Assessing Behavioural Guidance Methods to Reduce Turbine Mortality and Improve Downstream Passage of Out-Migrating Anguillid Eels

by

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Abstract

Hydropower infrastructure poses a great risk to fishes. The goal herein was to study how behavioural guidance could improve downstream passage of anguillid eels. First, I undertook a review of potential behavioural guidance methods for eel and found that light and sound seem most promising, and that these methods could be particularly useful if used to augment physical guidance. Second, I took part in a field assessment of light as an eel guidance mechanism using a 216 m light guidance device. I analyzed eels' vertical movement and various correlates of out-migration. In this chapter, I found that eels exposed to above-water light exhibited diving behaviour, and observed nocturnal migration coinciding with darkening lunar phases. This work consolidates evidence on eel sensory physiology and behavioural guidance, advances our understanding fishes' responses to anthropogenic light, and contributes to conservation and management efforts for a valuable and vulnerable family of fishes.

Acknowledgements

I would like to thank my co-supervisors Dr. Steven Cooke and Dr. Thomas Pratt for the opportunities, resources, and mentorship over the past two years, and I would like to equally thank Dr. Chris Elvidge for his close guidance. All three of you have contributed to my development in valuable and unique ways through this process, and I greatly appreciate the time you have taken to share your perspectives and expertise. I would also like to thank the numerous members of the Eel Passage Research Centre for similarly granting me the opportunity to work on this project, and for fostering my growth as a scientist and a professional with advice, good humor, and encouragement in all of our interactions. Thank you to Dr. Nicolas Lapointe for the support and advice both academically and professionally, and to fellow committee member Dr. Emily Standen for the insightful comments, questions, and suggestions in our meetings. During my studies I had the opportunity to undertake a side study regarding cumulative effects of small hydropower, and during that effort I was also lucky enough to be mentored by Dr. Lauren Stoot. Needless to say, throughout my time in the Cooke Lab I have benefited from an impressive network of support, expertise and diverse perspectives.

Finally, love and thanks to my parents for cheering me on with everything they've got as long as I've been alive, and to my wonderful partner Isabela for bringing me snacks, making me laugh, listening when I want to rant about why my R code wouldn't run for the past three hours, and simply doing everything you could to make the run to the finish line as easy on me as possible.

Co-Authorship Statement

A Review of Potential Behavioural Guidance Methods for Improving Downstream Passage of Out-Migrating Anguillid Eels

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This manuscript will be submitted to River Research and Applications. This paper was conceived by MacLeod, Cooke, Pratt, and Elvidge. All research, writing, and creation of figures was undertaken by MacLeod. All authors provided important feedback and edits to the manuscript.

Characterizing American Eel Out-Migration and their Vertical Movement Responses to an LED Behavioural Guidance Device

M. E. Cole MacLeod, Chris K. Elvidge, Thomas C. Pratt, and Steven J. Cooke

This project was conceived by Cooke, Pratt, Elvidge, and MacLeod. Processing of raw data was undertaken by Elvidge, statistical analyses were undertaken by MacLeod under the guidance of Elvidge, and all writing was undertaken by MacLeod. All authors provided important feedback and edits to the manuscript.

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Chapter 1: General Introduction

1.1 Global Cultural Context

Anguillid eels are a phylogenetically ancient clade and have been the subject of millennia of human inquiry, fascination, and reliance. Prominent historical figures including Freud and Aristotle were perplexed and captivated by eels and their cryptic origins and life history (Svensson 2021). Countless cultures including the Ancient Egyptians, the First Nations of eastern North America (Davis et al. 2004; Algonquins of Ontario 2012; Jarvis 2020), the Basques of southwestern Europe, and many Scandinavian and Japanese fishing communities have deep cultural connections to eels as a food source, spiritual source, and livelihood (Svensson 2021). In most of Europe, they were a staple food (and occasional currency) through the Middle Ages, early Modern period, and Industrial Revolution (Waxman 2020). Contemporarily, possibly owing to their declining abundance, eels are often regarded as a delicacy (Wight 2012; Randolph 2018).

Their historical popularity and ubiquity also means that eels have been aggressively harvested through time. By the 17th century, England had already depleted their eel stocks and was importing them from mainland Europe (Waxman 2020). Legally harvested American Eel *Anguilla rostrata* elvers are currently worth up to $5,000 CAD per kg, and lucrative black-market fisheries exist on the east coast of Canada and elsewhere (Withers 2023). Three common Anguillid species, the American *Anguilla rostrata*, European *A. anguilla*, and Japanese *A. japonica* eels hold IUCN Red List statuses of Endangered, Critically Endangered, and Endangered, respectively (Jacoby et al. 2015). American Eels are recommended for listing as Threatened by COSEWIC and are listed as Endangered in Ontario (COSEWIC 2012; Government of Ontario 2013).

1.2 Upper Saint Lawrence and Lake Ontario American Eel

Recruitment of American Eel to Lake Ontario, as measured at the Moses-Saunders Hydroelectric Dam eel ladder (the oldest monitoring site for eels in the Saint Lawrence Basin), has declined 95-99% since the 1970s (Cornic et al. 2021). Consequently, American Eels were classified as Endangered under Ontario's *Endangered Species Act, 2007*. While eel ladders are understood to be effective in facilitating upstream passage (Haro 2013), cumulative mortality resulting from the Moses-Saunders (Ontario-New York) and Beauharnois (Quebec) Hydroelectric Dams is estimated at 39.5% (Verreault and Dumont 2003). Approximately 99% of the flow at Moses-Saunders passes through the turbines, with similar volumes at Beauharnois, thus virtually all eels leaving the Saint Lawrence Basin are forced to pass these structures (EPRI 2018).

From 2006-2010, following dramatic declines and a near-total depletion of the naturally occurring Saint Lawrence Basin eel stock, an experimental stocking program was implemented. Approximately 3.8 million glass eels and elvers, captured in commercial fisheries in Nova Scotia and New Brunswick, were released at various sites around Lake Ontario and the Upper St. Lawrence River (Pratt and Threader 2011). A preliminary evaluation found early signs of success demonstrated by satisfactory growth rates and dispersion, but stressed the need for further monitoring (Pratt and Threader 2011). Later studies found that stocked eels grew and matured faster, migrated younger, smaller, and later in the season, and exhibited more males; all traits of the population contingent from their place of capture in the Maritimes (Stacey et al. 2015; Côté et al. 2015). This has cast significant doubt on the hypothesis that eel life history strategies are shaped primarily by their environment, and leaves uncertainty regarding the effectiveness of conservation stocking. Because most eels remaining in the system are stocked

(Côté et al. 2015), escapement is expected to continue declining as their numbers dwindle; facilitating the survival and successful reproduction of those remaining is of utmost importance to stakeholders (EPRI 2018).

Because physical guidance was not an option due to issues with scale (i.e., the Moses-Saunders GS is ~1 km wide, and mean discharge is ~8,000 m^3/s) and effects on generating capacity and debris accumulation, Ontario Power Generation (OPG) began operating a Trap and Transport (T&T) program to mitigate eel mortality. Specially licensed commercial fishers are compensated for large (> 2.2 kg or 80 cm) yellow-stage eels captured as by-catch. The eels are delivered to the Ontario Ministry of Natural Resources and Forestry (OMNRF) Glenora Field Station, where they are held and accumulated. They are transported via truck past Moses-Saunders and Beauharnois, and re-released with the expectation that they will mature and out-migrate within a few years. To improve the program, maturing eels need to be efficiently targeted and collected during their downstream migration, rather than incidentally capturing resident eels that may or may not be ready to migrate.

The Eel Passage Research Center (EPRC) was established in 2013 by the Electric Power Research Institute (EPRI). They are a bi-national group of biologists from EPRI, Fisheries and Oceans Canada, Hydro Quebec, New York Power Authority, Ontario Ministry of Natural Resources and Forestry, US Fish and Wildlife Service, Quebec Ministry of Forests, Wildlife, and Parks, New York Department of Environmental Conservation, and Ontario Power Generation. Carleton University was invited to join the group in 2019. The EPRC was formed to improve OPG's Trap & Transport program; their stated goal is to *develop the technology to behaviorally guide the eels to a collection point for capture and transfer around the Moses-Saunders Power Dam and the Beauharnois Generating Station* (EPRI 2018). Given physical guidance has been deemed infeasible, the EPRC began researching behavioural guidance as an alternative. They commissioned numerous laboratory studies and literature reviews on a number of potential stimuli including flow manipulation, electricity, light and sound; of these, the latter two had the strongest evidence base for altering eel movement on the St. Lawrence (EPRI 2017, 2018; Pratt et al. 2021). The present study, as part of the EPRC's research program, is the largest management-scale evaluation of light for behavioural guidance of eels.

Increasing the likelihood that these large, female (*i.e.* highly fecund; Hixon et al. 2014) individuals reach the Sargasso Sea and reproduce could not only help eels in Canada, but also increase the reproductive potential of the panmictic species throughout its range. Future implementation of this technology could involve directly diverting eels away from hazards and obstructions. This project, with its direct implications for management, could result in significant gains for a deeply imperiled and important species.

1.3 Thesis Objectives

In Chapter 2, I undertook a literature review regarding the development of behavioural guidance methods for Anguillid eels, with a practical focus on their real-world potential to improve fish passage at hydropower facilities. I summarized eel sensory biology; outlined and discussed potentially relevant methods and the senses they act upon; assessed the practicality of each using experimental evidence from laboratory and field trials; and considered factors such as costs and logistics. I concluded by discussing elements of optimal study design and outlined priority research areas.

In Chapter 3, I primarily assessed the effect of white Light Emitting Diode (LED) light on the vertical movement behaviour of out-migrating American eel. Using complementary data from light field mapping and acoustic telemetry, I visualized, categorized, and quantified eel responses to an above-water Light Guidance Device, comparing responses when the array was on versus when it was off. Secondarily, using complementary metadata, I characterized the nature of eel out-migration according to available environmental, spatial, temporal, and biological correlates.

Chapter 2: Reviewing the Potential for Behavioural Guidance to Improve Downstream Passage of Out-Migrating Anguillid Eels

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Abstract

Anguillid eels are some of the most imperiled freshwater fishes on the planet. Although they face numerous threats, hydro-electric dams and their turbine infrastructure represent a particularly insidious threat to semelparous and long-lived adult out-migrating eels en-route to marine spawning grounds. For decades, the hydropower industry, regulators, and researchers have undertaken efforts to guide eels away from turbines and towards safe passage routes. A subset of these efforts have involved exploiting sensory physiology (e.g. sight, hearing) to either attract eels to areas of safe downstream passage (including collection facilities for trap and transport) or repel eels from areas of danger. Here, we summarize efforts undertaken over the last few decades to evaluate the effectiveness of various eel guidance methods to reduce turbine entrainment. We collated relevant literature and organized it primarily based on guidance modalities of light, sound, flow, chemicals, magnetism, and electricity. Combined (multimodal) approaches were categorized under the primary behavioural stimulus. White (broad-spectrum) or blue (480 nm) light (standalone or multimodal) and low-frequency sound (multimodal) as repellants show the greatest promise as behavioural guidance stimuli. Ambient flow velocity has a large influence on the success of all methods, however, evidence for induced flow as a guidance mechanism is limited. More work is needed to develop reliable and effective behavioural guidance methods that facilitate safe passage for out-migrating anguillids; particularly, there is a need to continue to scale studies from the lab to the field to ensure ecological and management relevance.

2.1 Introduction

For much of our existence, humans have exploited other species' sensory physiologies to incite desirable behaviour in that species. Contemporary examples include uses of sound to repel pest animals (Gilsdorf et al. 2002), UV light and pheromones to trap or control insects (Shimoda and Honda 2013; Rizvi et al. 2021), and light to attract schooling fishes and enable capture (Nguyen and Winger 2019). In practice, this use of non-solid sensory stimuli to deter or attract a species can be broadly termed 'behavioural guidance' (adapted from 'non-physical deterrence': Noatch and Suski 2012; precedent for 'behavioural guidance': Scruton et al. 2003; Kemp et al. 2012; Piper et al. 2015, 2019; Ford et al. 2017; Hansen et al. 2018; Elvidge et al. 2018; Holgate et al. 2023). There is widespread interest and effort devoted to developing behavioural guidance tools for conservation and management goals (Laiolo 2010; Sorensen and Johnson 2016; Elmer et al. 2021). Existing methods include the use of electro-repulsive metals in fishing gears to reduce shark bycatch (Hutchinson et al. 2012) and electrical exclusion of invasive Sea Lamprey (*Petromyzon marinus*) from spawning streams around the Laurentian Great Lakes (Johnson et al. 2021). Relevant to the hydropower industry, behavioural guidance could help to improve passage outcomes for downstream migrating fish.

Hydropower is humanity's oldest and most widespread form of mechanical energy and is valued worldwide as a reliable source of renewable electricity (IEA 2021). However, the dams and turbine infrastructure associated with hydroelectric projects can have negative consequences on aquatic life (Nicola et al. 1996; Liermann et al. 2012; Chen et al. 2023). Diadromous fishes, including freshwater eels (Anguillidae; hereafter anguillid eels or eels), are particularly susceptible given they may need to pass these barriers multiple times in their lives to complete their life histories (Liermann et al. 2012; Reid et al. 2019). Migratory obstruction due to these barriers, particularly turbine entrainment, is concurrent with population declines in eel species worldwide (Liermann et al. 2012; Piper et al. 2013; Jacoby et al. 2015; Verhelst et al. 2018). Some of the most widely valued and studied of the 18 anguillid species (Teng et al. 2009), European Eel *Anguilla anguilla*, American Eel *A. rostrata*, and Japanese Eel *A. japonica*, are considered Critically Endangered, Endangered, and Endangered, respectively (Pike et al. 2020a, 2020b, 2023). Urgent action to reduce all sources of mortality, including circumventing the hazards associated with hydropower, is needed.

Anguillids are facultatively catadromous, reproducing in the ocean but spending most of their lives in fresh, brackish, or occasionally nearshore marine waters (Cairns et al. 2013). Larval eels reach the continental shelf and undergo a metamorphosis into an initial juvenile stage termed glass eel or elver. They spend most of their lives in their subsequent juvenile growing stage as yellow eels, which may reside across all continental aquatic habitats, but after 5 to 30 years they out-migrate to return to their oceanic spawning grounds as sexually mature silver eels (Figure 1) (Cairns et al. 2013). On rivers where barriers are present, elvers and young yellow eels may successfully pass using specially designed eel ladders (Haro 2013; EPRI 2018); however, facilitating the downstream passage of late yellow and silver eels remains a significant challenge for resource managers and scientists (Versar 2009; Piper et al. 2013; EPRI 2018; Verhelst et al. 2018; Pratt et al. 2021).

Numerous factors make eel passage particularly challenging. Physical fish passage methods do exist (e.g. screens and racks) and have been successfully installed at small hydroelectric stations, but many problems including biofouling, debris accumulation, reduced generating capacity, and poor passage efficiency and effectiveness can occur in attempts to use them to guide out-migrating eels, particularly at larger facilities (EPRI 2018). Eels' relatively poor burst swimming abilities (Bruijs and Durif 2009; Russon and Kemp 2011), preference for faster water currents (Bruijs and Durif 2009; Piper et al. 2013), and elongate bodies leave them especially vulnerable to being drawn into turbines or impinged against guidance structures. Moreover, their semelparity and long lifespan mean that mortality in out-migrating individuals is likely to be especially costly to subsequent reproduction and recruitment. For example, recent work on American Eel in the Saint Lawrence River and Lake Ontario watershed estimated a threshold of 25% mortality of out-migrants before population decline (Haxton 2022). Cumulative mortality from two hydropower dams on the Saint Lawrence River alone is estimated at 39.5% (Verreault and Dumont 2003), and there are 151 hydro facilities on the entire watershed (Verreault et al. n.d.). Similar situations are reported for anguillid stocks and species worldwide (Jacoby et al. 2015). These passage issues can occur from low flow, dam-and-reservoir sites (e.g. Mensinger et al. 2021) to high-flow, quasi-run-of-river stations (e.g. EPRI 2018; Pratt et al. 2021), but are generally more common at larger (i.e. deep and wide) facilities.

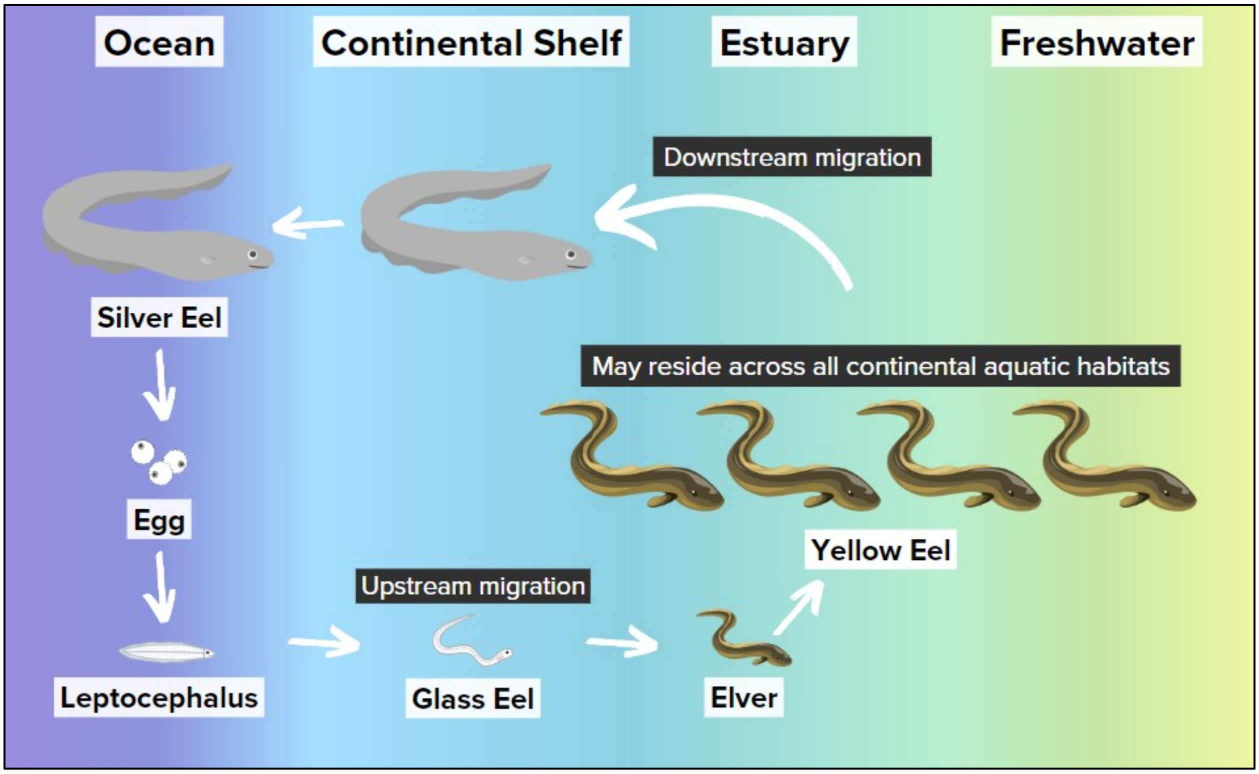


Figure 1. The life cycle of anguillid eels (adapted from Cairns et al. 2013). Born in offshore marine areas, eel larvae and juveniles float toward continental shelves on ocean currents, where they reside in nearshore marine areas or further inland. In approximately 5-30 years, surviving individuals out-migrate and sexually mature, returning to their place of birth to reproduce and die.

There is reason to believe behavioural guidance could improve various aspects of the management of fish movement, including passage technology, either by augmenting or replacing aspects of existing methods. To this end, laboratory and field guidance experiments have been undertaken using stimuli such as light, sound, and electricity with species including Atlantic Salmon *Salmo salar* (Scruton et al. 2003)*;* White Sturgeon *Acipenser transmontanus* (Ford et al. 2017)*;* Chinook Salmon *Oncorhynchus tshawytscha* (Hansen et al. 2018); Common Carp *Cyrprius carpio* (Kim and Mandrak 2017)*;* and anguillid eels (primarily American and European Eel; e.g. Hadderingh et al. 1999; Piper et al. 2015, 2019; EPRI 2016, 2018; Elvidge et al. 2018; Deleau et al. 2020a, 2020b; Miller et al. 2021, 2022). To develop rigorous knowledge regarding the potential for various methods to guide these fishes, it is necessary to understand the underlying physiology being targeted (Elmer et al. 2021). While eels are similar to the other teleosts listed at the levels of cellular and systemic structure, the morphological patterns and internal molecular processes of eel sensory systems can be quite unique, and can change throughout their lives to suit their dramatic habitat transitions (Tomoda and Uematsu 1996). Thus, inferences from other taxa are unreliable. Where such specificity is possible, it is important to primarily consider the sensory biology of, and behavioural guidance studies on, late yellow and silver stage eels (Versar 2009b; EPRI 2018; Popper et al. 2020).

Here, we synthesize existing literature related to the behavioural guidance of mature anguillid eels. We focus on guiding (i.e. repelling or attracting) out-migrating eels on rivers away from hydroelectric infrastructure and toward collection points or safe passage. We begin by providing a brief summary of the relevant aspects of anguillid sensory ecology (given relevance to behavioural guidance; Elmer et al. 2021) and outline possible guidance modalities. We then explain how site-specific characteristics may affect both the propagation of these stimuli and eel behaviour, given these interactions are referenced throughout. Evidence for how each modality may affect eel behaviour is evaluated, and the applicability of this evidence in the field is assessed using environmental, ecological, and logistical context. We consider elements of rigorous study design, summarize research directions, and discuss which modalities warrant prioritization or further investigation. Methods and results are sufficiently diverse to preclude quantitative analyses, so we embrace a narrative approach.

2.2 Sensory Ecology of Eels

The movement behaviour of eels can be driven by input and processing of numerous environmental cues including chemicals, light, sound, flow, and to a lesser extent, magnetism and electricity (Evans and Claiborne 2006; Trischitta et al. 2013; Horodysky et al. 2022). These stimuli are interpreted in accordance with factors such as life history stage and proximate behavioural priorities (e.g. feeding, evasion, migration, mating) to influence movement (Horodysky et al. 2022). Vision, hearing, and mechano/rheoreception may have the greatest role in acutely altering movement (Trischitta et al. 2013), whereas olfaction may have a greater role in guiding broader spatial activities such as foraging, homing, migration, and mate identification (Barbin 1998; Barbin et al. 1998; Trischitta et al. 2013). Eels possess magnetite throughout their bodies and may use the earth's magnetic field to guide their migrations (Moore and Riley 2009), but neither magnetism nor electricity has been implicated in 'day to day' behaviour. Eels do sense and respond to other stimuli such as temperature and pressure (Evans and Claiborne 2006), but these parameters are not practical to manipulate in field conditions so are not considered here.

2.3 Peculiarities and Challenges of Underwater Stimulus Propagation

Light, sound, chemicals, and electricity all behave differently underwater and present unique considerations in the development of a behavioural guidance system. High turbidity attenuates light, which can limit the distance at which fishes perceive and respond to it (Hamel et al. 2008; Putland and Mensinger 2019). Sound does not have this issue, but it does propagate relatively poorly in particularly wide or shallow channels and may lose obvious directionality (Noatch and Suski 2012; Pratt et al. 2021). Furthermore, infrasonic signals can travel through or along channel beds and walls; depending on channel shape and substrate composition, eels may detect this signal more strongly than through the water (Popper and Hastings 2009; Popper et al. 2020). Chemicals in water are dominated by ambient hydrodynamics, and thus disperse unevenly and uncontrollably (Allen et al. 2012). Finally, variability in water conductivity would likely influence the operational parameters of a hypothetical electrical guidance system (Miller et al. 2021). More broadly, ambient levels of the same or similar stimulus may decrease the relative intensity of the artificial signal compared to background levels; this is a particular concern at sites with light or noise pollution (Noatch and Suski 2012; Popper et al. 2020). Other interactions among various stimuli and other physical and environmental features are likely to occur, but many of these are not easily generalized or not well-understood.

2.4 Spatial Distribution and Behaviour of Out-Migrating Eels

Migration timing and pathing of maturing eels depends on a number of temporal, physical, and environmental factors. Out-migrants may distribute through the whole width and depth of a river and at all times of day (Versar 2009a), but move predominately at night (Smith and Saunders 1955; Helfman et al. 1983; Vøllestad et al. 1986), often in high flow velocities, during periods of high discharge, and along channel walls (Jansen et al. 2007; Bruijs and Durif 2009; Russon and Kemp 2011; Piper et al. 2013, 2015, 2017). However, Piper et al. (2017) demonstrated flow velocity alone may not explain a significant proportion of eel path choice, and some routes can be consistently avoided despite receiving the majority of discharge. Whereas silver eels in downstream flows exhibit relatively consistent directional transiting behavior, silver eels in still water exhibit slower, more non-directional exploratory behaviour (Behrmann-Godel and Eckmann 2003; Jansen et al. 2007). Contrary to their benthic reputation, eels transiting downstream through a large, high flow channel (approximately 800 m across, > 1 m/s depth-averaged flow velocity) were observed using the upper 2 to 3 m of the water column (EPRI 2024).

2.5 Guidance Modalities

In this section we summarize available knowledge of how eels sense and respond to light, sound, flow, odour, magnetism, and electricity[1]. We interpret this information as it pertains to the development of behavioural guidance systems for out-migrating eels at hydroelectric facilities.

2.5.1 Light

Ambient light allows eels to see and enables behaviours such as food detection, predator avoidance, and circadian rhythms (Noatch and Suski 2012). Relevant to the problem at hand, vision can mediate efficient movement through undesirable conditions. Eels perceive light using the ‘camera’ eye common across vertebrates (Figure 2). The pupil and lens behind it control the amount of light let through and the focus of the eye, analogous to the aperture and lens of a camera. After light passes through the lens it reaches the retina, which receives the stimulus and sends an electrical signal to the brain via the optic nerve, similar to imprinting and developing film (AMDF 2016). Juvenile eels are most sensitive to yellow-green light (520 to 550 nm), whereas late-stage yellow and silver eels are most sensitive to blue-green light (480 to 520 nm) (Pankhurst and Lythgoe 1983; EPRI 2017). This change reflects their transition from relatively shallow, often inland fresh and brackish water to deep blue oceanic waters.

[1] Although both flow and the non-pressure component of sound are sources of water motion and thus both act on mechanoreceptors, they are separated here for the sake of logical organization and clarity of discussion.

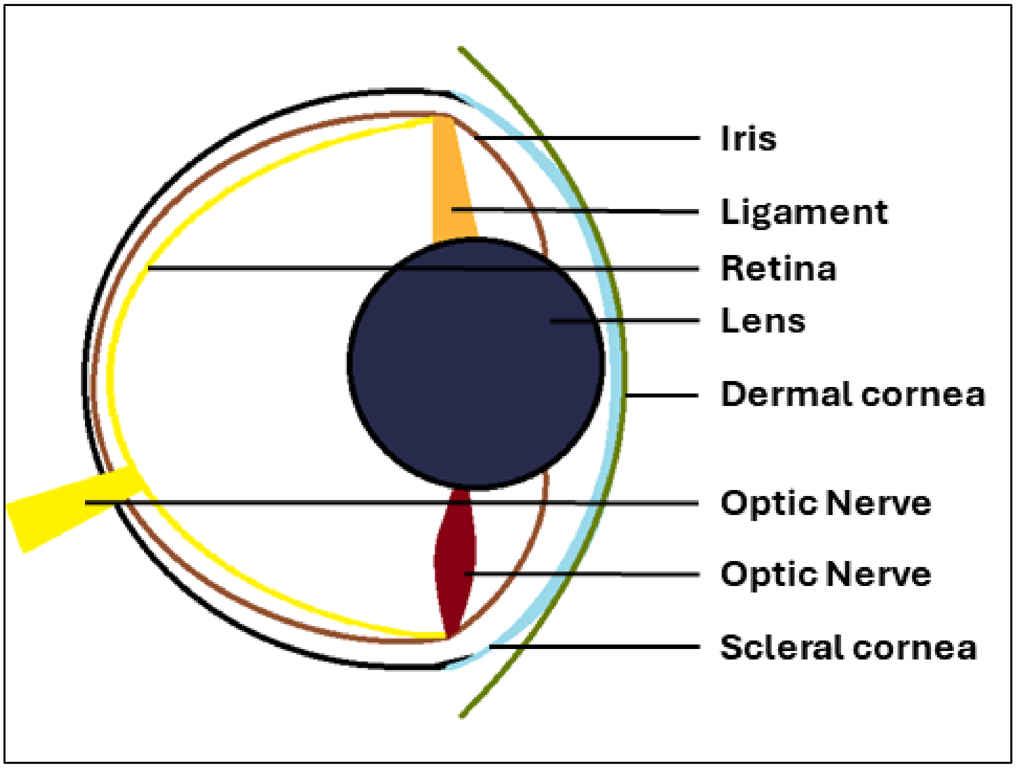


Figure 2. Simplified diagram of the teleost 'camera' eye (adapted from Nicol and Somiya 1989).

In nature, there is clear evidence that eels are negatively phototactic. They are most active and usually migrate at night, and peak migration periods tend to coincide with waning and new moons (i.e. low sky illumination) and greater cloud cover (Smith and Saunders 1955; Helfman et al. 1983; Vøllestad et al. 1986; McGrath et al. 2002; Stahl et al. 2023; EPRI 2024). Out-migrating eels also seem to generally avoid artificial light; adding lights to one section of an eel weir reduced silver eel catches in nets near that section (Cullen and Mccarthy 2000). A clear understanding of eels' photosensitivities, their primarily nocturnal migratory behaviour, and their aversion to light illuminates a clear path for developing a light guidance system.

Laboratory experiments on eels also encourage further development of light guidance technology. An early flume study found silver eels transiting in the direction of bulk flow were deflected by fluorescent light (Hadderingh et al. 1999). More recently, Elvidge et al. (2018)

exposed late-stage yellow eels to a Y-maze dichotomous choice test. One corridor was unlit, and one was illuminated by different LED colours; results were compared to unlit control trials. Eels entered the dark side more often and for a longer duration compared to light. Blue (480 nm) light elicited the greatest avoidance, consistent with eel retinal cells' ontogenetic shift in physiological sensitivity (Pankhurst and Lythgoe 1983; EPRI 2017), followed by full-spectrum white light. Elvidge et al. (2018) therefore suggest that these colours should be prioritized in field-scale evaluations of light guidance devices.

There have been field-scale light guidance experiments undertaken to variable but often positive results. On the River Test, UK, Bowen (2014) observed significant deterrence from white LED light in an experimental guidance system, but this river was quite small (15 m across) and interpretations were limited by a small sample size. Kruitwagen (2013) similarly observed significant deterrence from white LEDs in the North Sea Canal, NL (800 m across), which reduced the number of eels at a nearby trash rack by almost a full order of magnitude. However, the same LEDs were used by Bruijs and Vriese (2013) at the Linne Hydropower Plant, River Meuse, NL (225 m across). There, they observed no evidence of guidance, and listed potential nullifying factors including sub-optimal placement, high turbidity, turbulence, and ambient noise. McGrath et al. (2003) hung a series of halogen lamps in the water column upstream of the Iroquois Water Control Dam (IWCD), St. Lawrence River, CAN-US border (~700 m across) to create a 'wall of light'. Flow velocity was quite high at this site, approximately 1 m/s. Significant avoidance was claimed, but information is limited given no publication exists. Furthermore, this study did not employ a control phase to test the effects of the structure in the absence of light, leaving the likelihood open that the presence of the 'wall' altered hydrodynamics and acted as a physical deterrent in itself, similar to observations of eels avoiding a floating boom in Piper et al.

(2017). Versar (2009) also suggested infrasound due to vibrating moorings may have amplified the effect of the light platform. Finally, issues with debris accumulation and impractical maintenance requirements further discouraged the design as presented.

A second study on the St. Lawrence, also upriver of IWCD, used acoustic telemetry to describe *in-situ* responses in greater detail. Elvidge (unpub) deployed a floating, rather than hanging, light guidance structure upstream of the IWCD. The device sat at a 30° angle relative to the river axis and was equipped with downward facing white LEDs, which were turned off for 20% of nights as control treatments (Figure 3). The goal of this configuration was to horizontally deflect eels toward one side of the river for collection and downstream transport based on past telemetry data clarifying eels' major corridors. Tagged migrants that swam near the array while it was on did not deflect as predicted; there was only limited evidence of a small adjustment in horizontal trajectory with much individual variation. However, these eels slowed significantly and swam significantly deeper as they passed the floating array compared to those that passed during control periods. Control eels did still exhibit a much shallower dive, again consistent with Piper et al. (2017). Elvidge (unpub) demonstrates that downward-facing LED light can cause eels swimming downstream at velocities of >1 m/s to slow down and exhibit primarily diving behaviour, consistent with seeking darker waters. It is not immediately clear how this effect could be harnessed, but this result does stress the importance of proper device configuration in eliciting the desired response.

Figure 3. Photo of the 216 m long experimental light guidance array deployed upriver of the Iroquois Water Control Dam with the goal of behaviourally guiding out-migrating American Eel Anguilla rostrata to collection and safe passage, Fall 2022.

This body of evidence suggests that a light guidance system could be a useful tool for diverting out-migrating eels to reduce turbine mortality, in continuance with earlier predictions by Noatch and Suski (2012). However, there is little clarity of knowledge regarding how responses may change with manifold potential variations in device configuration and site characteristics, save for relatively simple considerations of in-water versus above-water lighting and the effects of flow, turbidity, and light pollution. With a greater understanding of operational parameters and the nature of eel responses, and with much site-specific development, light guidance may prove beneficial in particular situations. However, it is far from an out-of-the-box solution. Beneficial effects may also be obtained through a multimodal approach by pairing light with physical methods (e.g. for White Sturgeon *Acipenser transmontanus*: Ford et al. 2017, Staghorn Sculpin *Leptocottus armattus*: Mussen and Cech (2018)), or with other stimuli, such as sound (EPRI 2018). LEDs in particular are promising components of future light guidance devices as they are programmable to produce different colours, strobe rates, and intensities; can be adjusted while deployed; can incorporate UV anti-biofouling diodes; and are cheaper, more energy efficient, and have longer lifespans than alternative light sources (e.g. mercury, metal halide, incandescent) that were used in earlier field tests (EPRI 2017).

2.5.2 Sound

Acoustic cues (sound) can guide eel movement behaviour by providing information about the distance and directionality of prey, predators, and other relevant objects or phenomena (Sand and Bleckmann 2008; Popper and Hawkins 2019). Teleosts balance themselves, perceive their own motion in water, and detect the motion of water itself (including that from sound) through the octavolateralis system, which comprises the inner ear and lateral line (Popper 1996). The inner ear contains three otoliths in close proximity to a sensory epithelium containing mechanosensory hair cells (Figure 4). Since living tissue has a similar density and elasticity to water, particle motion travels through the body to the sensory epithelium. This motion impacts the otolith, which remains stationary due to its higher density, causing the sensory hair cells to bend (Popper and Hawkins 2018). Sound pressure is detected through the swim bladder, which reverberates analagous to the tympanic membrane (ear drum) of mammals (Popper et al. 2019). Eels' elongate bodies and lack of specialized anatomy to facilitate the latter process means that while they detect both, they respond primarily to the particle motion component of sound, rather than sound pressure (Popper et al. 2003; Ladich and Schulz-Mirbach 2016; Popper and Hawkins 2018).

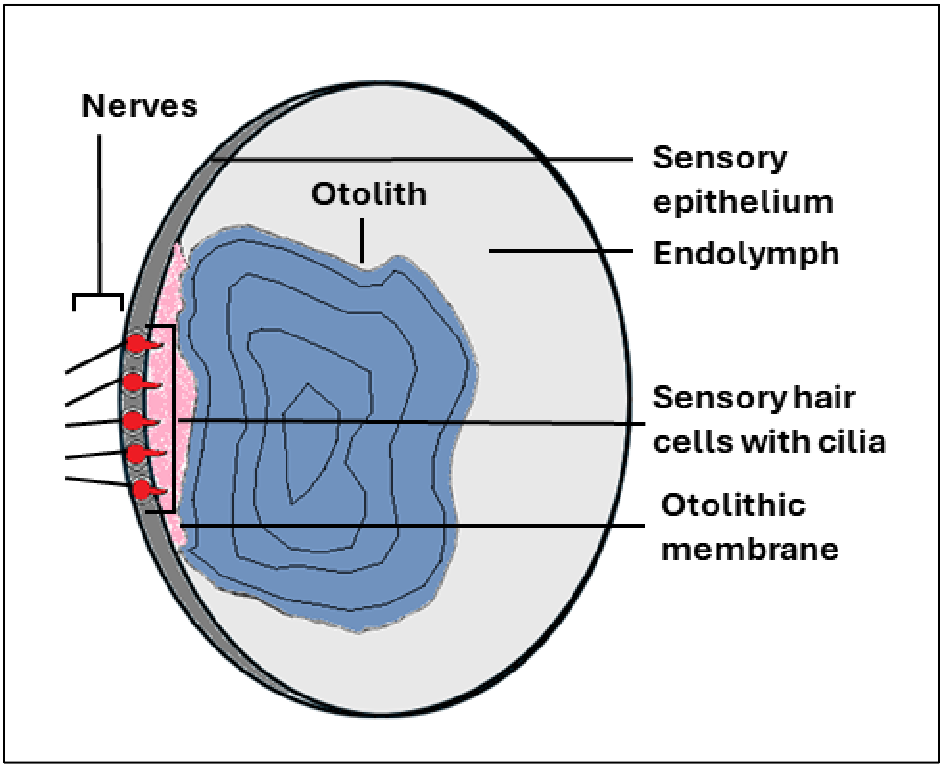


Figure 4. Simplified diagram of a teleost otolith organ inside the inner ear (adapted from Ibsch et al. 2004). As part of the octavolateralis system, otolith organs detect the particle motion component of sound and aid in the perception of balance and body acceleration.

The auditory range of anguillids is relatively narrow and of lower pitch compared to humans and other fishes. Eels can detect from < 1 Hz to 300 Hz (Jerkø et al. 1989; Sand and Karlsen 2000), whereas gadids (cod) and salmonids can hear up to 600 Hz, Goldfish *Carassius auratus* up to 3,000 Hz, and humans from 20 to 20,000 Hz. In eels, detection of particle motion through the inner ear predominates until about 100 Hz. From 100 to 300 Hz, particle motion is harder to detect and the swim bladder may play an equal role (Jerkø et al. 1989), but this secondary signal attenuates significantly as it travels to the lateral line and inner ear (Popper et al. 2003). Thus, <1 Hz to 100 Hz, one-fifth of which is below the threshold for infrasound (< 20 Hz), may be anguillids' optimal hearing range. However, recent evidence suggests audiogram measurements may not reflect optimal frequencies for behavioural responses (Holgate et al. 2023).

Though less compelling than light, there is also experimental evidence to support sound as a behavioural guidance mechanism. Recently, EPRI (2016) tested whether low-frequency sound (50 Hz, 100 Hz) or infrasound (10 Hz) could cause eels to avoid the source in a small fume, and if so, the extent of this response. Eels exhibited avoidance to all signals, but the strongest response was observed to 10 Hz and the weakest to 100 Hz, lending further evidence to the supposition that lower frequencies, particularly infrasound, could be more effective for behavioural guidance. Historically, laboratory and field experiments evaluating the efficacy of broadband (60 to 1000 Hz) and low frequency sound as behavioural guidance methods (i.e. analyzing path outcomes in downstream flow or similar, rather than a simple deterrent effect) report poor to mixed outcomes ('no guidance' to 57%; Sand et al. 2000; Bau et al. 2011; Piper et al. 2019; Putland and Mensinger 2019; Deleau et al. 2020b). However, advances in acoustic field mapping and acoustic telemetry have enabled more detailed analyses in newer experiments, revealing promising observations that could guide a more focused approach.

Piper et al. (2019) provides descriptions of eel responses to infrasound at a shallow (< 2 m) hydroelectric water intake channel with moderate flow velocity (0.5 m/s) compared against control periods when the sound source was turned off. The infrasound device was suspended in the middle of the channel at mid-depth by three floating buoys, and emitted a 12 Hz frequency at a Sound Pressure Level of 171 dB within 5 m of the device. As an outright deterrent this method was not very effective, with only a 28% decrease in entrants to the channel. However, eels that passed during ensonified periods moved erratically, spent less time in and around the intake channel, took longer to enter, and their movement trajectories were over twice as long compared to control eels.

Piper et al. (2019) demonstrates that eels responding to infrasound cannot be expected to predictably alter their trajectory, but instead may respond with hesitance and erratic movement. Capitalizing on this response would be particularly difficult at higher flow velocities, such as in Bau et al. (2011) and MacNamara et al. (2012) (flow velocities 1 to 1.5 m/s), where infrasound had no effect on outcomes (Piper et al. 2019). Nevertheless, such results do suggest infrasound could be useful as a secondary stimulus in a multimodal guidance system (Putland and Mensinger 2019; EPRI 2018; Pratt et al. 2021; Piper 2019; Deleau et al. 2019b). This conclusion is consistent with Versar (2009)'s supposition of an augmentative effect of vibrating moorings in the eel light guidance system described by McGrath et al. (2003), and with a study on Shiner Surfperch *Cymatogaster aggregata* which demonstrated vibration can enhance the effectiveness of physical screens (Mussen and Cech 2018)

Infrasound does not presently appear to have been tested in a multimodal experiment. However, Deleau et al. (2020a) set out to determine whether either continuous broadband sound (60 to 1000 Hz) or a low-frequency (100 Hz) pulse could improve a vertical bar screen's deflection of downstream swimming eels toward a bypass in a flume. Responses to the acoustic signals were compared against control trials wherein there was a screen but no sound. Most eels in all trials reached the bypass, but fewer failed to deflect during ensonified trials (3 control; 1 in each sound trial). Both acoustic modalities caused eels to reach the bypass sooner than during the control trial, though the 100 Hz pulse had a greater effect. While Deleau et al. (2019a)'s methods as described did successfully enhance the efficiency of the screen, infrasound appears to elicit a stronger response than higher frequencies under otherwise equivalent conditions (EPRI 2016), so it is possible an even greater effect could be observed if a similar experiment were undertaken using infrasound.

Further investigation of infrasound as a secondary deterrent is warranted but there are some obvious limitations. High ambient noise levels are common around generating stations, and particularly shallow or wide rivers may pose challenges due to requisite propagation distance or poor underwater acoustics (Noatch and Suski 2012; Pratt et al. 2021). Moreover, the cost and footprint of a device with the specifications necessary for field scale application, particularly in larger channels, may be prohibitive (Deleau et al. 2020b). Yet, if the predominant paths of out-migrating eels at the study site were determined in advance, it could be possible that a relatively small volume of the channel would need to be ensonified to affect a sufficient proportion of migrants (as in EPRI 2018). More studies with detailed quantifications of out-migrating eel responses to natural and anthropogenic sound are needed, particularly at varied sites with well-specified soundscapes (Popper et al. 2020).

2.5.3 Flow

Like most fishes, eels sense and respond to hydraulic patterns to maintain their intended position and direction, optimize swimming efficiency, and conserve energy (Liao 2007; Versar 2009a). As in the previous section, the octavolateralis system detects the movement of water, including flow. Whereas the inner ear orients and detects acceleration of the body (Figure 4), the lateral line is most responsible for detecting localized disturbances in water (Figure 5). The latter organ consists of water-filled canals lined with sensory cells, which detect hydraulic attributes including velocity, acceleration, and pressure (Kasumyan 2003). Using this sense eels tend to stay in higher flow velocities (Jansen et al. 2007; Bruijs and Durif 2009; Piper et al. 2013), though they may avoid high acceleration flows (Piper et al. 2015) and flow velocity alone does not predict a significant proportion of space usage (Piper et al. 2017). Nevertheless, initial evidence is sufficient to believe that manipulated flows could have the potential to behaviourally guide out-migrating eels.

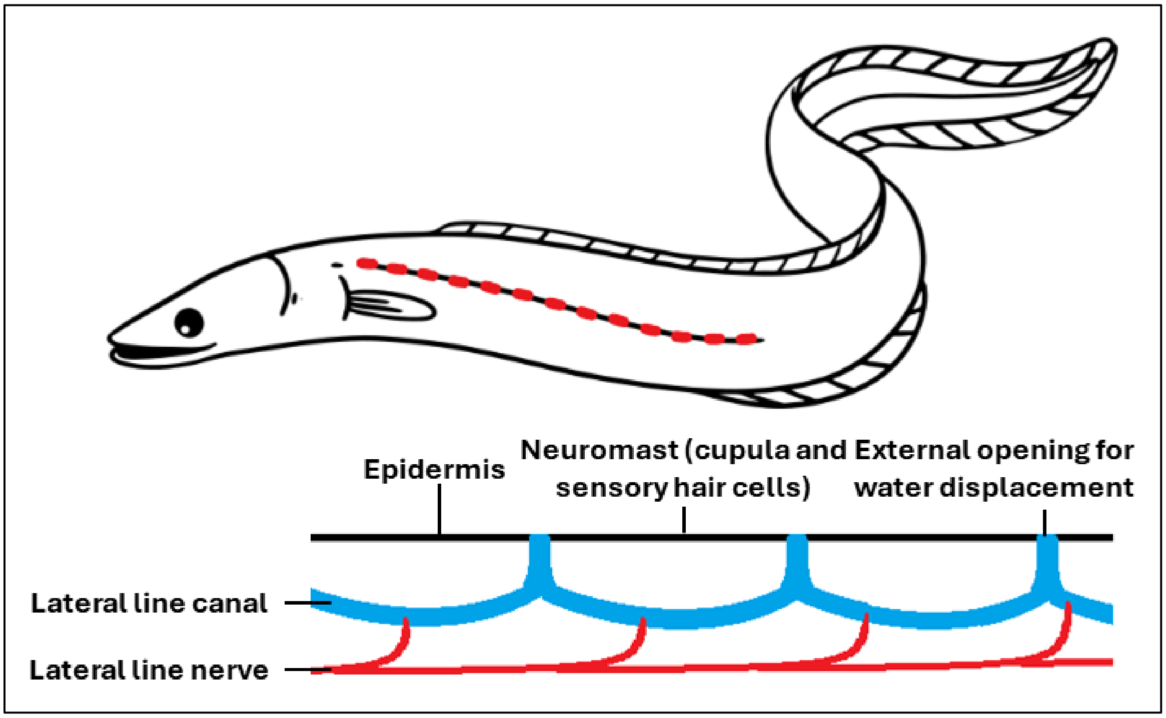


Figure 5. Simplified diagram of the lateral line system found in all fishes, including anguillid eels (adapted from Thomas Haslwanter 2012). As part of the octavolateralis system, the lateral line is primarily responsible for detecting localized water motion.

Experimental evidence for flow is more equivocal, though it may have potential in limited situations. In Hadderingh et al. (1999), silver eels in a flume were faced with corridors with different flow velocities; 75% of eels chose the greatest velocity. EPRI (2016) then attempted to use flow to guide eels to a target bin in a flume. Ambient water velocity was 0.9 m/s, and a flow velocity enhancement system was used to discharge 31 L/s from one side of the flume to generate a plume of enhanced flow toward the intended collection bin. The authors were not able to clearly define excess velocity within the enhanced plume, and there was no evidence for guidance. Moreover, eels tended to congregate upstream of the stimulus source, sometimes never swimming downstream at all. This behaviour was also observed during control and multimodal (flow and electricity) trials, with the same null effect in the latter. These findings were surprising given high ambient flow, and results may have been an artefact of study design (EPRI 2016). There are also multiple ways in which flow can be enhanced (e.g. nozzle diameter, velocity, volume) that could have unique effects on eel responses. Much more work needs to be done to define operational parameters for flow, and Pratt et al. (2021) discourages flow-electricity multimodal systems without developing a better understanding of the role of component stimuli.

It is important to elucidate other ways flow manipulation could affect eel behaviour. Rather than enhancing velocity, Piper et al. (2015) investigated how out-migrating eels in a redundant hydroelectric intake forebay responded to flow constriction and acceleration and compared these results to unmanipulated control periods. Ambient flow velocity in the forebay was moderate (0.6 m/s), and eels exhibited passive (i.e. swim speed similar to ambient velocity) benthic movement as they approached the experimental area. Upon sensing the constricted and accelerated flow field (0.2 m/s/s), eels quickly rejected it, strayed far back upstream, and took a relatively long time to pass. Control eels exhibited local exploratory behaviour, but passed sooner. These results suggest it would be important to moderate acceleration in any attractant-flow behavioural guidance system. More interesting, however, is the provenant opportunity to use accelerated flow as a deterrent to drive eels toward desirable routes, probably in tandem with other modalities (Piper et al. 2015). As of yet, no such experiment seems to have been undertaken.

It remains conceivable that manipulated flows could behaviourally guide out-migrating eels under certain circumstances, given further clarification of parameters and responses. Flume studies with similar goals, but different methods, from those in EPRI (2016) are an important first step, given the present lack of compelling laboratory evidence. If such an experiment has positive results, flow enhancement may warrant revisiting, particularly in relatively small channels with low to moderate flow velocity. On very large rivers, especially those with strong ambient flow, it may simply be energetically and economically infeasible to modify flow enough to reliably affect the behaviour of a useful proportion of out-migrating eels (Pratt et al. 2021). Aside from the feasibility of flow as an attractant stimulus, the novel observations by Piper et al. (2015) highlight the yet-unexplored potential for accelerated flow as a deterrent in a multimodal guidance system.

2.5.4 Chemicals

Eels may use olfaction for many purposes including feeding, mating, predator evasion, local navigation, and migration (Hara 1986). Eels 'smell' using an olfactory rosette, which then communicates a signal to the olfactory bulb in the brain (Huertas et al. 2008; Porceddu et al. 2022). These organs are most complex in juvenile followed by silver stage eels and regress dramatically during the intermediate freshwater yellow stage (Porceddu et al. 2022), consistent with the assertion that olfaction could be an important sense for migration (Barbin et al. 1998). Rather than any one chemical, eels may most effectively interpret cues from a 'bouquet' of odours (Sorensen 1986), particularly during the upstream migration where detritus and conspecific odours (e.g. bile and mucus) may label habitats as suitable based on prior residency (Huertas et al. 2008). Little is known of which odours silver eels may use to guide their downstream migration; a recent flume study found no evidence of a behavioural response to dead nor live conspecific chemical cues (Schmucker et al. 2017).

Many factors suggest chemical cues are not likely a solution for behavioural guidance of out-migrating eels. To develop an effective behavioural guidance system based on olfaction, one would need some idea of mature eels' upper and lower detection limits of an attractant or repellant odour, as well as estimates of the spectrum or intensity of behaviour elicited by the odour across its range of detection, ideally in the field (Versar 2009). To date, no concrete knowledge of any such odour exists, let alone any with this clarity of understanding. Moreover, given the uneven and uncontrollable dispersion and dilution of chemicals in rivers (Allen et al. 2012), eels would be moving in the same direction as the odour and the probability, concentration, and duration of exposure for each individual may be essentially random or negligible (Versar 2009a). Faced with this, it is quite unlikely that the release of an odour could induce a behavioural response reliably and predictably enough to guide out-migrating eels to collection or passage points.

2.5.5 Magnetism

Eels seem to be able to position themselves and navigate according to earth's magnetic field, a sense possibly used for long-range homing and likely most significant during migratory life stages in the ocean (Durif et al. 2022). Since magnetic fields can pass through tissue, sensory mechanisms could be located anywhere in or throughout the body, with no obvious structure needed (Lohmann and Johnsen 2000). Indeed, magnetite or other magnetic material is present in eels' lateral lines (Moore and Riley 2009), and could also be located in their olfactory lamellae, skulls, vertebrae, and pectoral girdles (studies reported in Versar 2009). The olfactory organs have also been proposed as a mechanism for magnetoception in other fishes including salmonids (Diebel et al. 2000) and tuna (Walker 1984).

Despite the widespread presence of magnetoception material in their bodies, there is little reason to believe magnetic fields could be used to behaviourally guide eels in the manner desired. Eels in lab and field studies may exhibit physiological responses and change their preferred body orientation in response to induced magnetic fields, but descriptions of the nature of these changes are highly inconsistent with no clear trend (Tesch et al. 1992; Westerberg and Bégout 2000; van Ginneken et al. 2005). It has also been proposed that physiological or behavioural changes observed in trials are not due to changes in the magnetic field, but rather a result of electrostatic shock generated when inducing electric currents to bring about the altered magnetic field (Versar 2009). Most recently, EPRI (2016) reported that silver eels exhibited no directional movement behaviour in response to an induced magnetic field in a flume. Their field strength was as strong or stronger (> 30 Gauss) than threshold levels reported by many previous studies, and their results leave extreme doubt concerning the utility of magnetism in the field (Pratt et al. 2021). It does not currently seem practical to endorse further investigation into using magnetism to behaviourally guide out-migrating eels, given discouraging preliminary findings and the availability of more sophisticated and promising methods. This is to say nothing of the logistical challenges of generating artificial magnetic fields at scales necessary for field application.

2.5.6 Electricity

Like most teleosts, anguillid eels have no dedicated electrosensory anatomy (England and Robert 2022). Electrical current directly stimulates the nerves of fishes and most responses are likely involuntary, or because swimming too close causes discomfort (Cowx and Lamarque 1990; Sharber and Sharber Black 1999; Noatch and Suski 2012). There is a theoretical 'sweet spot' of device intensity and distance from the device at which eels are uncomfortable enough to respond, but do not face more serious effects such as stunning, paralysis, impairment of neuromuscular function, musculoskeletal injury, or death (Noatch and Suski 2012). From this knowledge, there is reason to believe electrical fields could guide eels to safe passage or collection; however, electricity itself introduces considerable risks.

Indeed, decades of research have demonstrated that electrical barriers pose a serious danger to out-migrating eels. Hadderingh and Jansen (1990) described deleterious effects from early attempts to guide eels with electric fields, and a study covered in Versar (2009) reported thousands of mortalities after an electrical guidance system immobilized out-migrating eels in high flow, leading to mass impingement on an intake rack. Even if the eels were able to overcome the downstream flow velocity in an attempt to escape the intake, they could not move back upstream without enduring more electrical shocks. Recently, Meister et al. (2021) tested whether an electrified bar rack (i.e. an electrical-physical multimodal system) could guide eels in a flume. The effect of electrification did not significantly affect outcomes compared to the rack alone, and eels were observed hemorrhaging and/or vomiting due to contact with the electrified rack.

A recent flume study adds behavioural context to these observations. Miller et al. (2021) examined responses of mature eels to two electrical fields (0.15 V / cm; twitch threshold in still water, 0.30 V / cm; paralysis threshold in still water) across low (0.5 m / s) and high (1.0 m / s) flow velocities. Current strength alone had no effect, but 74% of eels exhibited a response to the field in low flow versus 31% in high flow. Of those that did respond under both flow conditions, nearly twice as many chose to accelerate through the field compared to those that changed their trajectory. Clearly, when attempting to conserve at-risk fishes, provoking headlong acceleration into a potentially deadly electrical field is not a desirable outcome.

Electricity could yet be useful for some aspect of facilitating downstream passage of eel; however, available evidence overwhelmingly suggests it is inappropriate as a barrier, which is how it has commonly been conceived of to date (likely following precedent set by the use of electrical barriers to restrict movement of non-native species [Noatch and Suski 2012; Johnson et al. 2021]). Countless untested variations in electrical field parameters and placement could reap potentially desirable and yet-undescribed behavioural effects. For example, electricity could be useful to attract (via induced galvanotaxis) and narcotize out-migrating eels for collection and transport in a multimodal guidance system. Further experiments are warranted but should be designed carefully to avoid potentially severe negative effects on eels.

2.7 Synthesis

No guidance modality is universally suitable or straightforward for fishes, and the approach is characterized by wide inter- and intraspecific variation, potentially even between sexes (Putland and Mensinger 2019; Elmer et al. 2021). However, there is evidence to support light, sound, and to a lesser degree flow as modalities that could potentially guide out-migrating eels (Figure 6). Full-spectrum white or 480 nm blue light has potential as a standalone method, has been shown to improve the efficacy of a physical barrier for other species (Ford et al. 2017; Mussen and Cech 2018), and has the potential to be combined with sound (EPRI 2018) or accelerated flows (Piper et al. 2015). Evidence does not support infrasound as a standalone deterrent, but it can increase the efficacy of physical methods (Deleau et al. 2020a) and likewise could augment other stimuli. Sound may have some theoretical advantages over light, but current clarity of knowledge is insufficient (Popper et al. 2020). Enhanced flow velocity may attract, but its potential is probably limited to lower flow systems and parameters remain undefined (Pratt et al. 2021). Accelerated flows have newfound potential as a deterrent in a multimodal system (Piper et al. 2015), but this approach is in its infancy. Electrical barriers may be useful for behavioural guidance in other situations, but they introduce too much risk to an endangered species in downstream flow. There is little reason to believe chemicals or magnetism are appropriate for the task at hand.

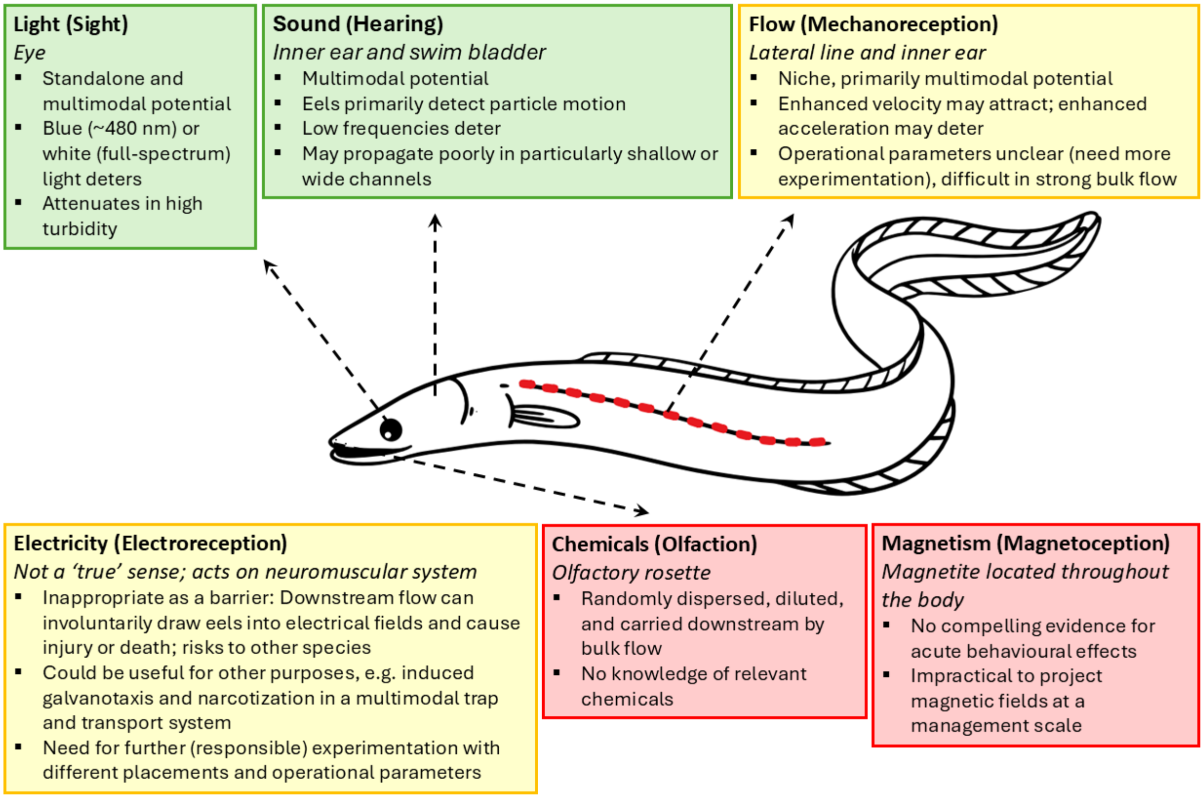


Figure 6. Schematic diagram describing the physiological mode of action and feasibility of various stimuli for behaviorally guiding out-migrating anguillid eels away from hydroelectric infrastructure.

Pairing behavioural guidance with existing physical systems could be of particular interest. Sound or light additions could be a cost-effective addition in proportion to their potential benefit, especially compared to physical retrofits (Miller et al. 2022). These additions could see immediate marginal gains to passage efficiency, whereby incremental advancements amount to meaningful improvement at a larger scale (Miller et al. 2022). Because multimodal systems act on multiple senses at once, they may simulate more biologically realistic conditions (Versar 2009). Whereas there is not currently a clear path to a reliably effective behavioural guidance system for any one modality, a physical-behavioural multimodal approach for existing physical guidance systems is more straightforward and could bring immediate benefits.

Three aspects of flow are quite relevant to the development of a behavioural guidance system. At higher velocities, the effect of a behavioural guidance device may be dampened and a greater stimulus intensity may be required to elicit the same response observed in lower velocities (Hadderingh et al. 1999; Versar 2009a; Putland and Mensinger 2019; Miller et al. 2021). Even if the stimulus intensity is great enough to induce the desired behaviour, eels' responses may be physically limited when bulk flow velocity begins to compete with their burst swimming capacity (1.35 to 2.12 m/s; Russon and Kemp 2011), or if the stimulus is not detected at a sufficient distance to allow for the intended path adjustment in downstream flow. Finally, eels may exhibit avoidance to physical objects that create hydraulic disturbances (Piper et al. 2017), which could be a convenient multimodal effect depending on the design of a behavioural guidance device.

Overall, avoidance is more readily elicited, and perhaps more biologically realistic, than attraction. Flow manipulation is the only method with any evidence for attracting eels via enhanced flow velocity, but high acceleration flows can also deter. There is interest in attractant sounds or odours (Schmucker et al. 2017; Popper et al. 2020), but little headway has been made in this regard. A possible explanation stems from the understanding that fishes interpret sensory stimuli in accordance with factors including their behavioural state and life history stage (Horodysky et al. 2022). Out-migrating anguillid eels undergo extensive morphological changes, swim thousands of kilometres, stop eating, and catabolize their internal organs in hopes of reaching distant marine spawning grounds (Tesch and Thorpe 2003). An animal in such an engrossed state may not easily be attracted to anthropogenic cues, which are unlikely to be more biologically relevant than the prospect of reproducing before death. In contrast, acute bouts of avoidance due to unpleasant stimuli may demand less relevance and thus be easier to induce.

Acoustic telemetry, or ideally less invasive methods such as sonar, are a critical advancement for monitoring responses to stimuli. With their advent, in-situ monitoring of behavioural responses has become a non-negotiable element of behavioural guidance field study design (Noatch and Suski 2012; EPRI 2018; Putland and Mensinger 2019; Popper et al. 2020). Pre-study monitoring allows for a baseline understanding of how eels naturally move through target sites, the importance of which is twofold. First, understanding preferred channels could dramatically decrease requisite coverage of a guidance device. Second, these paths can be compared against experimental treatment and control data to not only isolate the effect of the stimulus, but also determine whether the structure itself has a meaningful hydraulic effect. In-situ monitoring has delivered much recent progress by allowing for detailed observation of unanticipated behaviours in the field, rather than relying on outcomes alone (Piper et al. 2013, 2015, 2017, 2019; studies reviewed by Pratt et al. 2021; Elvidge unpub). Tracking wild fish also allows determination of peak migration periods, which is pertinent information for management-scale application.

Behavioural guidance sites and technologies need to be selected and developed based on detailed knowledge of site-specific characteristics (Noatch and Suski 2012), and there should be reliable estimates of the proposed stimulus intensity and coverage. Furthermore, it would be helpful to begin to standardize terminology and protocols for measurements and reporting results to facilitate quantitative comparisons among studies (Popper et al. 2020). Some common issues include insufficient reporting of contextual data, poorly described responses, misrepresenting the magnitude of a response, variable and proprietary designs, poor stimulus mapping, and the use of improper metrics (e.g. sound pressure) (Putland and Mensinger 2019; Popper et al. 2020). These data need to be accurate and represented in a useful manner to bolster interpretations and be more useful to future studies.

As for more practical benefits, behavioural guidance devices generally have a smaller spatial footprint and less impact on hydrology than physical barriers (Noatch and Suski 2012). They are less permanent, and can be temporarily deployed or remotely controlled to meet peak migration periods. They tend to be less susceptible to debris accumulation and biofouling which interfere with generating capacity, can be dangerous to fish, and are costly and hazardous for humans to remove (Noatch and Suski 2012). Advancing knowledge of the behavioural responses of fishes and growing recognition of the need to diversify from historically typical fish passage technologies (Silva et al. 2018) suggest behavioural guidance's importance is likely to grow into the future (Elmer et al. 2021).

2.8 Conclusion

Behavioural guidance strategies hold great promise for improving survival outcomes during downstream fish passage through high-risk sites including generating stations. As obligate migrants, anguillid eels are a problem taxon for fish passage and species worldwide are endangered. Here, we summarized what is known of eel sensory biology, discussed potentially relevant modalities, assessed the practicality of each, and commented on study design and future directions. Light and infrasound seem most promising overall, though flow manipulation also has niche undeveloped potential. Ambient flow velocity may limit the effectiveness of all modalities by limiting eels' time and capacity to respond. Multimodal approaches are likely most practical in the short term, and their installation at existing sites could lead to immediate marginal gains for out-migrating eels. Fine-scale monitoring of responses in the field is a critical component of contemporary behavioural guidance research and has enabled many recent advancements. Studies need to collect and report results and contextual data in sufficient resolution, using relevant and comparable protocols and metrics. Behavioural guidance offers a suite of appealing advantages over physical barriers, and its role in fish passage technology may continue to grow. We also emphasize the importance of other efforts to mitigate mortality, including innovations in fish friendly turbines (Yang et al. 2018; Niño Del Río et al. 2023). Hopefully, this paper provides a useful starting point for hydropower proponents and researchers interested in using behavioural guidance to reduce eel mortality.

Chapter 3: Characterizing American Eel Out-Migration and their Vertical Movement Responses to an LED Behavioural Guidance Device

Abstract

The use of abiotic stimuli to exploit sensory physiology and alter the behaviour of animals in a desirable manner (behavioural guidance) could help fishes safely pass hydroelectric dams. The complex life history of Anguillid eels, requiring both up- and downstream migration, leaves them particularly vulnerable to hydropower infrastructure. Laboratory and flume trials on late yellow-stage eels have demonstrated that they exhibit an avoidant response to light, and eels often migrate at night, indicating that light could be an effective stimulus in a field-scale behavioural guidance system. We deployed an above-water 216 m light guidance device fitted with a series of white light emitting diode bulbs at the Iroquois Water Control Dam, on the St. Lawrence River. Late yellow-stage eels ($N = 398$) were acoustically tagged, and migrants' movements at the experimental site were logged in three dimensions by an acoustic receiver array. Here we characterize migrant eels using environmental and spatial data, given relevance of such knowledge to a behavioural guidance system, and describe the vertical movement patterns exhibited by tagged eels that passed during the experimental period. Most eels were detected at night, during two waning moons, and in the upper 3 m of the water column independent of the guidance device. Individuals exposed to the light field slowed down, dove more often, and dove significantly deeper than those that swam near the device when the lights were off. Responses were variable among individuals and it not clear how a diving response could be harnessed in a behavioural guidance system; however, such findings do hold promise for the use of light in other configurations. Significant challenges remain to develop an effective downstream passage solution for eels using light.

3.1 Introduction

Behavioural guidance, the use of non-solid sensory stimuli to deter or attract a species (adapted from 'non-physical deterrence': Noatch and Suski 2012), has been employed by humans for countless generations and can include methods as simple as yelling to scare a potential predator or the visual stimulus of a scarecrow. Contemporarily, behavioural guidance has been used to repel domestic and agricultural pests (Gilsdorf et al. 2002), control insects (Shimoda and Honda 2013; Rizvi et al. 2021) or to attract fishes for capture (Nguyen and Winger 2019). There is a growing field of research focused on using behavioural guidance to create more specialized ecological management tools (Laiolo 2010; Sorensen and Johnson 2016; Elmer et al. 2021). Fisheries-specific developments in this field include the use of electro-repulsive metals in fishing gear to reduce shark by-catch (Hutchinson et al. 2012) and electricity to block the spawning behaviour of invasive Sea Lamprey (Johnson et al. 2021) or exclude invasive xenocarp (Kim and Mandrak 2017). Behavioural guidance has the potential to improve fish passage at riverine barriers, such as hydroelectric facilities, by deterring or attracting individuals away from hazards and toward either safe routes or concentration and collection facilities. This could be particularly useful as a conservation tool for at-risk diadromous species such as Anguillid eels, given their reliance on watershed connectivity (Reid et al. 2019).

Anguillidae are a family of 18 species of panmictic, semelparous, facultatively catadromous eels (Teng et al. 2009). That is, they consist of a single (or in rare instances a few) breeding population(s), undergo a single reproductive cycle before death, and usually live in fresh to brackish water but must undertake migrations from and to their marine spawning grounds twice in their lives (Cairns et al. 2013). These migrations, and the years between them, are accompanied by successive life stages with distinct punctuations in eel appearance, physiology, and behavioural strategy (Figure 7). Relevant here is the term 'yellow eel'; the subadult stage which predominates the eel's continental life, and 'silver eel'; the sexually mature adult eel which returns to its birthplace to reproduce (Cairns et al. 2013). The transition between these stages is gradual and maturation co-occurs with migration, so the term 'late-yellow stage' is also used throughout this paper to refer to eels preparing for or undertaking their out-migration.

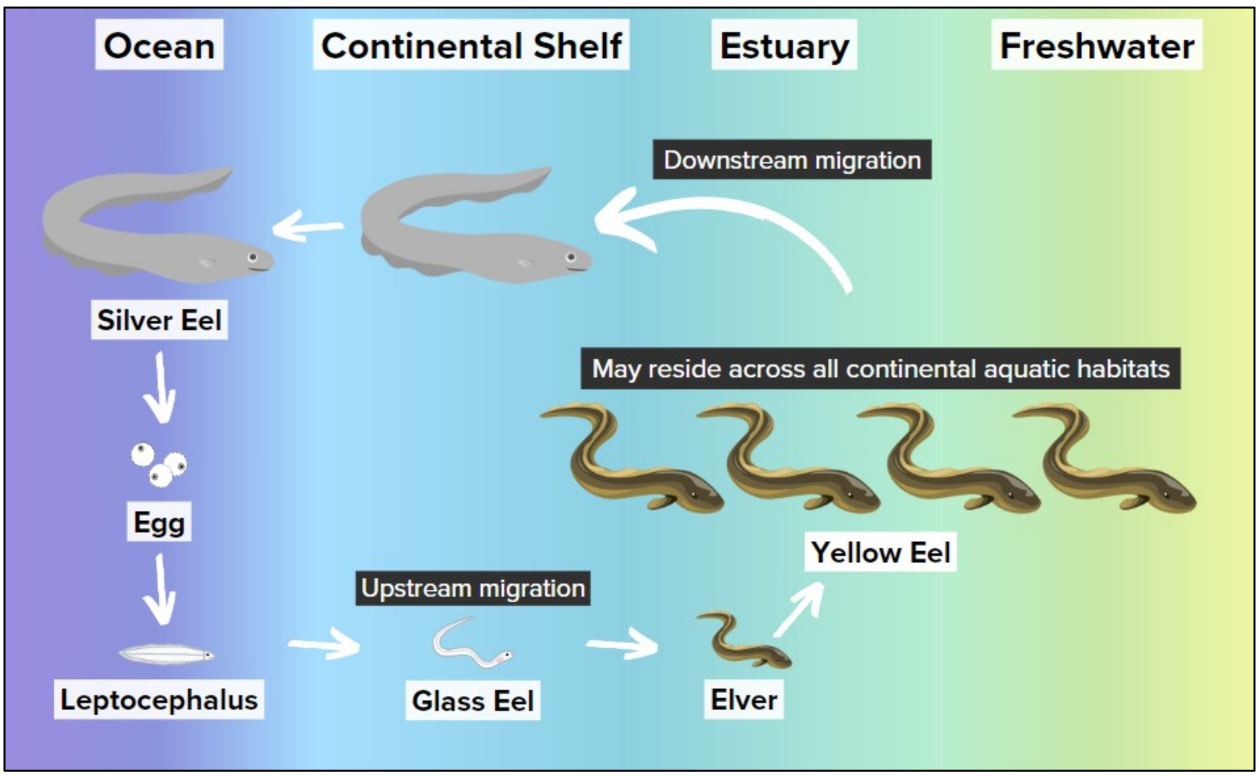


Figure 7. Diagram of the life cycle of Anguillid eels (adapted from Cairns et al. 2013). These fishes are born in cryptic marine areas, and are carried as larvae and juveniles on ocean currents toward the continental shelves. There, they reside in nearshore marine areas, estuaries, or further inland in freshwater. After rearing in these habitats for 5 to 30 years, eels begin to sexually mature and migrate back to their birthplace to reproduce.

Estimates of anguillid eel abundances have decreased precipitously worldwide, up to 99% in some areas (Verreault and Dumont 2003; Jacoby et al. 2015; Verreault et al. n.d.). The conservation status of widely valued and studied species such as American Eel *Anguilla rostrata,* European eel *Anguilla anguilla,* and Japanese Eel *Anguilla japonica* range from Endangered to

Critically Endangered (Pike et al. 2020a, 2020b, 2023). Eels encountering hydroelectric infrastructure during downstream migration can be delayed, injured, or killed, and these structures are widely considered a significant threat to the survival and recovery of many Anguillid species (Liermann et al. 2012; Piper et al. 2013; Jacoby et al. 2015; Verhelst et al. 2018, 2021).

Innovation is needed to mitigate the threats hydroelectric facilities pose to diadromous fishes. While relatively straightforward physical methods to improve downstream fish passage do exist (e.g. barriers, bypasses), there is extensive site, species, and intraspecific variability (Silva et al. 2018). This is particularly true for eels, which can be especially problematic to pass successfully. Out-migrating eels prefer greater flow velocities (Jansen et al. 2007; Bruijs and Durif 2009; Piper et al. 2013), which leaves them vulnerable to being drawn into turbine intakes and impinged against barriers in high flow, and their long bodies increase their likelihood of turbine strikes or entrainment compared to smaller-bodied fish. Eels' semelparous and panmictic nature mean that late-life mortality, particularly in regions where large, fecund females predominate (Hixon et al. 2014), could have outsized effects on subsequent recruitment. Also, their energetically taxing out-migration from the continents to deep marine areas means sublethal or even sub-injurious encounters may have serious knock-on effects on reproductive success. Problems can occur across site types, from low flow dam-and-reservoir facilities (Mensinger et al. 2021) to higher flow quasi-run-of-river systems (EPRI 2018; Pratt et al. 2021; Verreault et al. n.d.). Issues may be particularly apparent at relatively large facilities equipped with deep and wide water intakes, where accumulation and biofouling may necessitate prohibitively dangerous and/or expensive maintenance, and physical guidance structures can reduce generating capacity to an unacceptable degree (EPRI 2018). Fish passage science continues to evolve to incorporate richer data and more diverse areas of expertise (Silva et al. 2018), and behavioural guidance is increasingly considered for many juvenile and out-migrating diadromous fishes including salmonids (Hansen et al. 2018), sturgeon (Ford et al. 2017, 2018), and anguillid eels.

Anguillid eel life history and general behavioural observations indicate that they avoid both natural and artificial light. Eels are generally more active in low light, tend to out-migrate at night, and peak migration periods may occur during the waning and new moons and greater cloud coverage (Smith and Saunders 1955; Helfman et al. 1983; Vøllestad et al. 1986; Jellyman and Unwin 2017; Verhelst et al. 2018, 2023). Additionally, Cullen and Mccarthy (2000) report that artificial lighting near weir nets reduced catches of silver eel in those nets. Thus, out-migrating eels appear to avoid anthropogenic light just as they do sunlight.

Overlapping with the refinement of field observations, laboratory trials were undertaken in attempts to understand the nature of, and thresholds for, eels' putative avoidant response to light. Hadderingh et al. (1999) undertook a test in which eels transiting downstream in a flume were exposed to two corridors; one contained a fluorescent lamp, the other was dark. 65% of eels chose the darkened corridor. This effect was dampened but still significant when avoiding the light would cause eels to exit the area of greatest flow velocity. Elvidge et al. (2018) undertook a similar study in which late-yellow and silver eels were faced with various Light Emitting Diode (LED) spectra in one corridor, and the other was left dark, with additional control trials in which both corridors were left dark to test for a natural preference. Eels again exhibited avoidance to the illuminated corridor. Eels responded most strongly to blue (480 nm) and white (broad-spectrum) light, generally consistent with the shifting optical physiology of maturing eels (Pankhurst and Lythgoe 1983; EPRI 2017). These studies reinforce support for light's deterrent effect on out-migrating eels and provide justification for scaling to field experimentation.

Important takeaways include the prioritization of blue and white light, as well as the potential mitigating effect of high flow velocity.

Concurrent with laboratory developments and refinement of field observations, a number of experimental light guidance devices (LGDs) have been deployed in the field in recent decades. The earliest, and possibly most relevant study available is McGrath et al. (2003), wherein a series of halogen lamps were deployed vertically in the water column upstream of the Iroquois Water Control Dam (IWCD), St. Lawrence River (the same site as the present study; ~700 m across) to create a "wall of light". This study reported significant avoidance (77.6%), but information is limited given no publication exists. The halogen lights were not energetically efficient, debris accumulation on the lights required regular, relatively impractical on-site maintenance, and similar concerns were cited regarding biofouling. This device also did not influence a sufficient proportion of all out-migrating eels, thus there were doubts about the feasibility of the approach at a management scale. Furthermore, the experiment did not employ control periods, leaving the likelihood open that the presence of the physical structure to support the lights altered hydrodynamics and potentially acted as a physical deterrent in itself (Piper et al. 2015, 2017; Ford et al. 2017). Yet, these early results were nuanced enough to support continued experimentation, albeit with varied designs.

More recent field experiments continue to encourage development, but also emphasize caution and nuance. Bowen (2014) observed that strobing white LED light significantly deterred eels from an experimental LGD, but a small sample size and the fact that this was on a relatively small river limited interpretations (River Test, UK; 15 m across). In the much wider North Sea Canal, NL (800 m across), Kruitwagen (2014) used white LED light to reduce the number of eels observed near a trash rack (50 m wide) by a full order of magnitude. However, Bruijs and Vriese

(2013) used the same device and found no evidence for guidance on the River Meuse, NL (225 m across). There, they cited poor placement, high turbidity, turbulence, and ambient noise as potential causes for failure. Behavioural guidance methods are often characterized by broad variability in outcomes across sites (Elmer et al. 2021), and that is indeed what has been observed among past efforts to guide eels with light.

Logically, then, knowledge development regarding light guidance should emphasize adaptability. Yet, there is a scarcity of research regarding the acute behavioural effects of light on eels, particularly peer-reviewed studies, and the level of detail in much of the available work is inadequate for practical field application (Versar 2009a; EPRI 2018). Thus, there is little clarity regarding optimal device design, operational parameters, response thresholds, the nature of responses elicited, or how any of these factors may vary. In particular, there are not yet any studies which undertake altered methods at the same site as a previous experiment. This makes comparisons between specific methods difficult, given site-specific variability. Additionally, fundamental knowledge of eel-outmigration (e.g. space usage, phenology, timing) is lacking in many systems, further limiting informed decision-making regarding device design, placement, and operation.

With a more complete understanding of eel out-migration, eels' responses to light in the field, and with the correct methods, a full-scale light guidance system may be a useful tool for protecting eels in the St. Lawrence River and similar systems worldwide. Many recent developments could enable progression in this regard. Advancements in acoustic telemetry allow for management-relevant, fine-scale monitoring of behaviour in the field; Elvidge et al. (2018) has identified ideal light spectra for eliciting avoidance in maturing eels; and LED lighting offers many advantages (e.g. energetic and spatial efficiency, programmable, remotely controllable, equippable with UV anti-biofouling bulbs) over older technologies. Issues encountered by McGrath et al. (2003) suggest submerged lights are too susceptible to debris loading in this system, and above-water lighting could be necessary. Yet, the capacity for above-water light to guide out-migrating eels has not been tested before.

3.1.1 Present study

Here, we use fine-scale acoustic telemetry to characterize the responses of out-migrating American Eel to downward-projected white LED light under natural conditions, with the hypothesis that maturing eels avoid artificial light (McGrath et al. 2003; Hadderingh et al. 1999; EPRI 2017, 2018; Elvidge et al. 2018). Specifically, we deployed a floating 216 m long LGD at 30 degrees to the river/flow axis, upstream of the IWCD, St. Lawrence River, Canada – US border. Using acoustic telemetry data from past years, we identified pre-existing preferred paths of out-migrating eels and placed the LGD where it could affect over 50% of eels that passed through the system while covering less than 20% of the river's width, making this the first known management-scale assessment of light to behaviourally guide American Eel. To control for potential hydraulic or physical effects, we examined tagged eels' responses to the light stimulus against responses during periods when the lights were off but the LGD was present. The applied goal of this experiment was to horizontally divert eels toward one side of the dam to a theoretical collection device for trap and transport (see Piper et al. 2020). This effort (i.e. characterization of horizontal trajectories and a site-specific practical discussion) is reported on in EPRI (2024). Here, we primarily focus on the LGD's effect on vertical movement responses – given this was emphasized less in EPRI (2024) – and interpret results with a broader scope. We also report temporal, environmental, and spatial characteristics of eel out-migration, given they are foundational to the practical implementation of a light guidance device. Our research aims can thus be summarized with two distinct objectives:

Objective 1: Test whether a downward-projected LED light field can alter the vertical movement behaviour of out-migrating yellow and silver stage eels by qualitatively and quantitatively characterizing movement patterns of treatment (lights on) and control (lights off) groups passing within the measured light field and analyzing data for differences in depth or diving behaviour (e.g. swimming speed, depth and changes in these) across categories.

Objective 2: Report ecological, environmental, temporal, and spatial correlates of eel out-migration, including: migration rate of all tagged eels, potential size-dependent tendencies for out-migration, moon phase, discharge, dates, time of day and overall swimming depth.

3.2 Methods

3.2.1 Experimental Site

Iroquois Water Control Dam is located at the Canada-US border, near Iroquois, Ontario and Waddington, New York (Figure 8). It is 774 m across and equipped with 32 spillways, which are used to maintain water levels upstream and prevent high water downstream. All of its gates stay open outside exceptional circumstances, and the structure is not understood to hinder fish movement (EPRI 2018). The channel geometry and hydrology directly upstream of IWCD is characterized by a relatively straight-walled and flat-bottomed channel 10 to 15 m deep, average flow is about 8,000 m^3/s at a velocity of 0.6 to 1.5 m/s, and currents are fairly straight but tend diagonally toward the US shore (Figure 9; EPRI 2018). IWCD is located at the narrowest point upstream of the St. Lawrence River's two generating stations (Figure 8). In all likelihood all out-migrating Upper Saint Lawrence River and Lake Ontario (USLRLO) eels swim through it, so it is an ideal experimental site and an ideal site for concentration, collection, and downstream transport (EPRI 2018)

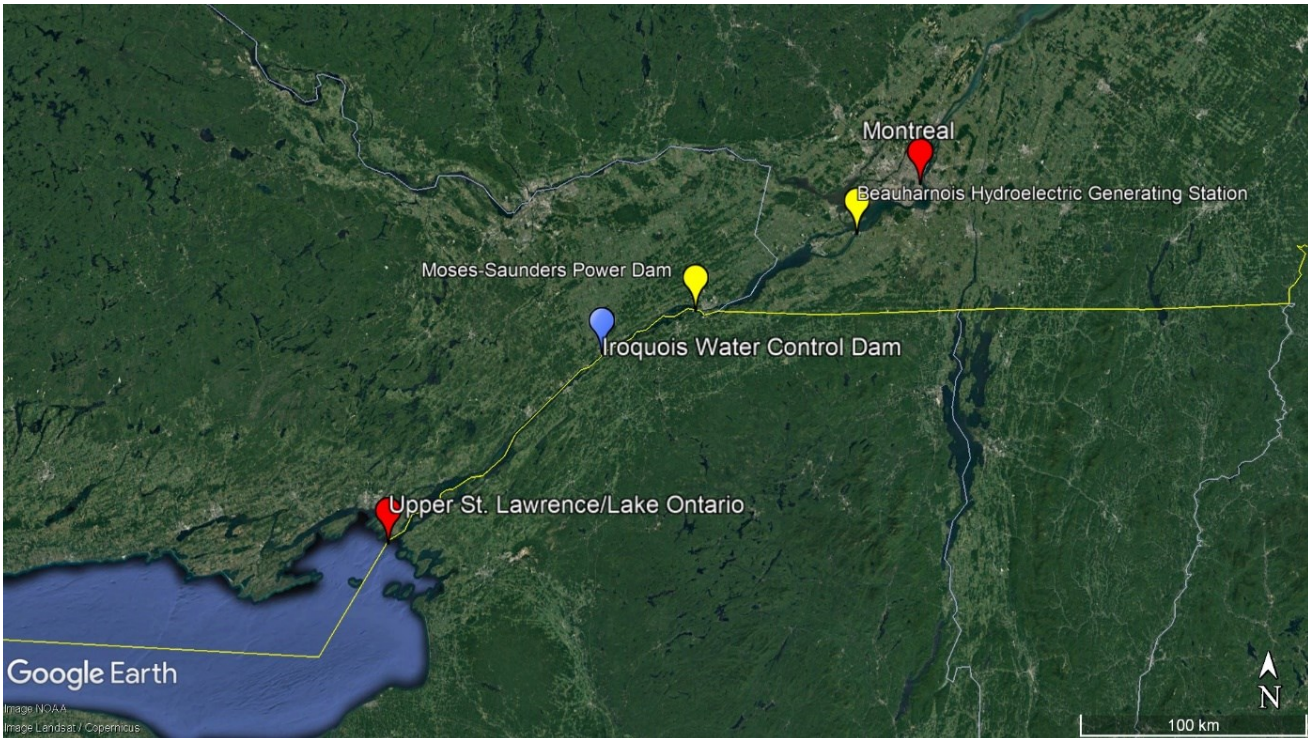


Figure 8. Map centered on Lake Ontario and the Saint Lawrence River, with the study area, Iroquois Water Control Dam, CAN-US border (blue pin). IWCD is approximately equidistant to the mouth of Lake Ontario and Montreal, QC (red pins), and is located upstream of the St. Lawrence's two hydroelectric generating stations (yellow pins).

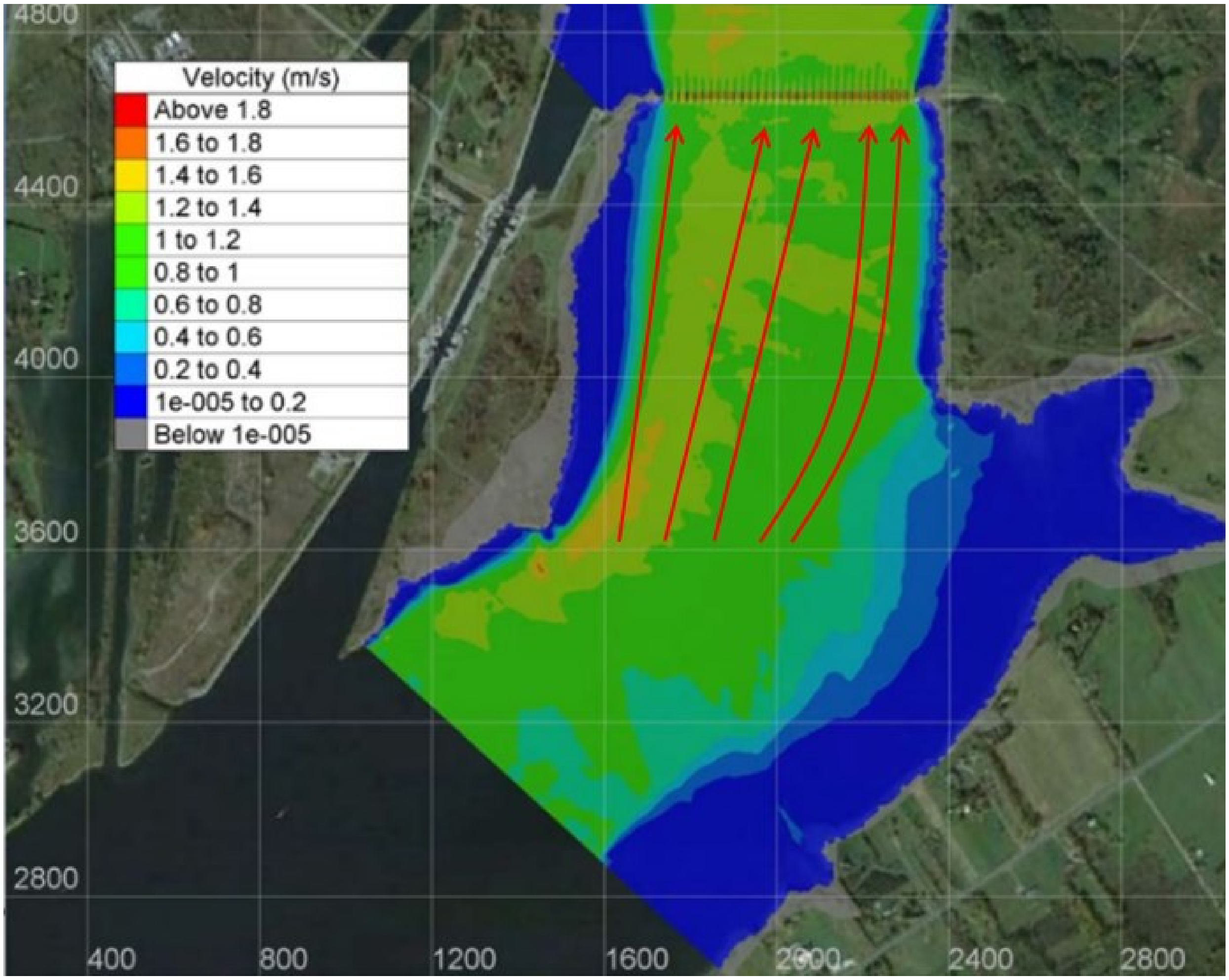


Figure 9. Flow velocity heatmap of the channel upstream of Iroquois Water Control Dam, with red arrows added to represent dominant currents. Adapted from EPRI (2018).

3.2.2 Light Array Construction and Installation

Light array construction was completed during August 2022. A series of $N = 32$ DuraBrite standard-series Light Emitting Diode flood light modules (35,000 lm, 5000 K colour temperature, 76º beam angle) were mounted on a 216 m long series of $N = 32$ floating ice barriers, faced toward the eastern (US) shore at a 30° angle relative to the river axis and anchored against the current using heavy chains attached to cement blocks resting on the riverbed (Figures 10; 11). Each LED module was focused using 45° top and bottom and 60° side shrouds, resulting in a band of bright, continuous white light toward the water surface at ~ 40°. The array's placement in the river was meant to maximize eel encounters based on prior telemetry results indicating that up to 66% of eels migrate closer to the US shore (EPRI 2024). The light array was operated (on during treatment nights, off during control nights) from sunset to sunrise, 17 August to 12 December 2022 (see Experimental Period for details).

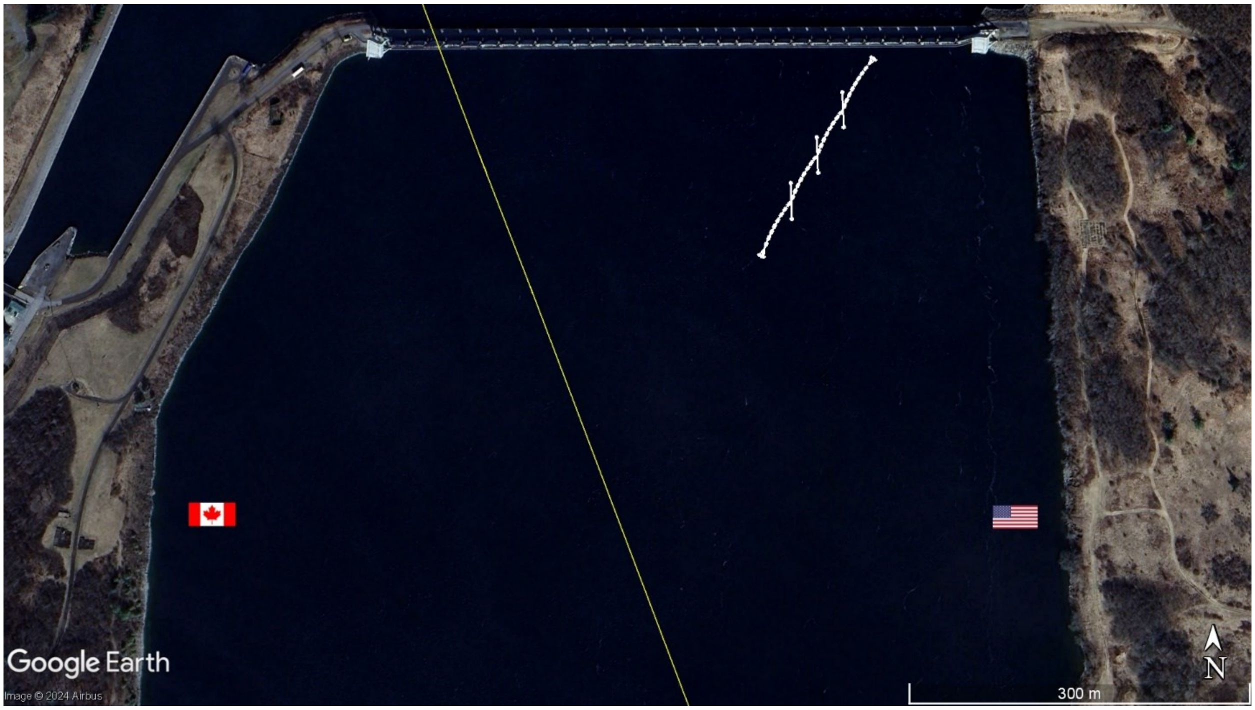


Figure 10. Satellite image depicting the floating light guidance device deployed at Iroquois Water Control Dam, St. Lawrence River, September 2022. The dotted diagonal line represents the floating booms and LEDs (i.e. the device itself), while the flared ends of the diagonal line and the vertical lines passing through it represent anchor chains tethered by cement blocks. Canadian and US flags represent their respective sides of the river, and the international border is demarcated by the yellow line.

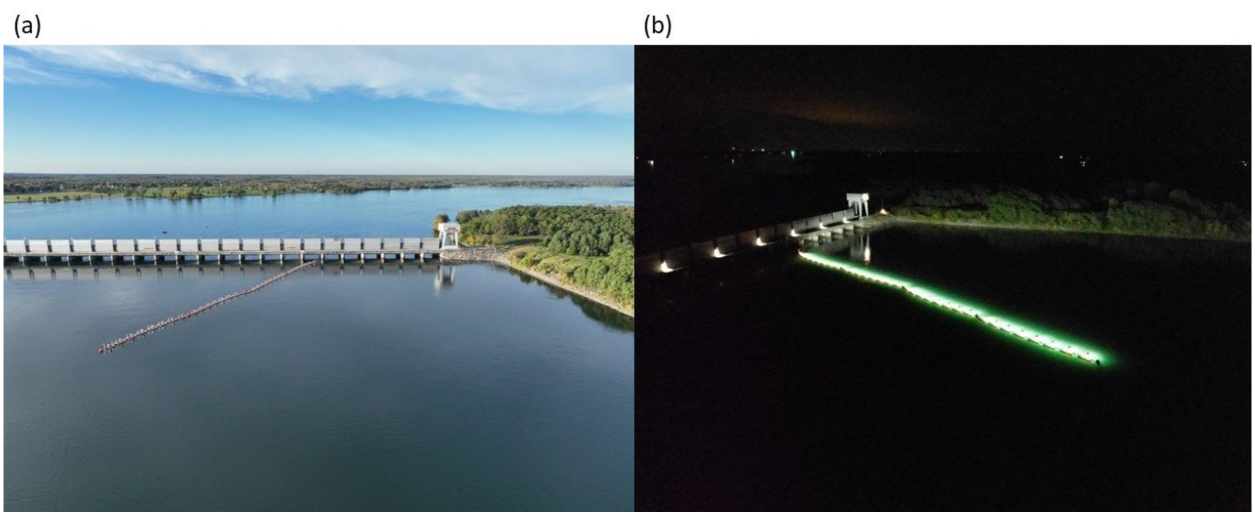
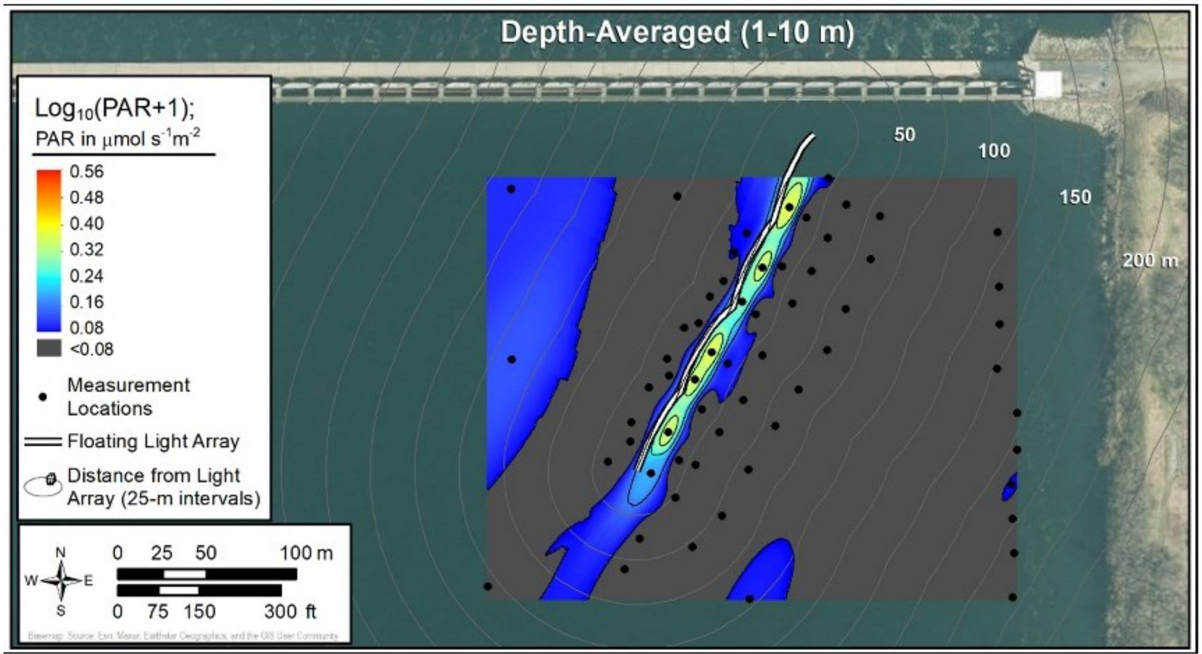


Figure 11. Photos of the 216 m floating light guidance device (a) during the day and (b) at night outside Iroquois Water Control Dam, St. Lawrence River, September 2022. Images from A. Weinstock (New York Power Authority).

Light field mapping

Light field mapping was undertaken the night of 28 October 2022 (waxing crescent moon, 4 day moon age, 13% illumination, 17% relative luminosity; www.nextfullmoon.org). *N* = 61 locations around the light array were sampled to 10 m depth in 1 m intervals using a LI-COR LI-193SA spherical underwater quantum sensor equipped with a LI-COR 2009S lowering frame, YSI EXO2 multiparameter sonde depth sensor, and GPS locator. Data were recorded using a LI-COR LI-1400 logger. Light was measured as Photosynthetic Active Radiation (µmol s^{-1} m^{-2}). Contour maps were produced to represent the vertical and horizontal extent and magnitude of the light field against ambient conditions. The depth-averaged effective range was up to 25 m from the array, and up to 5 m depth (Figure 12a). The furthest detectable extent of the light at any sampling location or depth was 51 m from the array (Figure 12b). EPRI (2023) contains a full report on the light field mapping process.

(a)



(b)

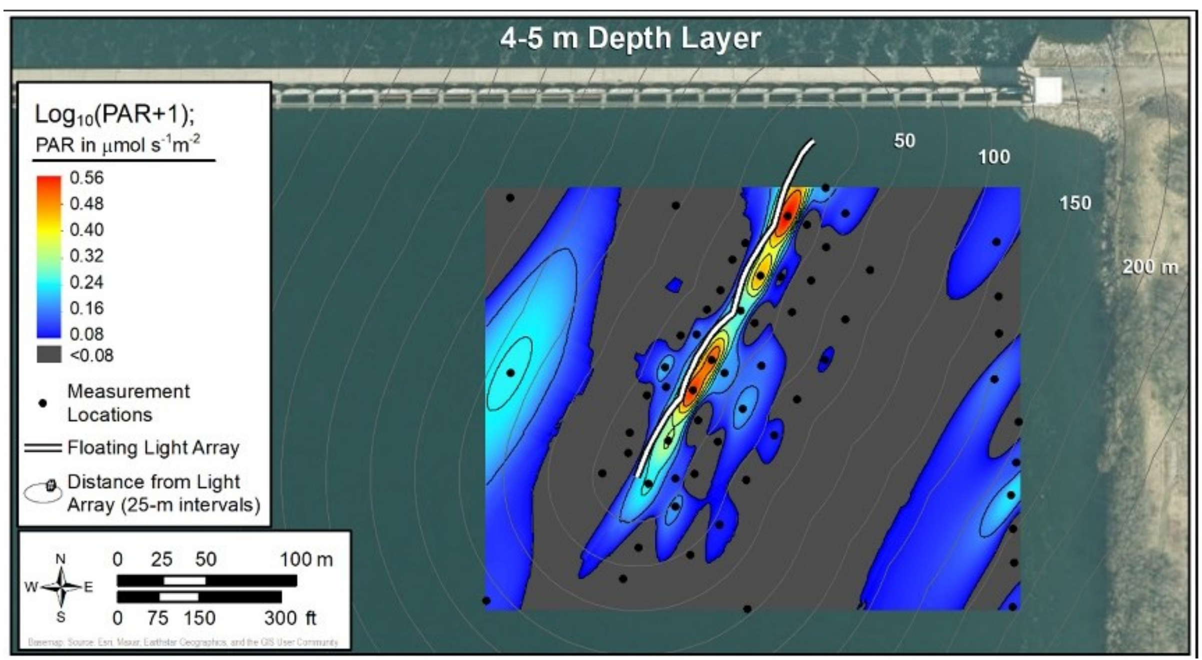


Figure 12. (a) The depth-averaged (1-10m) effective range of the experimental light guidance array (white diagonal line) deployed at IWCD was determined to be 25 m; sampling transects denoted with black dots. **(b)** The furthest detectable extent of the light array; luminosity was greater than background levels at 51 m from the array in the 4 to 5 m depth range. Figure was adapted from EPRI (2023).

3.2.3 Eel Selection & Tagging

All field work was undertaken at the Ontario Ministry of Natural Resources and Forestry (OMNRF) Glenora Fisheries Station in Glenora, Ontario from 10 May to 3 June and from 9 to 23 September 2022. Eels were obtained by OMNRF from specially licensed commercial fishers, who caught them as by-catch in a trap net fishery on Lake Ontario. Eels selected for tagging before researchers arrived were held according to OMNRF Trap and Transport protocols (J. LaRose et al.). After researchers were on-site but before tagging, eels were held in a tank containing approximately 2000 L of water circulated (200 L/min) from Lake Ontario using a submerged pump.

Work associated with the current trap & transport program for USLRLO eels (OMNRF 2008) indicated 90 cm Total Length (TL) as a threshold size for out-migration, which corresponds to ~ 1.78 kg. For tagging, OMNRF staff retained eels ≥ 1.8 kg which appeared to be in good condition. Researchers then prioritized the largest of those retained, with the assumption that larger eels would be increasingly likely to out-migrate. N = 398 eels were tagged, n = 199 per season Tagged eel mass ranged from 1.90 to 4.92 kg ($\bar{x}$ = 2.62 ± 0.44 kg) and TL ranged from 92 to 121 cm ($\bar{x}$ = 104.0 ± 5.44 cm) (Table 1; Figure 13).

Table 1. Mean plus standard deviation, median, and range of American Eel *Anguilla rostrata* total length and mass by tagging period, May to June and September 2022.

	Spring		**Fall**	
	Length (cm)	Mass (kg)	Length (cm)	Mass (kg)
Mean +/- SD	103.3 ± 5.2	2.40 ± 0.32	105.8 ± 5.4	2.83 ± 0.43
Median	103	2.33	105	2.74
Range	92 to 119	1.90 to 3.31	92 to 121	2.14 to 4.92

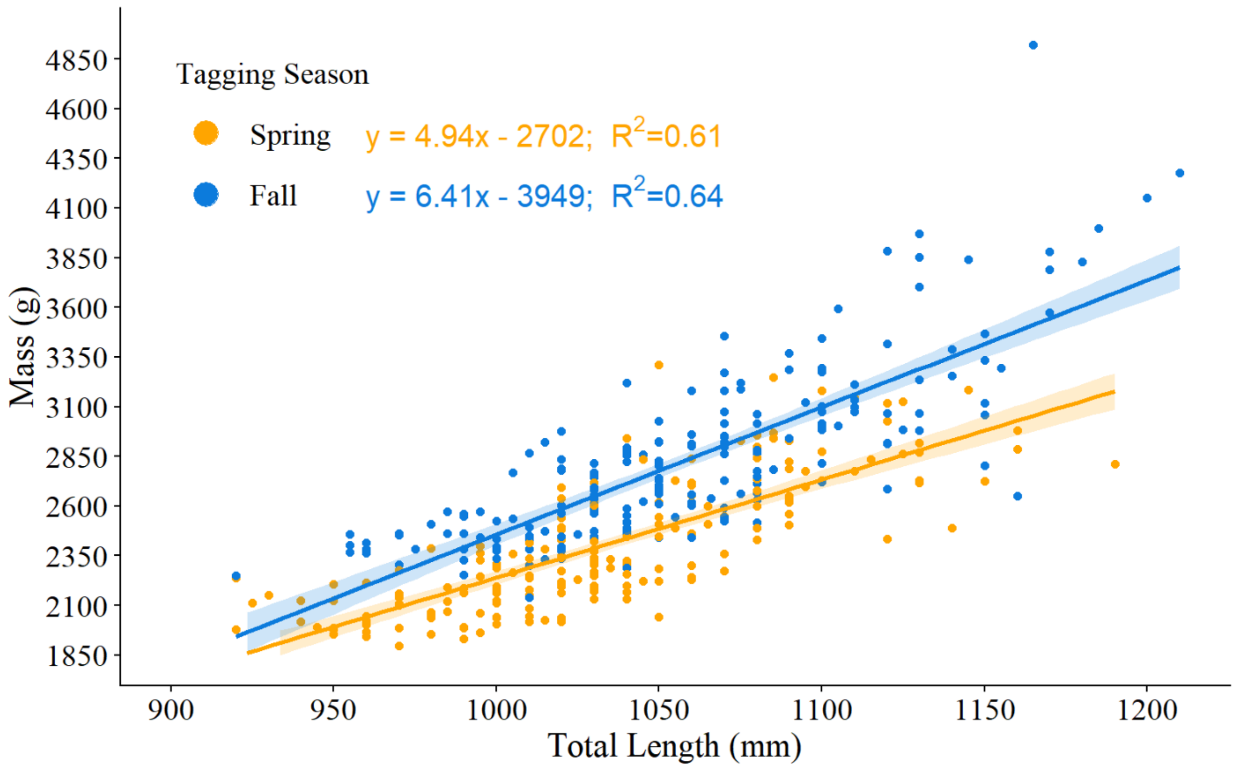


Figure 13. Linear regression of acoustically tagged American Eel *Anguilla rostrata l*ength (mm) and mass (g) by tagging season. Eels were tagged at the Ontario Ministry of Natural Resources and Forestry (OMNRF) Glenora Fisheries Station, Glenora ON, Spring and Fall 2022, and were sourced from the OMNRF-Ontario Power Generation Trap & Transport program.

To prepare the anaesthetic bath, a clove oil solution was prepared from 2 mL clove oil and 18 mL anhydrous ethanol. 15 mL of this mixture was added to 10 L Lake Ontario water in a 60 L cooler for a final concentration of 150 ppm (0.15 mL/L) clove oil in water. Preliminary trials found this concentration elicited sufficient sedative effects (i.e. unresponsiveness and loss of equilibrium) in ≥ 1.8 kg eels after ~4 minutes. Eels were individually netted from the 2,000 L holding tank and placed in the bath for 4 to 7 minutes, until sufficient sedative effects were observed. Anaesthetic bath temperature was monitored using digital aquarium thermometers, and a new bath was prepared if there was a change of > 2°C, if the anaesthetic seemed to be losing its potency (i.e. eels were taking longer to be sedated), or if the water became visibly dirty. Sedated eels were netted and weighed in lb (converted to kg using *0.453592) on a Pro Tournament

Scales Model 357 digital scale (accurate to ± 5g). Then, they were transferred to a 1.4 m surgical trough with 2 L of water from Lake Ontario, measured in cm, and tagged. The trough water was changed every 10 fish, or sooner if it appeared dirty.

During tagging, one researcher held the eel in the trough with a pair of steel mesh gloves attached to a Compass Health Brands TENS 7000™ unit (50 µS, 60 Hz, normal wave form, intensity setting 3-4 (37.5-50 mA)) as a form of secondary electrosedation due to the difficulty associated with handling large eels. Unit settings were determined in preliminary trials; researchers watched for lightly tensing (not rigid, nor entirely relaxed) musculature upon contact with the gloves. Another researcher wearing powder-free nitrile gloves and using a FEATHER® No22 disposable scalpel, made a small (1 to 2 cm) ventral incision in each eel, about 6 cm superior to and 3 cm lateral of the cloaca. An Innovasea V9P-2x-180kHz HR acoustic transmitter (9 mm diameter; 2.8-3.2 s signal frequency; depth sensor to 34 m, 0.15 m intervals, ±0.5 m accuracy) was inserted in the coelom parallel with the body, and the incision was closed with 1-2 suture(s) (Ethicon® PDS*II 3-0 violet monofilament, FS-1 24mm 3/8c reverse cutting needle; Figure 14). All surgical equipment was sterilized in 5% Purdue Pharma BETADINE® for 30 seconds before being rinsed with pure distilled water, and all surgeries were undertaken by the same researcher to ensure consistency. Surgeries generally took less than 2 minutes from the time an eel was netted from the anaesthetic bath. Eels were then moved to a 378 L Rubbermaid® cattle trough with water from Lake Ontario flowing through. Most individuals recovered immediately; a minority took 1 to 5 minutes. Once an eel appeared to be fully recovered (i.e. regained equilibrium, alert, responsive), it remained in the bath for at least another 15 minutes before being released back into Lake Ontario. Time of release for each eel was noted and all were returned to Lake Ontario within 48 hours of their arrival at Glenora.

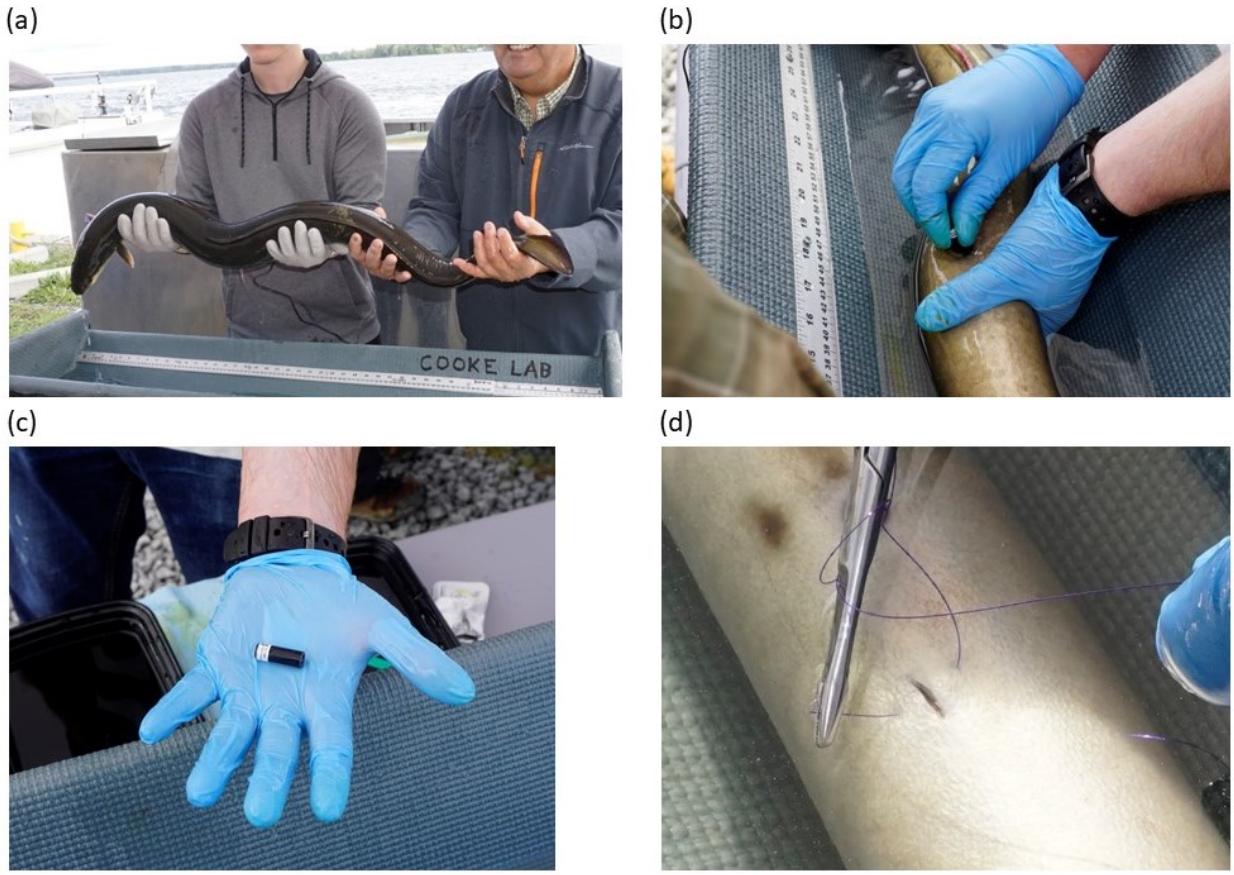


Figure 14. (a) Cole MacLeod, left, and Dave Stanley, right, holding a >1 m American Eel *Anguilla rostrata* before acoustic tagging. **(b)** Intracelomic implantation of an American Eel with an InnovaSea V9P-2x-180kHz HR acoustic transmitter. **(c)** An InnovaSea V9P-2x-180kHz HR acoustic transmitter (9 mm diameter; 2.8-3.2 s signal frequency; depth sensor to 34 m, 0.15 m intervals, ±0.5 m accuracy). **(d)** Suturing of the ~1 cm tagging incision located on the ventral side of the eel near the cloaca. Images from John Sanna (Ontario Power Generation).

3.2.4 Receiver Array

InnovaSea HR2-180kHz receivers (*N* = 27) attached to 69kHz Acoustic Release (AR) receivers were attached to concrete anchors and deployed ~100 m apart in a grid pattern below the light array to detect tagged eels from 23 August to 5 December 2022 (Figure 15). The AR receivers were not collecting data from the tagged eels; they were only used to ensure retrieval of the HR2 receivers. Because half of the eels had been tagged in the spring, an initial 'gate' of *n* = 3 HR2-AR pairs were deployed perpendicular to the river axis, ~300 m apart, ~500 m upstream of IWCD from 18 July to 23 August 2022 to detect any early summer migrants (Figure 16). The full receiver array could not be deployed at this time due to logistical delays. These receivers were retrieved, data were downloaded, batteries changed, and they were redeployed in the full array with the other *n* = 24 receivers on 23 August 2022. All receivers were retrieved via remote release on 5 December 2022, and raw data were downloaded and provided to InnovaSea Systems, Inc. to position (*i.e.* calculate latitude, longitude, depth; project on a virtual XYZ grid with meter units) eels detected by ≥3 receivers using the proprietary VEMCO Positioning System (VPS) (S. Schlueter, pers. comm. 2023). InnovaSea returned the VPS data at the end of March 2023.

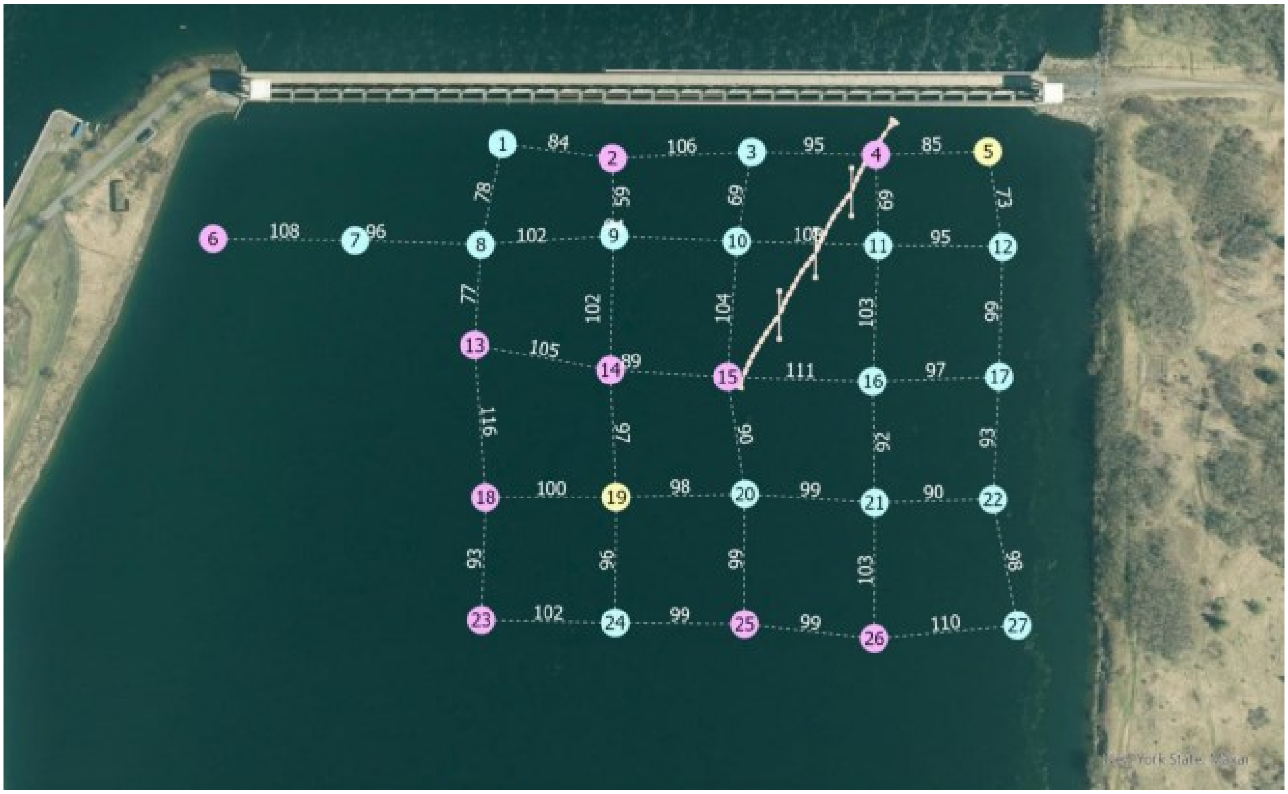


Figure 15. Satellite image of Iroquois Water Control Dam where the bold diagonal white line is the Light Guidance Device, and the numbered circles are $N = 27$ Innovasea 180kHz HR2 receivers deployed to record the responses of acoustically tagged American Eel *Anguilla rostrata* to the light field. Numbers on the receivers are IDs, numbers on the dotted lines between receivers represent distances in metres. Image from J. Ecret and S. Schlueter (US Fish and Wildlife Service). Receivers were deployed from 23 Aug to 04 Dec 2022.

Figure 16. Satellite image of Iroquois Water Control Dam with locations of *N* = 3 Innovasea HR2-180kHz receivers (white squares, ~300 m apart) deployed in Summer 2022 before full deployment of the Light Guidance Device and *N* = 27 receivers to detect early migrant American Eel *Anguilla rostrata*.

3.2.5 VPS

Many telemetry studies aim to maximize detections (i.e. retain up to 80%; Meckley et al. (2014)) at a cost to positioning accuracy. Because the intent here was to produce fine-scale movement tracks over a short geographic area with a high degree of confidence, potential error was minimized by filtering positions more conservatively than usual. VPS data have two calculated error terms which convey the accuracy of a given position: Root-mean-square error (RMSE) and horizontal positioning error (HPE). RMSE measures error resulting from physical deflections of acoustic signals, and HPE measures error as influenced by the receiver array's effective coverage. Both suggest greater potential error with greater values. Positions with RMSE <2 were retained and positions >2 were discarded, per InnovaSea's recommendation. Positions with HPE <0.4 were retained and positions >0.4 were discarded; this threshold was calculated by approximating how far an eel traveling at 1-1.5 m/s (slightly faster than ambient flow velocity) may realistically move between detections (2.8 to 3.2 s transmission rate; ~4 m between signals).

3.2.6 Experimental Period

The experimental period (i.e. the temporal overlap of the full receiver array and light array deployment) spanned 23 August to 5 December 2022, based on the observed migration timing of native and translocated (see Pratt and Threader 2011) USLRLO eels and the onset of winter. We planned for the experimental period to consist of approximately 20% control nights, 80% treatment nights (3 out of every 14 nights would be control nights) reflecting a compromise between ensuring sufficient sample sizes for statistical significance while maximizing the number of eels that encounter the light array. However, logistical issues regarding accessing the array's power supply caused delays in implementing control periods early in the experiment, and the nature of winter field work meant the receiver array needed to be retrieved a week earlier than planned. These constraints resulted in a split of 16% control nights, 84% treatment nights (*i.e.* the lights were off for n = 17 out of N = 104 nights) (Table 2).

Table 2. Schedule of operation of the Light Guidance Device deployed upriver of Iroquois Water Control Dam from August to December 2022 to target out-migrating American Eel *Anguilla rostrata*; "on" denotes continuous operation until next "off" date.

Week	Nights Off	Off	Off	On
22-Aug	0			23-Aug
29-Aug	0			
5-Sep	0			
12-Sep	0			
19-Sep	0			
26-Sep	2	28-Sep	29-Sep	30-Sep
03-Oct	1	05-Oct		06-Oct
10-Oct	2	12-Oct	13-Oct	14-Oct
17-Oct	1	19-Oct		20-Oct
24-Oct	2	26-Oct	27-Oct	28-Oct
31-Oct	1	31-Oct		01-Nov
07-Nov	2	08-Nov	09-Nov	10-Nov
14-Nov	1	16-Nov		17-Nov
21-Nov	2	22-Nov	23-Nov	24-Nov
28-Nov	1	01-Dec		02-Dec

3.2.7 Analyses

Guidance candidate categories were defined based on measured light field intensity (i.e. 51 m max extent [peripheral contact]; 25 m average extent [full contact]; and 0 m [swam beneath LGD]). Each eel's closest point of detection to the LGD was identified and calculated (m) using the Google Earth ruler tool, and individuals were categorized accordingly. This closest point was also used as the reference for calculating LGD distance for the remainder of each eel's VPS positions. These calculations were undertaken using a Visual Basic for Applications (VBA) function for calculating distance between two sets of coordinates using the Haversine formula in Microsoft Excel® (Figure 17). A categorical variable for depth responses was constructed with possibilities defined as 'no dive', 'minor or equivocal dive' (< 2 m depth change), and 'dive' (> 2 m depth change) were constructed. Eels were categorized via visual inspection using top-down GIS tracks laid over satellite images (Figure 18) and side-view depth plots (Figure 19), with colour codes and the y axis representing swimming depth, respectively. An 'ascending' category was also anticipated, but no guidance candidates were observed swimming from depth to surface as their dominant vertical movement pattern across detections.

```
Public Function getDistance(latitude1, longitude1, latitude2, longitude2)
earth_radius = 6371
Pi = 3.14159265
deg2rad = Pi / 180

dLat = deg2rad * (latitude2 - latitude1)
dLon = deg2rad * (longitude2 - longitude1)

a = Sin(dLat / 2) * Sin(dLat / 2) + Cos(deg2rad * latitude1) * Cos(deg2rad * latitude2) * Sin(dLon / 2) *
Sin(dLon / 2)
c = 2 * WorksheetFunction.Asin(Sqr(a))

d = earth_radius * c

getDistance = d

End Function
```

Figure 17. VBA function used to calculate distances between detection points of acoustically tagged out-migrating American Eel *Anguilla rostrata* swimming upstream of Iroquois Water Control Dam.

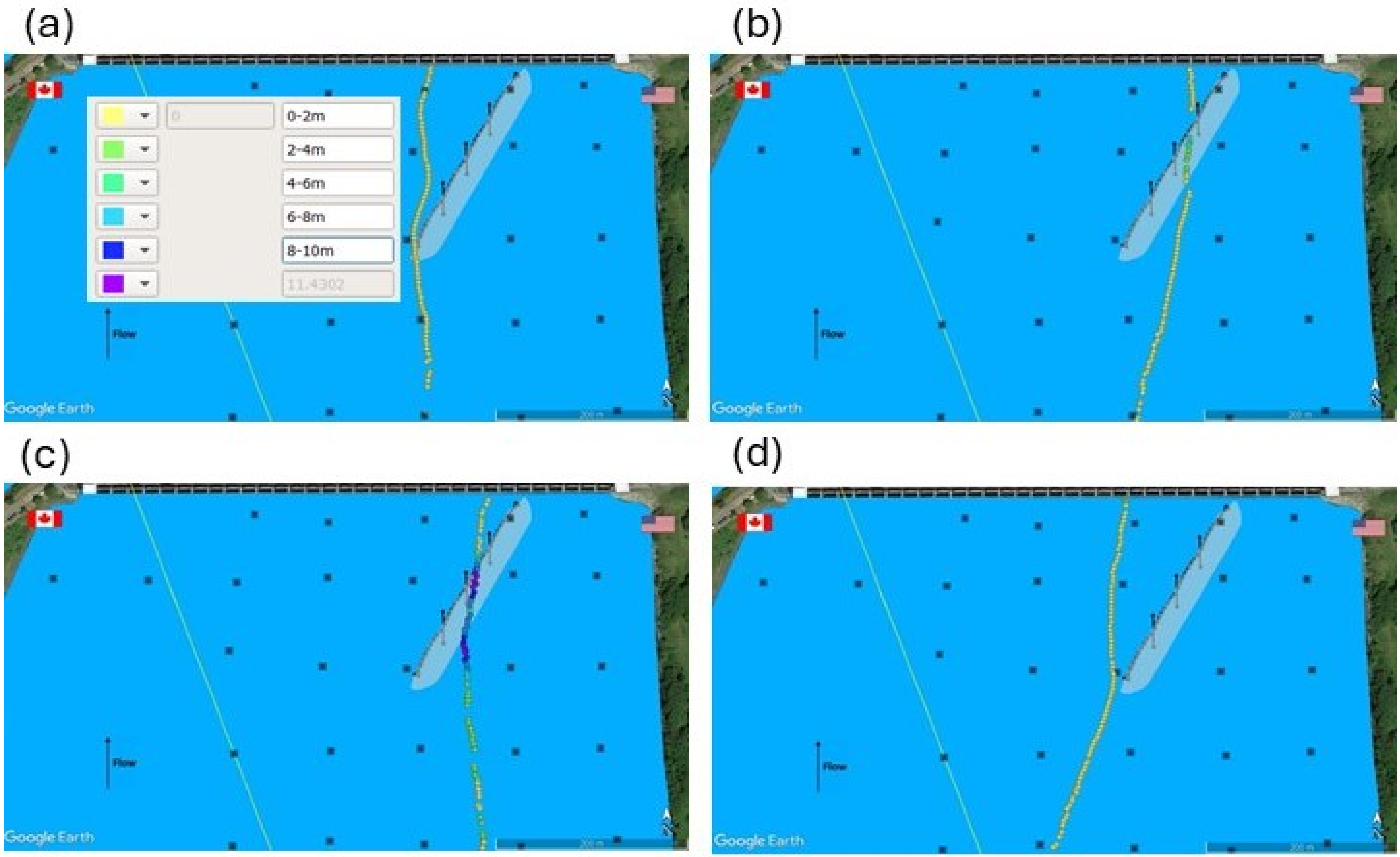


Figure 18. Satellite image and GIS track examples of American eel *Anguilla rostrata* categorical depth responses to the floating Light Guidance Device deployed upstream of Iroquois Water Control Dam, Fall 2022: **(a; d)** no response; **(b)** weak response (< 2 m change); **(c)** diving response (> 2 m change). Adapted from EPRI (2024).

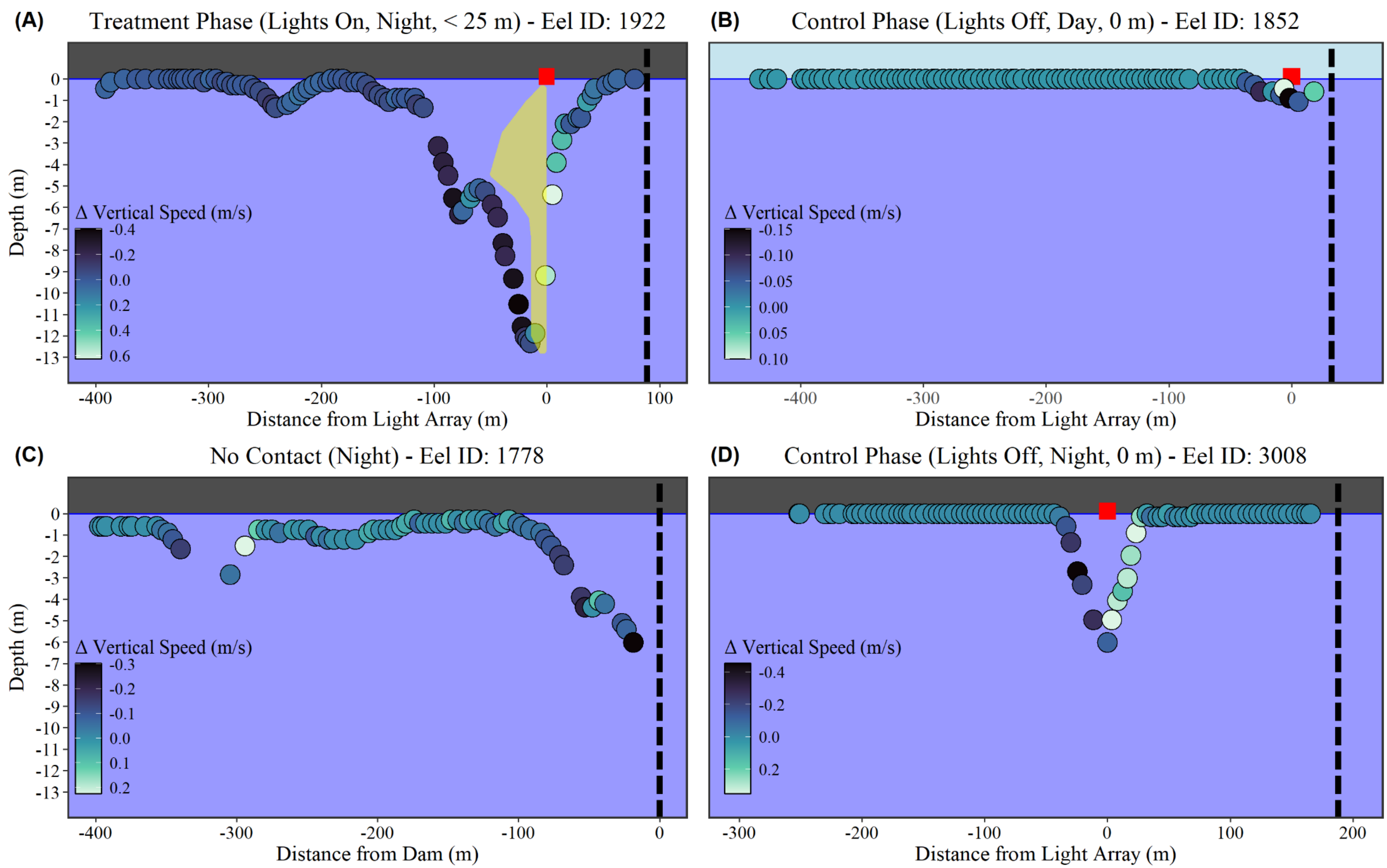


Figure 19. Depth plot examples of American eel *Anguilla rostrata* **(C)** general non-contact path, **(A; D)** dive, and **(B)** weak response (< 2 m change) to the floating Light Guidance Device deployed upstream of Iroquois Water Control Dam, Fall 2022. Red square represents the LGD and the shaded yellow area is the estimated light field.

Numerous variables were externally sourced or secondarily calculated using primary data. Lunar phase progression and daily photoperiod durations across the temporal range of the experiment were retrieved from https://nextfullmoon.org/moon-phase-any-date and https://timeanddate.com, respectively. Mean daily discharge (m^3/s) measurements were sourced from Ontario Power Generation's monitoring station at the Moses-Saunders Power Dam approximately 45 km downstream of IWCD (Figure 2) as a stand-in for conditions at the experimental site. Changes in vertical swimming speed (± m/s) were calculated based on distances and times between detections, and the distance from the LGD at which eels began to dive (if they did so) was estimated from visual inspection concurrent with categorizing diving behaviour.

All statistical tests were undertaken using $p < 0.05$ (i.e. > 95% confidence or a < 5% chance of a Type I error) as the threshold for significance. To assess the efficacy of using size metrics to predict potential out-migrants for tagging, the out-migration rate of tagged eels was compared against 50% using a Chi-squared contingency test, and the migration rates of Spring and Fall tagged eels were compared against each other likewise. The effects of TL and Mass on out-migration rate were estimated using Binomial Generalized Linear Models (GLMs), and their fit was compared against the null model (i.e. Migration~1) using the likelihood-ratio test. Mean depth (m) of non-candidate eels (i.e. > 51 m from the LGD) was calculated according to photoperiod and day and night groups were compared using Welch's two-sample t-test. Differences in depth response categories between control and treatment eels were evaluated using a Chi-squared contingency test. Mean distance from the LGD upon beginning to dive was calculated according to treatment period and compared using Welch's two-sample t-test. Linear Mixed-Effect models (LMEs) were used to estimate the effects of treatment period, distance from the LGD, the treatment-distance interaction term, and random individual variability (eel ID) on eel swimming depth and vertical swim speed. The swim speed LME was singular (see Figure 23 in Results for interpretation), so an Analysis of Covariance (ANCOVA) was undertaken using the same covariates, sans random error term.

Data cleaning, transformations, and analyses were undertaken using Microsoft Excel® or R (4.4.1) / RStudio (2024.04.2+764 "Chocolate Cosmos") with the following R packages: ‘tidyverse’ (Hadley Wickham) packages, particularly ‘dplyr’ (Hadley Wickham et al.) for transformations; ‘lubridate’ (Vitalie Spinu et al.) for handling dates, times, and datetimes; ‘rstatix’ (Alboukadel Kassambara) for ANCOVAs; ‘diptest’ (Martin Maechler) for Hartigan’s dip test; and ‘lme4’ (Douglas Bates et al.) and ‘lmerTest’ (Alexandra Kuznetsova et al.) for LMEs. All figures were generated using R/RStudio using: ‘tidyverse’ packages, particularly ‘ggplot2’ (Thomas Pedersen et al.) for plot design and specification; ‘cowplot’ (Claus Wilke) for further plot specification; ‘lubridate’; and ‘ggforce’ (Thomas Pedersen et al.) for creating polygons on plots.

3.3 Results

3.3.1 Detection and Path Categories

Overall, 207 eels were detected at IWCD, with 199 detected during the experimental period (23 Aug to 04 Dec). Of these, 4 were detected in the experimental area over multiple days and appeared to pass the light array multiple times, and 2 were positioned only once. Because we could not discern a singular encounter with the array for these fish, they were excluded from further spatial analyses. The remaining 193 experimental period migrants had viable paths (N = 12 969 filtered positions, $\bar{x}$ = 67.2 per eel, σ = 47.7). Of the viable eels, 120 had no contact with the light field (*i.e.* never swam within 51 m). Seventy-three tagged eels did make contact (< 51 m); 61 of those passed on treatment nights, and 12 passed during control periods. Twenty-two tagged eels made peripheral contact (25 to 51 m); 18 during treatment periods, 4 during control periods. Fifty-one tagged eels passed within the full light field or swam directly beneath the array (i.e. 25 m to 0 m); 43 treatment, 8 control. Figure 20 and Table 3 summarize outcomes for all tagged eels.

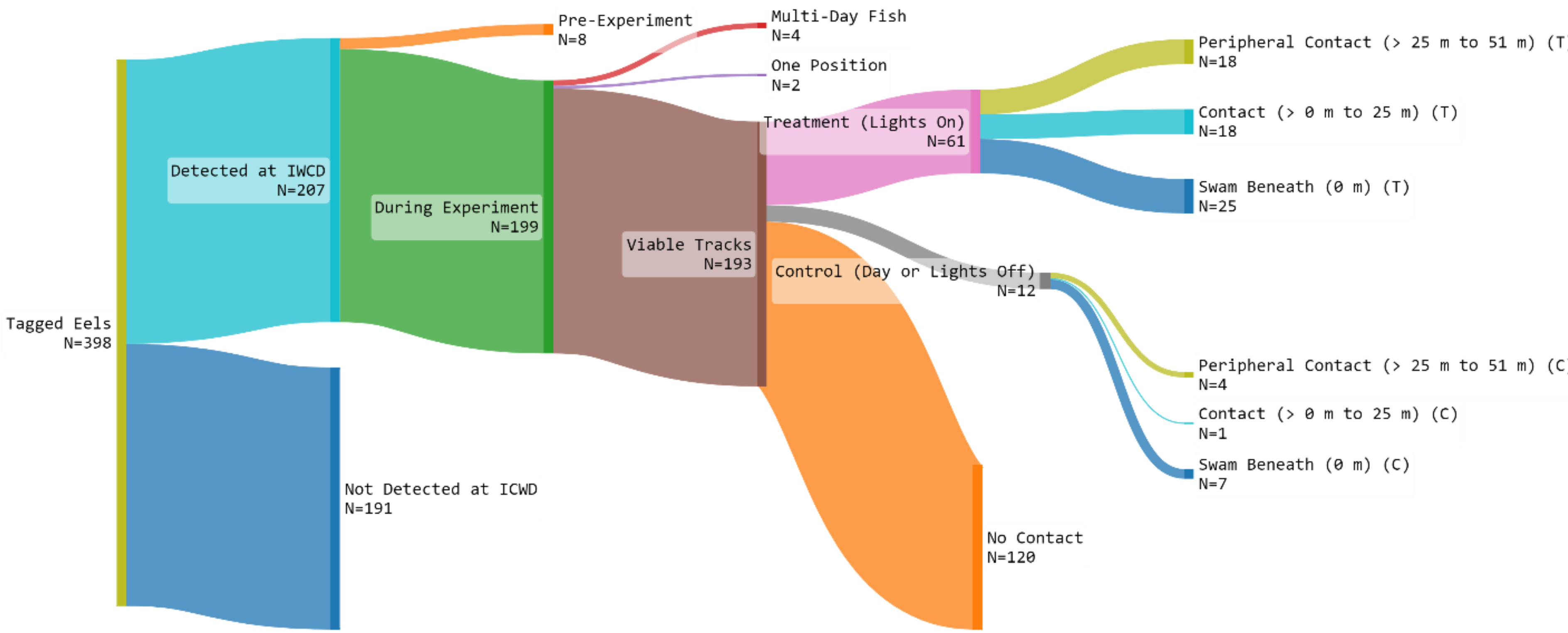


Figure 20. Sankey diagram showing outcomes of N = 398 American Eel *Anguilla rostrata* acoustically tagged in Spring and Fall 2022 at the Ontario Ministry of Natural Resources Glenora Fisheries Station, Glenora ON in a field-scale assessment of light as a behavioural guidance mechanism for out-migrating late yellow and silver-stage eels. Figure generated using www.sankeymatic.com.

Table 3. Outcomes of N = 193 American Eel *Anguilla rostrata* acoustically tagged in 2022 at the Ontario Ministry of Natural Resources Glenora Fisheries Station, Glenora ON and later detected by an array of N = 27 acoustic receivers at the Iroquois Water Control Dam, Canada-US Border

	Closest point to LGD (m)			**Detected with VPS**	***n* During Day**	***n* During Night**
	0	**25**	**51**			
n Total	32	51	73	193	9	184
n Treatment	25	43	61	144	0	144
n Control	7	8	12	49	9	40

3.3.2 Characteristics of Out-Migration

Of N 398 tagged eels, 52.5% (n = 209) out-migrated; 2 individuals that were not detected at IWCD were detected further downstream in a receiver array maintained by Hydro-Quebec. This out-migration rate was not significantly different from 50% (chi-squared test: $\chi^2_{(1)} = 1.005$, $p = 0.316$); however, the out-migration rate of eels tagged in the Spring was significantly greater than that of Fall-tagged eels (62.3% versus 42.7% respectively; chi-squared test: $\chi^2_{(1)} = 14.549$, $p < 0.001$). Eels were detected from 19 July to Dec 4, though only Spring-tagged fish were detected before 26 September (Figure 21). 96% of eels at IWCD (n=198) were detected overnight, between sunset (20:41 to 16:20; Jul. to Dec.) and sunrise (05:33 to 07:31; Jul. to Dec.; Figure 22). Unique detection frequency peaked during two waning moons (Waning Gibbous, Third Quarter, and Waning Crescent; 90% of unique detections [n=179]; Figure 23). Unique detections had no apparent relationship to discharge, which decreased with seasonal changes over time (Figure 23). Neither TL (Binomial GLM Migration~TL: likelihood ratio test $\chi^2_{(1)}$ = 0.103, $p = 0.748$) nor mass (Binomial GLM Migration~Mass: $\chi^2_{(1)} = 0.925$, $p = 0.336$) predicted propensity to out-migrate significantly better than the null model (GLM Migration~1). Eels that did not encounter the LGD at all (i.e. > 51 m) generally swam through the channel in the upper 3 m of the water column (Figure 24a). Mean swimming depth for this group was significantly greater during daylight hours (2.32 m) than in the dark (1.34 m; Welch's two-sample t-test: $t_{(367)}$

= 8.05, $p < 0.0001$; Figure 24b). Eels appeared to dive slightly upon the final 50 m approach to IWCD (Figure 24).

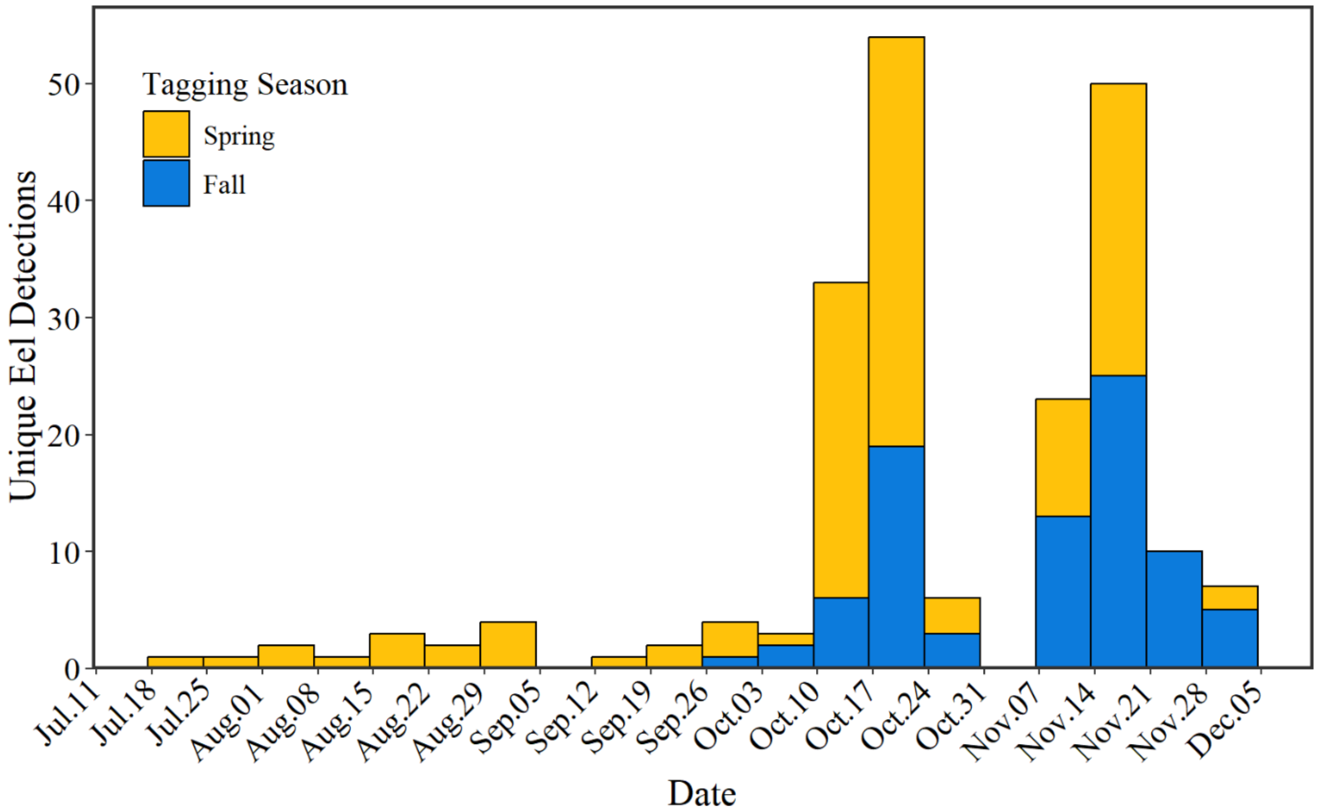


Figure 21. Detection frequency by date and tagging season of American Eel *Anguilla rostrata* acoustically tagged in Spring and Fall 2022 at the Ontario Ministry of Natural Resources Glenora Fisheries Station, Glenora ON and later detected downstream in an array of $N = 27$ acoustic receivers at the Iroquois Water Control Dam, Canada-US border.

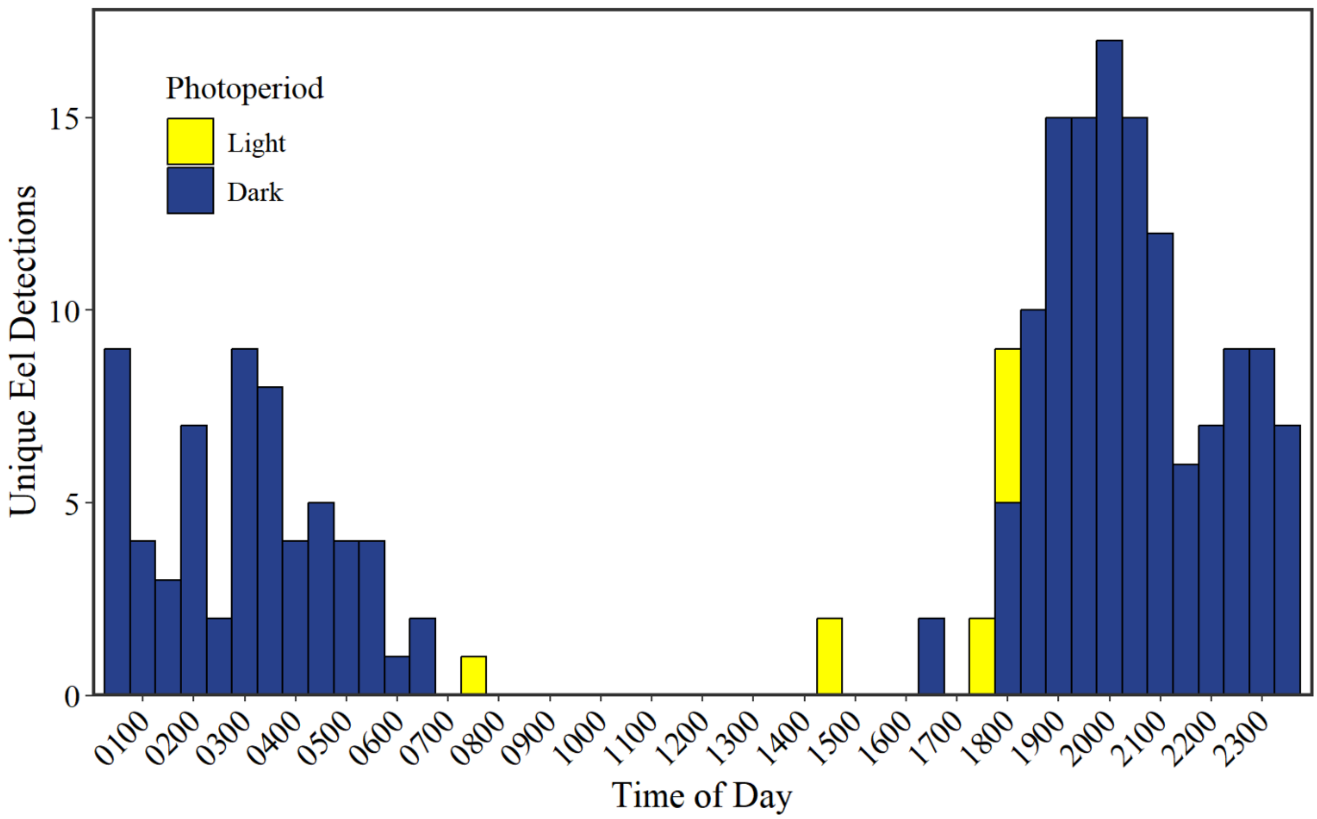


Figure 22. Detection frequency by time and photoperiod of American Eel *Anguilla rostrata* acoustically tagged in Spring and Fall 2022 at the Ontario Ministry of Natural Resources Glenora Fisheries Station, Glenora ON and later detected downstream in an array of $N = 27$ acoustic receivers at the Iroquois Water Control Dam, Canada-US border.

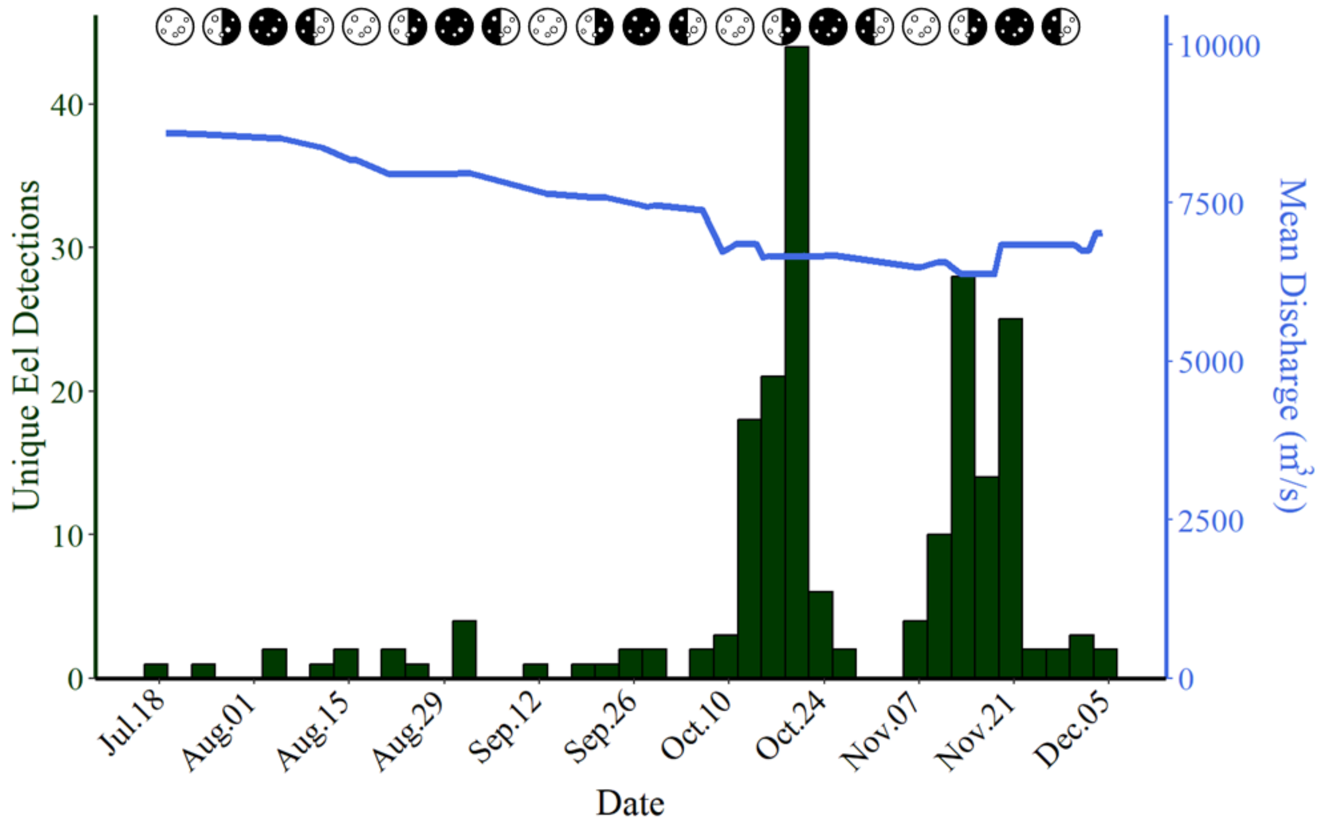


Figure 23. Detection frequency by date overlain with discharge (right y axis) and lunar phase (top) for American Eel *Anguilla rostrata* acoustically tagged in Spring and Fall 2022 at the Ontario Ministry of Natural Resources Glenora Fisheries Station, Glenora ON and later detected downstream in an array of $N = 27$ acoustic receivers at the Iroquois Water Control Dam, Canada-US border.

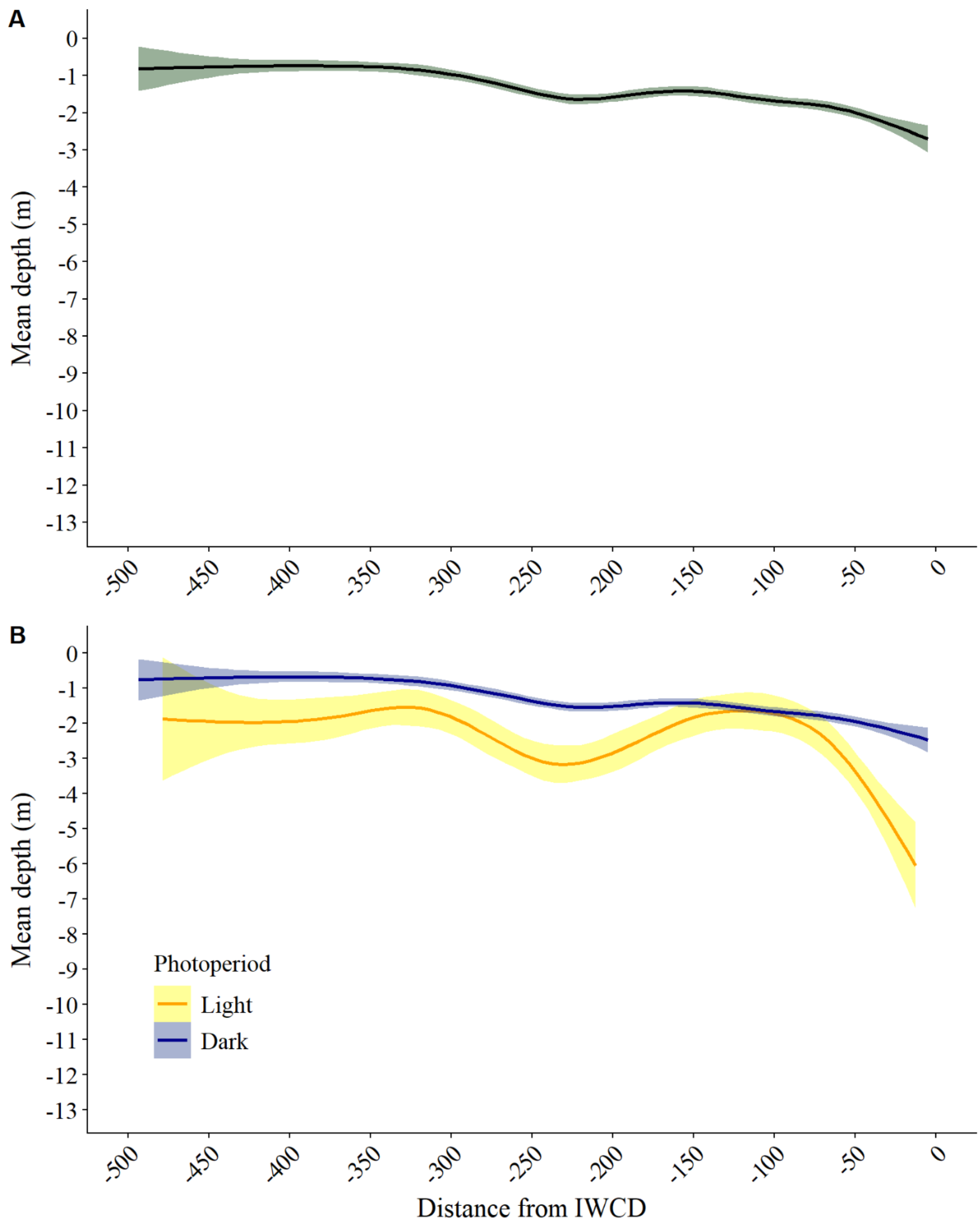


Figure 24. (A) Mean depth of American Eel *Anguilla rostrata* approaching Iroquois Water Control Dam (IWCD), excluding individuals that contacted the floating Light Guidance Device; **(B)** the same data separated and colour-coded by photoperiod. Shaded area represents standard error (95% confidence).

3.3.3 LGD Responses

Categorical depth responses (dive [> 2 m change], equivocal [0 to 2 m change], no dive) were not significantly different between control and treatment periods for the individuals that swam within 51 m of the array (chi-squared test: $\chi^2_{(2)} = 4.45$, $p = 0.108$), but they were for the 25 and 0 m categories (chi-squared test: $\chi^2_{(2)} = 8.90$, $p = 0.012$; $\chi^2_{(2)} = 16.471$, $p = 0.0003$; Figure 25). Light treatment eels in the 51 m category started to dive at a significantly greater distance from the LGD (Welch's two-sample *t*-test: $t_{(15.335} = 2.649$, $p = 0.018$). Treatment eels that swam closer (i.e. 25 and 0 m categories) exhibited almost double or greater mean distances at dive compared to those of control eels, but this difference was not significant, possibly due to the relatively small sample size for controls in these categories (Welch's two-sample *t*-test for 25 m group: $t_{(4.178)} = 1.924$, $p = 0.124$; Welch's two-sample *t*-test for 0 m group: $t_{(3.586)} = 2.549$, $p = 0.071$; Figure 26). While mean depth was greater across all categories (Figure 27), light treatment was not a significant predictor of depth for 51 m fish, though it was for 25 and 0 m (Linear Mixed-Effects Model [LME]; Table 4). However, distance from the LGD, the interaction of treatment and distance, and individual variability (i.e. random effect), were all significant predictors of depth across all categories (Table 4). Light treatment eels first slowed slightly on approaching the LGD, but then sped up noticeably as they swam beneath it (Figure 28). LME fit for changes in vertical swim speed (± m/s) was singular – that is, the random effect variance was near zero, and the specified co-variates (treatment, distance from LGD) were not sufficiently informative to change this (Figure 29). Thus, a two-way Analysis of Covariance (ANCOVA) was undertaken, which found no evidence of significance for treatment's effect on vertical swim speed across any distance category; however, the ANCOVA did reveal significant effects of distance from the LGD and the treatment-distance interaction term (Table 5).

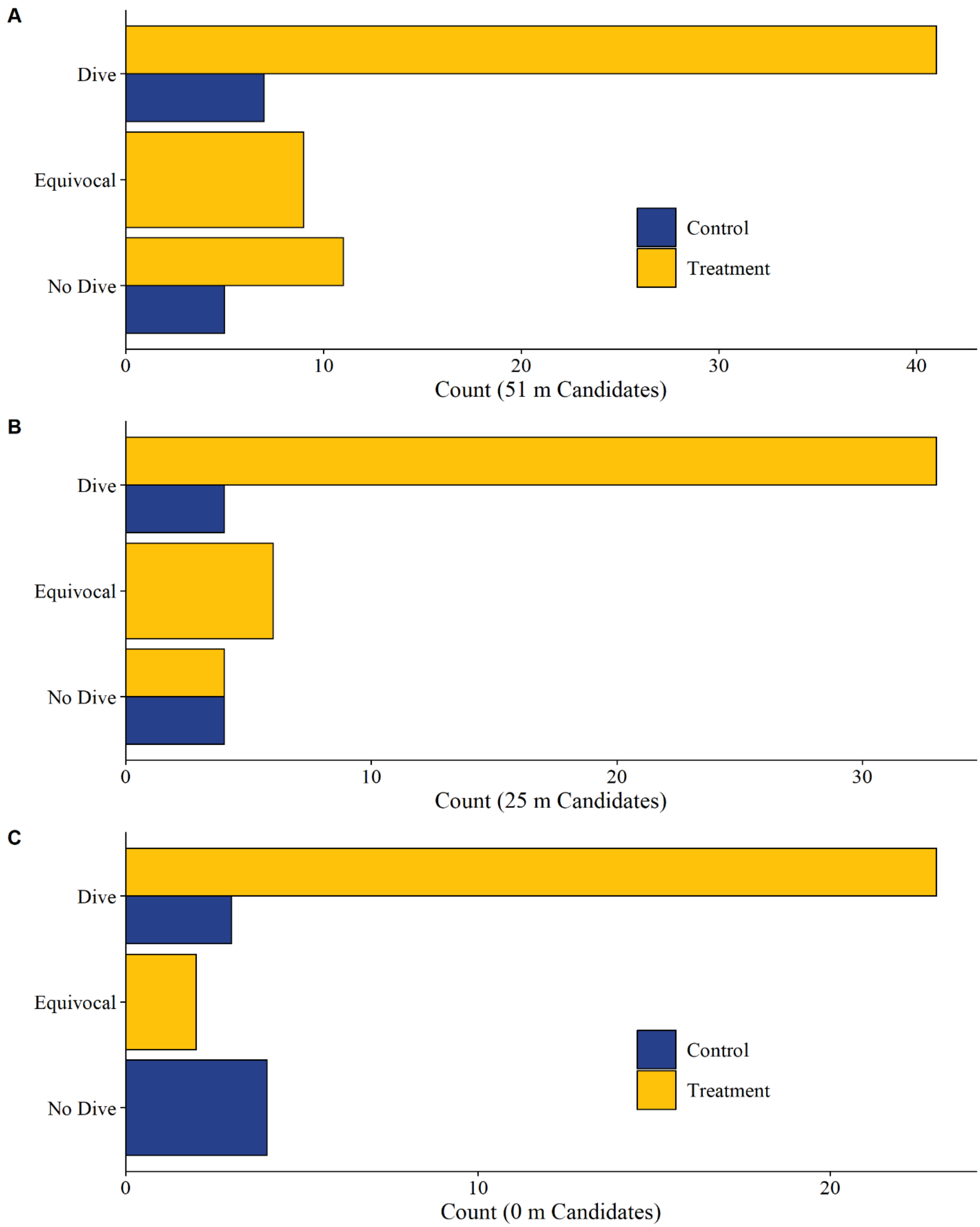


Figure 25. (A) Depth response categories of American Eel *Anguilla rostrata* that swam within 51 m of a floating Light Guidance Device located upstream of the Iroquois Water Control Dam, Can-US border, by treatment period and candidate category; **(B)** within 25 m; **(C)** within 0 m.

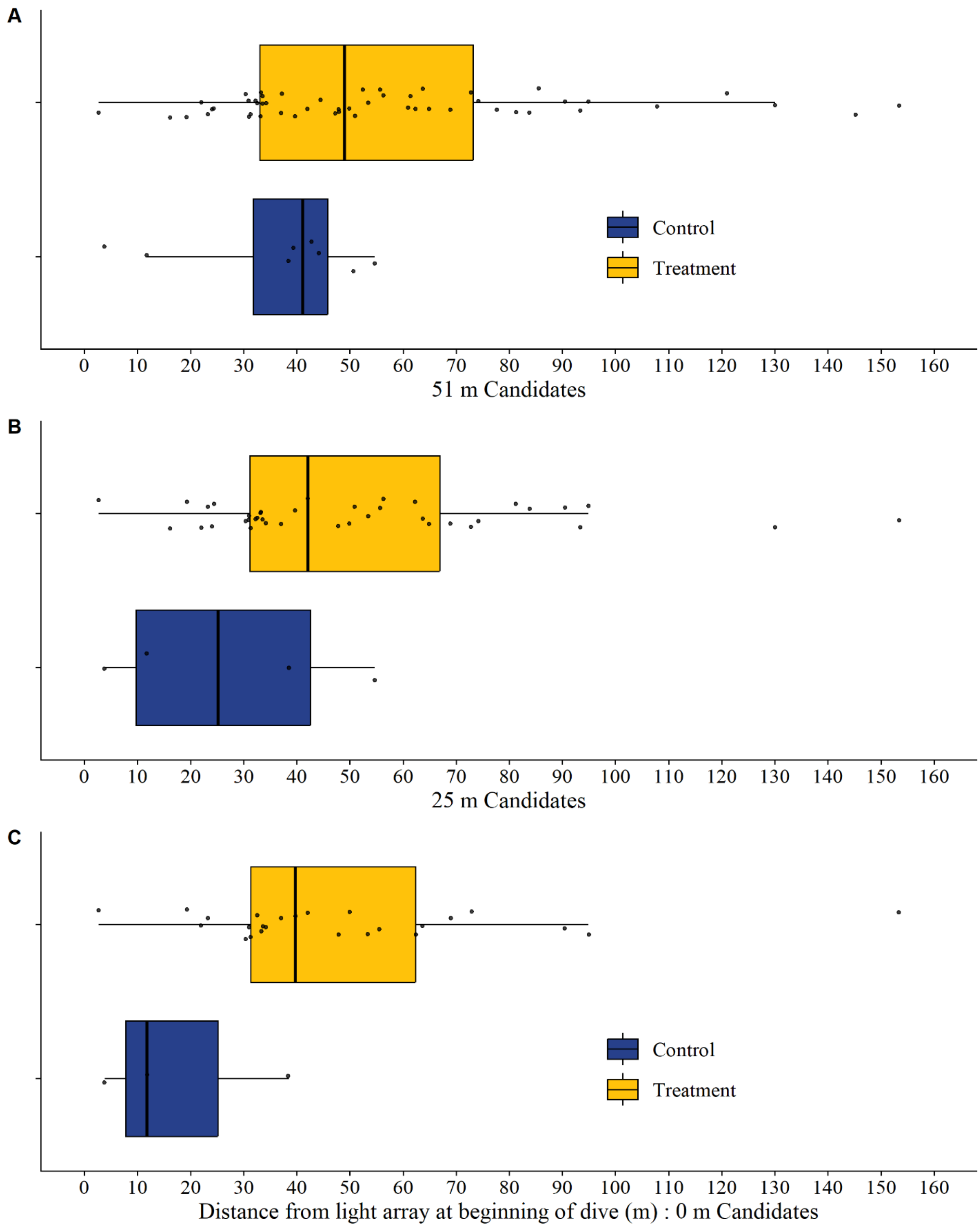


Figure 26. (A) Distance of American Eel *Anguilla rostrata* from a floating Light Guidance Device upon commencing diving behaviour (51 m category); **(B)** 25 m category; **(C)** 0 m category.

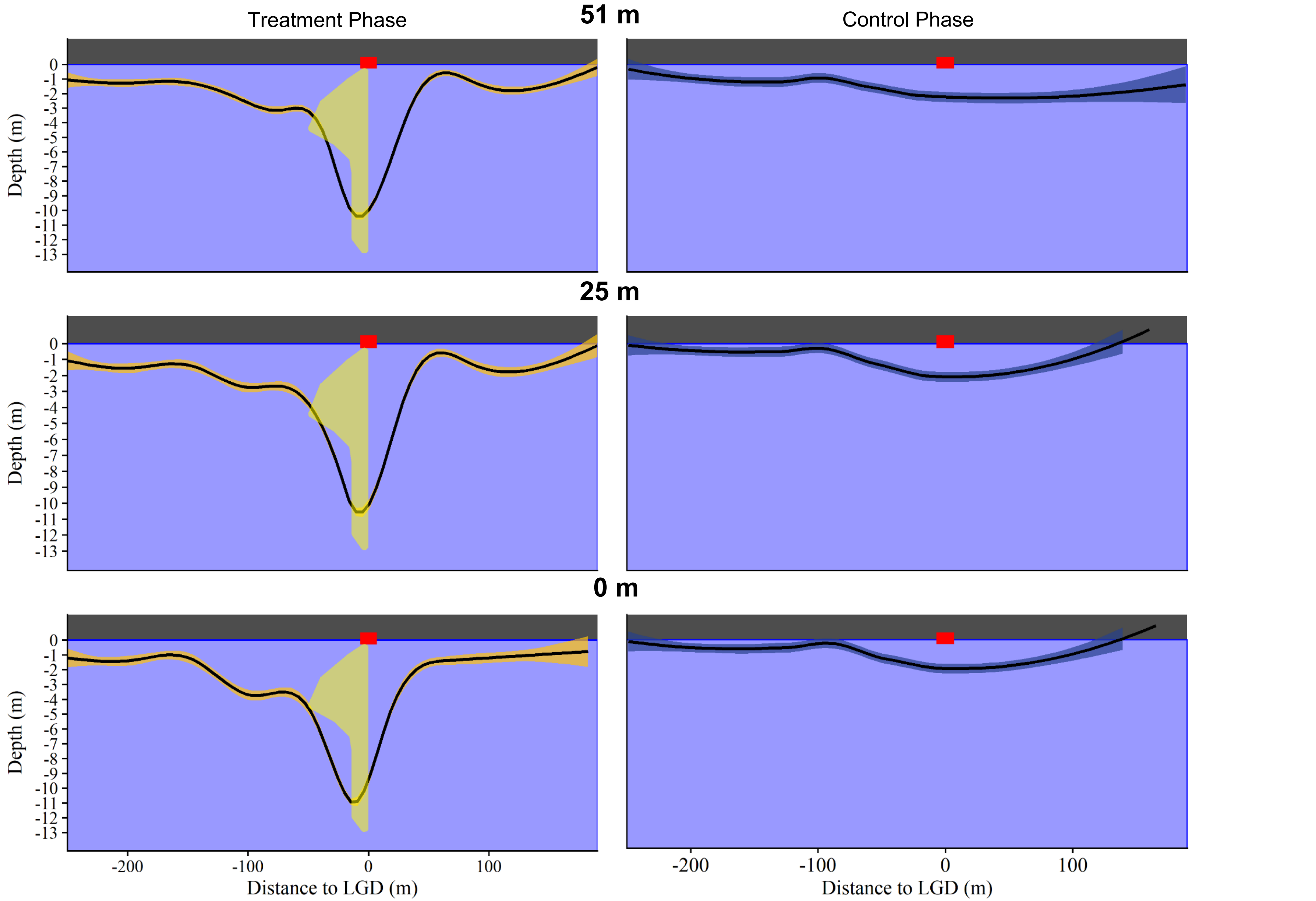


Figure 27. Mean swimming depths of American Eel *Anguilla rostrata* by treatment period (control, light) and candidate category (51, 25, 0 m). Shaded area on lines represents standard error (95% confidence). The red rectangle represents the floating Light Guidance Device, and the yellow shaded area beneath it, its light field.

Table 4. Linear Mixed Effect Model output for estimating the effects of various covariates on the depth (m) of eels, separated by distance category. All predictors significant across all distances except treatment in the 51m category.

Distance Category	Predictor	F	df	P
0 m	**Treatment**	13.793	1, 29.72	**<0.001**
	Distance from LGD	245.100	1, 3140.53	**<0.0001**
	Treatment*Distance	65.398	1, 3140.53	**<0.0001**
	Eel ID	LRT χ^2 = 1347.9	1	**<0.0001**
< 25 m	**Treatment**	5.440	1, 48.9	**0.0226**
	Distance from LGD	197.288	1, 4645	**<0.0001**
	Treatment*Distance	20.906	1, 4645	**<0.0001**
	Eel ID	LRT χ^2 = 2988.1	1	**<0.0001**
< 51 m	Treatment	0.842	1, 71.9	0.362
	Distance from LGD	243.367	1, 6111.7	**<0.0001**
	Treatment*Distance	4.510	1, 6111.7	**0.0337**
	Eel ID	LRT χ^2 = 3971.8	1	**<0.0001**

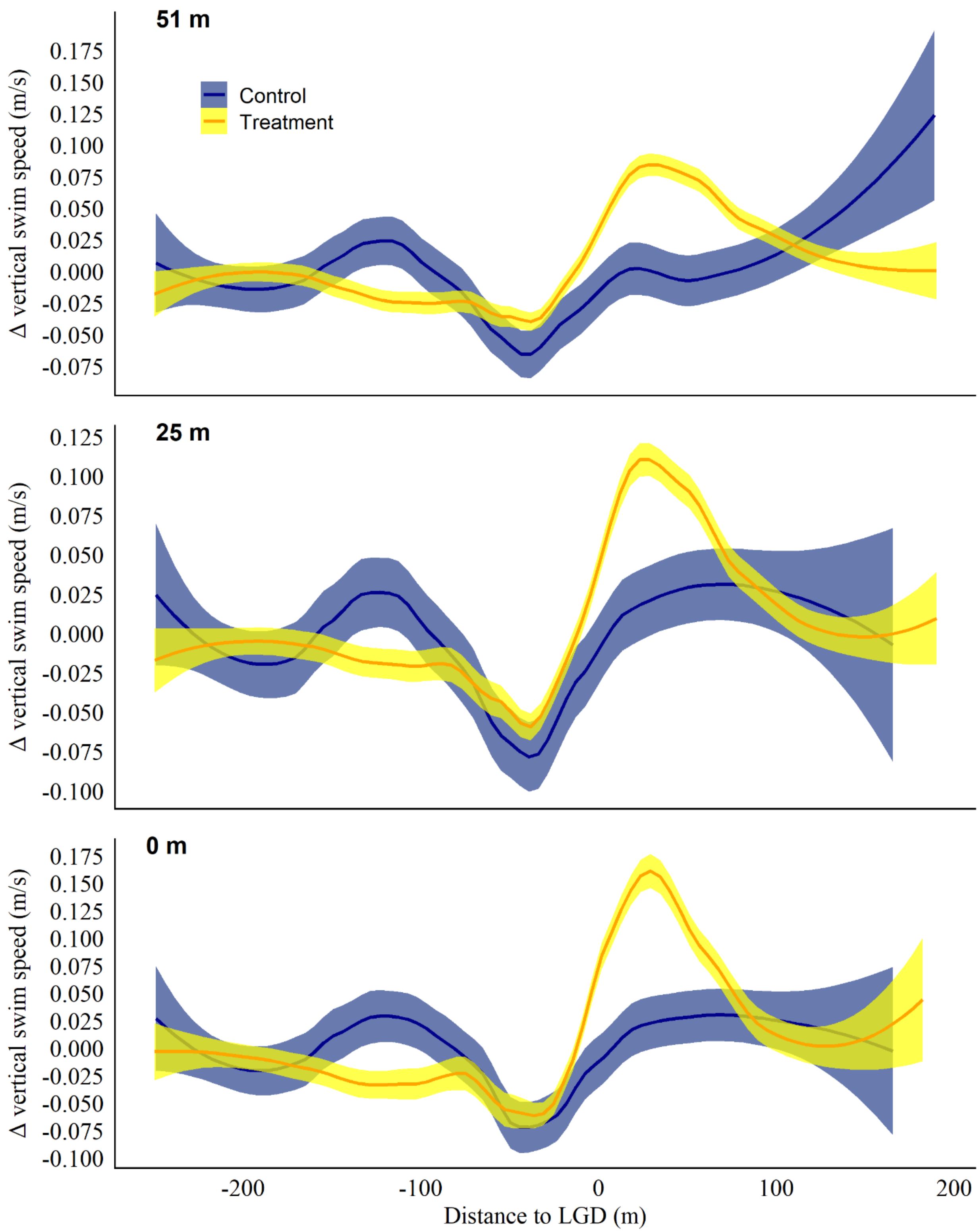


Figure 28. Changes in American Eel *Anguilla rostrata* vertical swim speed (± m/s) upon approaching a floating Light Guidance Device, by treatment period and distance category. Shaded area represents standard error (95% confidence).

```
> speedlme25=lmer(SpeedDepth~Treat*DistanceArray+(1|ID),
                  data=tracks %>% filter(Candidate25==1))

boundary (singular) fit: see help('isSingular')
```

Figure 29. RStudio 2024.04.2 (R version 4.4.1) output from attempting to fit a Linear Mixed-Effects model with vertical speed changes (± m/s) as the dependent variable; treatment and distance from the LGD (m) as predictor co-variates; and eel ID as a random effect (i.e. individual variability). Model singularity can have numerous causes and interpretations, but in this case it is likely that the random error term had an estimated effect variance near or equal to zero, and the specified co-variates were not sufficiently informative to alter this estimate.

Table 5. ANCOVA output for estimating the effects of various covariates on changes in vertical swim speed (± m/s) of eels approaching a floating Light Guidance Device (LGD), separated by distance category. Distance from the LGD and the treatment period-distance interaction term were significant across all categories, but treatment period alone was significant for none.

Distance Category	Predictor	F	df	P
0 m	Treatment	0.846	1, 3111	0.358
	Distance from LGD	23.779	1, 3111	<0.0001
	Treatment*Distance	7.905	1, 3111	0.0054
< 25 m	Treatment	0.483	1, 4608	0.487
	Distance from LGD	16.102	1, 4608	<0.0001
	Treatment*Distance	4.776	1, 4608	0.029
< 51 m	Treatment	1.288	1, 5494	0.256
	Distance from LGD	16.238	1, 5494	<0.0001
	Treatment*Distance	6.314	1, 5494	0.012

3.4 Discussion

Eels out-migrated from the Upper St. Lawrence and Lake Ontario between July and December 2022, reflecting both native (Summer and Early Fall) and stocked (Fall and Early Winter) individuals (Pratt and Threader 2011; Stacey et al. 2015). Detection frequency was bimodally distributed with peaks in mid-October and mid-November, and was neatly concentrated within two waning moons. Whether this bimodality is due to the existence of two distinct groups (i.e. native and stocked) or simply a natural phenomenon cannot be stated definitively, but given the first peak was already well into the Fall and the majority of eels remaining in the system are stocked (Côté et al. 2015), it seems unlikely that this distribution is reflective of distinct cohorts. 96% of eels migrated at night, in accordance with a large body of evidence (Smith and Saunders 1955; Vøllestad et al. 1986; Jellyman and Unwin 2017; Verhelst et al. 2018, 2023). Additionally, the few eels detected during the day appeared to swim at greater depths than their nocturnally migrating conspecifics, which has also been observed for out-migrating Longfin Eel *Anguilla dieffenbachii* (Jellyman and Unwin 2019). Given established context, it would be reasonable to assume this difference is indicative of light avoidance. Contrary to their benthic reputation, eels swimming through this channel rarely maintained depths greater than 3 m unless avoiding the LGD or light field.

Downward-projected white LED light caused eels to initially slow down, dive, and then speed through the light field, and light field mapping paired with both qualitative and quantitative analyses of eel behaviour confirm 25 m was the optimally effective threshold distance for the methods used here. However, the LGD itself also caused eels to exhibit these behaviours to a lesser extent, likely secondarily acting on eel rheoreception by disrupting local hydrology (Versar 2009a; Piper et al. 2017). As EPRI (2024) explores, eels in this experiment did not horizontally divert as they did in McGrath et al. 2003. The diving behaviour described here, however, is a novel observation and is likely a first step toward explicitly describing the role of device placement for light guidance of eel. Whereas McGrath et al. (2003) used vertical in-water lighting to elicit horizontal deflection (likely also with hydraulic effects/acting as a barrier itself, e.g. Ford et al. 2017; Piper et al. 2017), here we observed that above-water lighting elicits depth-seeking. In both cases, eels were deflected directly opposite the source. Given almost all natural light comes from the sun (i.e. above) and horizontal movement would do nothing to avoid it, diving may also simply be more the more evolutionarily likely mode of behaviour for an eel avoiding light, in the absence of the secondary effects of an in-water LGD. Unfortunately, there is not sufficient information available on many of the European industry studies cited in the Introduction for meaningful comparisons, other than to say that deflection behaviour was clearly observed and we did not have a null result (versus e.g. Bruijs and Vriese 2013). It is not immediately clear how to harness the response observed using the current methods or if it would be possible to do so, but this work nevertheless constitutes one of the largest field-scale evaluations of eel guidance with light and confirms that it can elicit obvious avoidance behaviour.

This, then, suggests that light could remain useful under a different configuration, i.e., in-water LGDs that satisfy debris maintenance needs and other practical considerations. Potentially more immediately promising is the use of light in a multimodal guidance system. Though the device described here technically did act on multiple sensory stimuli, the type of multimodal approach being suggested here would involve the use of light to augment a more effective but presently unsatisfactory physical guidance method. There is clear evidence for the subtly positive cumulative effect of using multiple guidance modalities to improve passage outcomes (framed as ‘marginal gains’ by Miller et al. 2022), and many recent works echo the importance of prioritizing the development of these methods (for light guidance of eels; EPRI 2018; Pratt et al. 2021; guidance of eels using other stimuli e.g. sound and flow; Piper et al. 2015, 2019; Putland and Mensinger 2019; Deleau et al. 2020; Popper et al. 2020; Miller et al. 2022; and in a broader scope of various stimuli and species Ford et al. 2017; Mussen and Cech 2018; Putland and Mensinger 2019; Jesus et al. 2021). Additionally, equipping existing physical guidance structures with behavioural guidance devices could be relatively cost-effective compared to otherwise necessary improvements to the physical structure itself (Miller et al. 2022). In a more distant future, with further refinement of component stimuli, a multimodal approach could also involve explicitly targeting multiple sensory modalities, such as light and sound or light and manipulated flows (EPRI 2018; Piper et al. 2015; Pratt et al. 2021).

The advancements in this study and many other recent behavioural guidance studies have been enabled in large part by developments in acoustic telemetry technology. This study constitutes one of the first detailed analyses of eel responses to light in the field – rather than describing outcomes alone – thanks to the ability to track eel positions to every < 3 seconds while they were in the experimental area. This increase in data resolution enabled unexpected observations which led to new research directions in a study on sound guidance of anguillids (Piper et al. 2019), and also allowed us to observe the unanticipated diving response described in this paper. Pre-study telemetry undertaken in past years allowed for analysis of the spatial distribution patterns of out-migrating eels (EPRI 2024), though the LGD we deployed here failed to be encountered by the predicted >50% of out-migrating eels. It is possible that the combined presence of the structure and light affected eel distribution across the width of the channel in ways that were not observable on the scale captured by the receiver array. This will be investigated in future research by comparing lateral space usage to the same data from past telemetry work.

Site-specific characteristics should be considered carefully before attempting behavioural guidance in the field. Flow velocity is an important consideration for any fish guidance system, particularly for out-migrating eels with a strong preference for greater flows (Jansen et al. 2007; Bruijs and Durif 2009; Piper et al. 2013). In the case of light guidance, it is important that the extent of the light field reaches a sufficient distance at a sufficient intensity to overcome eels' reluctance to respond to behavioural stimuli when it would cause them to leave greater flow velocity (Hadderingh et al. 1999), or to give time to respond when bulk flow velocity is so great that it competes with eels' burst swimming capabilities (1.35 to 2.12 m/s; Solomon and Beach 2004; Russon and Kemp 2011). Flows were quite high here (often > 1 m/s), but a clear effect was observed as far as 51 m, and more reliably at 25 m. Other hydrogeomorphic characteristics of the present site, such as it being the narrowest point upstream of the two hydroelectric facilities, its relatively straight current, and its relatively shallow, flat bottom (i.e. its canalized structure) all made it an ideal experimental and theoretical collection site. Other studies may wish to seek sites with similar characteristics. Finally, light avoidance could be limited by attenuating factors such as turbidity and light pollution, and light guidance may not be appropriate on such systems.

3.4.1 Conclusion

Numerous species of Anguillid eel are endangered worldwide; to reduce the mortality out-migrants suffer due to hydroelectric facilities, there is a need to develop past typical engineering-dominated fish passage methods in favour of more diverse solutions (Silva et al. 2018). Light guidance provides potential advantages such as a smaller spatial footprint; potentially lower impacts on site hydrology, generating capacity, and maintenance needs; and high configurability (Noatch and Suski 2012). With further development, behavioural guidance could be a valuable conservation and management tool not only for eel but also other fishes. Here we described results from a field-scale experiment using an above-water Light Guidance Device, which primarily caused eels to seek greater depths to avoid the light field. We also analyzed environmental, biological, temporal, and spatial data to describe aspects of eel out-migration given relevance to the practical operation of a behavioural guidance system. Eel out-migration from the St. Lawrence River was observed to be primarily nocturnal, bimodally distributed, and predominately occurring within two waning moon phases (i.e. during lower sky illumination). The methods used here were not appropriate for the practical operation of a light guidance system. However, the results described do continue to signal potential for light guidance, and could contribute to the development of more successful methods, particularly in a multimodal system. Nevertheless, we acknowledge the practical uncertainties and high up-front costs of undertaking such work.

Chapter 4: Conclusions and Future Research Directions

Freshwater biodiversity and abundance is declining at an unparalleled rate (Balian et al. 2008; Darwall et al. 2018; He et al. 2019; Reid et al. 2019). A common driver of these declines is habitat alteration and fragmentation, which on rivers frequently takes the form of anthropogenic barriers, like hydroelectric dams (Liermann et al. 2012). Diadromous fishes, such as Anguillid eels, are particularly susceptible to losses from these structures due to their need to pass such barriers multiple times to complete their life history (Jacoby et al. 2015). The effectiveness of traditional physical guidance methods to move fish around dams is highly variable and greatly influenced by site- and species-specific constraints and characteristics (Silva et al. 2018). Thus, various potential methods of behavioural guidance are being researched as alternatives (EPRI 2018; Popper et al. 2020; Jesus et al. 2021). The goal of this thesis was to assess current knowledge on behavioural guidance of Anguillid eel, and to undertake a field-scale experiment on behavioural guidance of American Eel *Anguilla rostrata* using light.

Chapter 2 of this thesis was a review of behavioural guidance methods. Here, my primary goal was to summarize and synthesize new knowledge from diffuse literature regarding the behavioural guidance of maturing Anguillid eels. To do so I collected relevant literature and organized it based on guidance modality, categorizing multimodal approaches under the primary behavioural stimulus. I summarized relevant aspects of the sensory biology of anguillids, given the importance of understanding the sensory system being targeted. To give my work a practical focus, I also considered the role of various site-specific hydrogeomorphic and environmental characteristics that could interact with how stimuli or eels move through the environment, and discussed some logistical realities of field-scale deployment.

My main conclusion from this work was that light and sound seem most promising for behavioural guidance of eel, particularly in a multimodal system with existing physical guidance methods, and that these stimuli could be implemented relatively easily (compared to a standalone behavioural guidance system) and would likely result in immediate passage gains. No standalone behavioural guidance method is universally effective, but there has been some success with standalone methods using light. I also contributed a concise summary of eel sensory biology and behavioural responses to various anthropogenic stimuli, which will be a useful resource for new behavioural guidance proponents, as well as others interested in how eels move through their environments or the effects of anthropogenic stimuli on fish behaviour. It seems eliciting avoidance is more likely than attraction, which is biologically logical given the focused behavioural state of an out-migrating eel. There is a need to scale laboratory experiments to the field and to begin to standardize study design, and as that happens behavioural guidance's role in fish passage technology may continue to grow. Keeping these considerations in mind, future research should prioritize developing promising technologies in the field, and should focus more on how behavioural guidance could be used to augment physical guidance methods. There is a lack of such studies, despite available evidence indicating it could be the easiest avenue to success, at least on rivers where some form of physical guidance remains feasible. Knowledge development regarding behavioural guidance of eel – as with all fishes - is still in its early stages, but there have been important breakthroughs in the past decade, often due to advancements in technologies such as acoustic telemetry and LED light.

Chapter 3 was a field-scale assessment of light as a behavioural guidance mechanism by tracking the responses of acoustically tagged out-migrating American Eel to a 216 m light guidance device deployed upstream of Iroquois Water Control Dam on the St. Lawrence River.

To supplement work undertaken by the Eel Passage Research Centre, a bi-national organization of researchers and decision-makers spanning industry, government, and academia, I characterized eels' vertical movements in response to the light field, and also provided information on the environmental, biological, spatial and temporal variables correlated with out-migration and subsequent detection. Here, I found that eels that passed while the light array was active dove more often, dove sooner and deeper, and slowed on approach but swam faster upon diving. I also confirmed that eels tend to migrate at night, and observed that they tend to swim deeper during the day, that their migration timing seems to be correlated to particular lunar phases, and that eel migration frequency may be bimodally distributed, at least on the St. Lawrence.

This work, the first of its kind, clearly demonstrates that artificial light can be used to deter eels, even on deep, wide, high-flow rivers. In that regard it is an important advancement in our understanding of how fishes, particularly eels, respond to anthropogenic light. However, it is unclear how a diving response could be harnessed on its own under the configuration tested. Yet, deploying lights in a different manner (i.e. a hypothetical non-invasive in-water method, rather than above-water), or by using light in a multimodal approach (as covered in Chapter 2), light could still be a useful behavioural guidance method, or an augment for physical approaches, and this is an important future research direction. As I concluded in Chapter 2, much work remains to develop reliably effective behavioural guidance methods. This knowledge has importance outside of the applied question at hand, such as by improving our understanding of the effects of light pollution on fishes, particularly migratory fishes. More broadly again, by using cutting-edge acoustic telemetry technology to address important questions relating to renewable energy infrastructure and endangered species conservation, this chapter adds evidence to the Cooke et al. (2022) assertion that movement ecology can and should be used to inform complex management decisions.

Anguillid eels are an iconic and charismatic clade that have played an integral role in the human experience for millennia. They were deified by Ancient Egyptians, studied intensely by founders of modern Western thought such as Aristotle and Freud, and have been of great economic importance since at least the Middle Ages. Today, many species are Endangered or Critically Endangered, and given they are often considered a delicacy there is a voracious market for increasingly few eels. Aside from directed harvest, these fishes also often face devastating mortality when encountering hydroelectric facilities. There is a need to mitigate this mortality if species are to stabilize or recover, and existing fish passage technology is insufficient. Thus, there is a need to explore novel possibilities, including behavioural guidance. Hopefully, this body of work constitutes a valuable advancement to this end, and there is an embrace of methods that reduce eel mortality and contribute to the recovery of one of Earth's most unique animals.

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