric screen was found to be 95% effective at eliciting ide (*Leuciscus idus*) and European perch (*Perca fluviatilis*) to avoid an area, but this efficiency was not achieved (approx. 70%) at a small water intake in the field albeit with a wider range of species (Hadderingh and Jansen, 1990). However, the effectiveness of any behavioural guidance system will always be limited if accurate knowledge of responses to the stimuli is not obtained (Coutant, 1999). Although not specifically covered in this research project it might also be useful to further understand the physiological mechanisms of how fish perceive and detect electric fields. In this way, it is still important that research be performed in the laboratory to obtain fundamental responses and sensory capabilities of species in a controlled environment. These responses must then be validated in the wild with respect to environmental and site-specific variables present. Ultimately, a cross collaboration of both field and laboratory work is required to advance the field of research and the effectiveness of any behavioural device must be tested under a range of environmental conditions (Popper and Carlson, 1998; Perry *et al.*, 2014).

Future studies also need to evaluate the effectiveness of electric barriers with respect to management needs. For example, in Chapter 5, under the most optimal treatment (i.e. 1.22 Vcm^{-1} and 2 Hz) just over three-quarters (78.3%) of juvenile eel showed a preference to pass a route of lower electric field strength (LEF). However, within fisheries management any fish barrier that is not 100% effective is sometimes considered ineffective and not a practicable option (Clarkson, 2004). Whilst it is considered, and supported by the results here, challenging to attain 100% effectiveness with a behavioural guidance system, currently there is not enough data to justify this. Therefore, it might be possible to achieve this efficiency through careful testing and planning of parameters (O'Farrell *et al*., 2014). In addition, there might be situations where a barrier with < 100% effectiveness might be acceptable such as where the goal is reducing injury and mortality at water intakes in comparison to complete exclusion of species (i.e. invasive species) (Noatch and Suski, 2012).

Once a guidance system is proved effective in the wild for the management needs, the operational functioning would need to be checked to ensure stimuli worked over long distances and large areas and showed no signs of decreased effectiveness over time (Popper and Carlson, 1998). The operational management would also have to work to optimise behavioural stimuli in terms of economic effectiveness. For example, it is thought that behavioural guidance is more cost-effective than physical devices due to lower capital and maintenance expenses (Turnpenny *et al.,* 1998; Turnpenny and O'Keeffe, 2005) but there is not enough data and results to accurately quantify this (Popper and Carlson, 1998). It is possible that, through further research into the optimisation of parameters associated with their design, these devices would be more effective both in terms of guidance and costs.

8.2 Conclusions

The overall aim of this thesis was to advance scientific knowledge of the responses of fish to electric fields as a potential guidance system. To realise this aim, six objectives were formulated (see Chapter 3). The conclusions drawn are summarised in relation to each of the objectives below.

Objective 1: Review current literature to identify research trends and knowledge gaps on the conservation of European eel, cyprinid invasive species management and fish response to electric fields.

A literature review in Chapter 2 revealed that river infrastructure is one of the main contributors to the decline of freshwater species. Current methods to mitigate the negative impacts of infrastructure on fish have primarily focused on physical devices (e.g. screens, bar racks, fish passes). However, these have several drawbacks including high costs, possible injury and mortality and inadvertently enabling the spread of invasive species. Consequently, the use of behavioural stimuli (e.g. light, acoustics, bubbles, electricity) to control fish movements has been suggested as a possible alternative or enhancement. In terms of eel guidance, most research has focused on downstream migrating adults (silver-phase) using acoustics and light with relatively little known about the applicability of electric fields. For invasive cyprinid management, electric barriers have been implemented in the field but ensuring species selectivity through the quantification of electrosensitivities has not been performed. Furthermore, some of the research that has been undertaken has failed to accurately quantify the electric field parameters (i.e. field strength, pulse frequency and width) tested, or has focused within the context of electrofishing. Hence, the effects of these parameters on fish guidance requires more attention and research addressing this needs to be performed.

Objective 2: Quantify the physiological responses of fish to PDC electric fields.

Threshold field strengths for key physiological responses (*twitch*, *loss of orientation* and *tetany*) were obtained with respect to pulse frequency and width for adult (silver-phase) European eel, grass and common carp (Chapter 4 and 7). The results showed that physiological responses occurred at distinct field strengths for all species, but differences were present with respect to pulse frequency and width. Adult eel exhibited *tetany* at lower field strengths under the higher pulse frequency tested (10 Hz). *Tetany* was also elicited at lower field strengths under longer pulse widths for both adult eel and grass carp. These results highlight the importance of accurately quantifying responses with respect to electric field parameters tested.

Objective 3: Quantify the behavioural responses of eel to PDC electric fields.

Avoidance and guidance behaviours were assessed for three life-stages of European eel, juvenile (glass), yellow-phase and adult silver-phase. Higher field strengths increased avoidance and guidance efficiency in juvenile eel (Chapter 5). Neither avoidance nor guidance efficiency was affected by field strength for yellow- and silver-phase eel (Chapter 4 & 6). Further, in contrast to predictions, a lower pulse frequency treatment (2 Hz) was also found to be more optimal at guidance for juveniles (Chapter 5) but no relationship was observed for adult silver-phase eel (Chapter 6).

Objective 4: Assess the effectiveness of electric fields with respect to water velocity for downstream migrating silver-phase eel guidance.

The effectiveness of an electric barrier was compared across two water velocities for downstream migrating adult (silver-phase) eel (Chapter 4). Under the higher water velocity (1.0 ms^{-1}), less *acceleration* and *rejection* and more *no change* occurred. The results suggest that water velocity might be a limiting factor to the effectiveness of electric barriers for downstream migrating eel.

Objective 5: Quantify the behavioural responses of yellow-phase eel to electric fields with respect to direction of travel.

Behavioural responses of yellow-phase eel to electric fields were compared between upstream and downstream approaches. Yellow-phase eel were more likely to exhibit avoidance on upstream approaches but guidance efficiency was not effected by direction of travel. These results offer some support to the theory that electric barriers might be more effective for fish moving upstream.

Objective 6: Compare the electrosensitivity of cyprinid and anguillid species.

The threshold field strengths for physiological responses (*twitch*, *loss of orientation* and *tetany*) were directly compared between two cyprinids (grass and common carp) and one anguillid species (adult European eel) (Chapter 7). The results found that adult eel had a higher electrosensitivity than both cyprinid species likely attributed to the longer body length of eel (i.e. greater voltage gradient). This chapter highlighted the potential for designing species selective fish guidance systems based on electrosensitivity.

8.3 Research impact

As a result of this thesis a number of novel contributions to the existing knowledge have been made in the area of fish responses to electric fields and its potential as a guidance system:

- A literature review (Chapter 2) highlighted key research gaps in the knowledge of fish responses to electric fields and its application as a guidance system. The use of both static and flowing water conditions was highlighted to assess fundamental (physiological) and behavioural (guidance) responses of fish to electric fields.
- The physiological and behavioural responses of adult (silver-phase) European eel were assessed (Chapter 4) under both static and flowing water conditions. Firstly, the quantification of key physiological responses (i.e. electrosensitivites) of adult silver-phase eel was performed with respect to both pulse frequency and width. Secondly, eel were tested under flowing water conditions to test both the influence of field strength and water velocity on behavioural responses. This was the first study to accurately obtained physiological responses of adult eel with respect to electric field parameters and assess the effectiveness of an electric field barrier under flowing water conditions. The results from this Chapter have been published in Ecological Engineering. This paper is titled "Behavioural response of downstream migrating European eel (*Anguilla anguilla*) to electric fields under static and flowing conditions". The results from this Chapter were also presented at the Easter Animal Behaviour Virtual Meeting 2021.
- Chapter 5 used a novel set-up to assess the behavioural responses of upstream migrating juvenile (glass) eel to a two-choice test with a High and Low Electric Field Strength Route (H/LEF). Guidance to the LEF and avoidance was assessed across five different field strengths and two different pulse frequencies. This work has been published with PLoS ONE as Miller *et al.,* "Response of upstream migrating juvenile European eel (*Anguilla anguilla*) to electric fields: application of the marginal gains concept to fish screening".
- Chapter 6 assessed the responses of both yellow- and silver-phase eel to a two-choice test with an Electrified and Non-Electrified Channel. Guidance to the Non-Electrified Channel and avoidance was assessed with respect to electric field parameters (i.e. field strength and pulse frequency) and direction of travel. This work will be submitted to Journal of Fish Biology as Miller *et al.,* "Behavioural response of European eel (*Anguilla anguilla*) to two-choice electric field test".
- A direct comparison of electrosensitivities was performed in Chapter 7 between species and families (i.e. cyprinid vs. anguillid) to assess the potential of electric fields for selective fish guidance. This work will be submitted to Scientific Reports as Miller *et al.,* "Developing electric deterrents for selective-fish guidance: Interspecific variation in response to pulsed direct currents".

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