SIGNALS IN THE STREAM: USING TELEMETRY TO UNRAVEL THE INFLUENCE OF CURRENTS, GEOMORPHOLOGY, AND PREDATOR CUES ON SEA LAMPREY MIGRATION

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Fisheries and Wildlife – Doctor of Philosophy

2025

ABSTRACT

The spawning migration is a critical life stage for many fishes, demanding effective navigation, energy management, and risk avoidance strategies. This is particularly challenging for non-homing, semelparous species like the sea lamprey (*Petromyzon marinus*), which undertakes extensive riverine migrations fueled solely by endogenous energy reserves while facing novel predation threats. Understanding the behavioral mechanisms underlying this migration extends beyond the increasing our knowledge of the movement ecology and animal behavior. It is crucial for both controlling invasive populations in the Laurentian Great Lakes and conserving native populations elsewhere. This dissertation integrates fine scale acoustic telemetry, computational fluid dynamics (CFD) modeling, and field-based experimental manipulations to investigate how migrating sea lampreys respond to key environmental signals—hydrogeomorphology, hydrodynamic currents, and chemical risk cues—within a natural river system.

First, we demonstrate that sea lampreys utilize persistent geomorphological features for navigation. Tracking revealed that migrants consistently follow river thalwegs (deepest channels), swimming near the substrate. This behavior conferred a mean energetic saving of 5.8% compared to near-surface swimming and likely enhances safety from shoreline predators. We propose a novel navigation mechanism, hydrostatic pressure-guided rheotaxis, facilitates this efficient and potentially safer movement strategy. Second, we provide field-based validation of energy optimization theory by examining swim tactics in varying currents. Sea lampreys adjusted their swim speed to maintain a relatively constant ground speed (mean 0.92 body lengths s^{-1}), consistent with minimizing the cost of transport according to exponential models. Minor decreases in speed in deeper water suggest potential trade-offs with perceived risk. Third, we investigated responses to predation risk using conspecific alarm cues. Exposure induced structured changes in movement consistent with odor-guided rheotaxis, including a localized intensive search phase (reduced speed, increased tortuosity). Critically, when navigating the risk cue, lampreys prioritized immediate avoidance of the odor plume, splitting paths around the source, rather than selecting routes through deeper, putatively safer, habitat.

Collectively, these studies reveal that sea lamprey migration is guided by a sophisticated integration of environmental signals, resulting in predictable, context-dependent movement patterns. This research enhances our mechanistic understanding of migration ecology and provides actionable insights for management and conservation, informing the placement of control or passage devices and the application of behavioral manipulation strategies by highlighting the importance of river morphology, flow dynamics, and sensory cue interpretation.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. C. Michael Wagner, for taking a chance on me. I am a better scientist due to your mentoring, teaching and advice. Many thanks to my graduate committee, Dr. Christopher Holbrook, Dr. Erin Dreelin, and Dr. Brian Roth, for their guidance and support. I would like to give special thanks to Dr. Chris Holbrook for his collaboration and mentoring on all things acoustic telemetry. Dr. Dan Zielinski was responsible for creating the computational fluid dynamics models used in Chapters 2 and 3. I thank all personnel at United States Geological Survey Hammond Bay Biological Station and United States Fish and Wildlife Service Ludington Biological Station for their help in animal capture, housing, transportation and providing laboratory space and technical support, particularly during the COVID-19 pandemic restrictions. I give a huge shoutout and thanks to the dedicated colleagues and research technicians for their hard work, creative problem solving and support during these projects: Mikaela (Hanson) Feder, Emily Mensch, Taylor Haas, Dr. John Hume, Sharon Carpenter, Ceridwyn Hunter, Taylor Whipple, Nick Plants, and Laura Lepek. Lastly, but certainly not least, I must thank my family. Mom and Dad for their incredible support in everything I've tried, including my Ph.D. journey. And finally, my husband for not letting me give up on me or anything else and his love and support.

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CHAPTER 1

UNDERSTANDING SEA LAMPREY MIGRATION: FROM RIVER NAVIGATION TO CONSERVATION

ABSTRACT

The spawning migration of the sea lamprey (*Petromyzon marinus*) represents a critical, terminal life stage characterized by complex behaviors essential for locating suitable reproductive habitats. This review synthesizes current knowledge on the multi-stage migratory process, beginning with detachment from the host and orientation towards shorelines. Navigation into and within river systems relies heavily on olfaction, with larval pheromones indicating suitable spawning streams and guiding upstream movement, complemented by rheotaxis and responses to environmental cues like flow and temperature. Migrants employ specific strategies, such as bottom-oriented thalweg following, to navigate efficiently, conserve energy, and minimize predation risk in novel riverine environments. These behaviors are underpinned by significant physiological shifts and energetic trade-offs inherent to their semelparous reproductive strategy. Understanding sea lamprey migratory behavior is crucial due to their dual status as detrimental invaders in the Laurentian Great Lakes and species of conservation concern in their native Atlantic range. This review highlights how knowledge of their movement ecology—including navigation mechanisms, swim strategies in varying flows, and responses to chemical cues like alarm signals—can inform and improve management interventions. Specifically, insights into predictable behaviors like thalweg preference and responses to olfactory cues offer opportunities to enhance the efficacy of control tools (e.g., traps, barriers) and conservation measures (e.g., fish passage design, population assessments). Integrating behavioral ecology into management frameworks is vital for developing more effective, targeted, and context-specific strategies for both controlling invasive populations and conserving native ones.

LITERATURE REVIEW

The spawning migration in sea lampreys is unique to both the lamprey life cycle and among other migrating animals. The spawning migration begins when a sea lamprey detaches from its host, either in the lake for landlock populations or in the ocean for anadromous population. As a parasitic feeder, the starting point for this solitary migration is largely based on the host's behavior (Clemens et al., 2010; S. Silva et al., 2014). The nocturnal sea lamprey begins the search for appropriate spawning habitat by orienting to and travelling toward the shoreline (Meckley et al., 2012, 2017). Rather than homing to predetermined streams, sea lampreys rely on odors to label a river as suitable for reproduction (Bergstedt & Seelye, 1995; Meckley et al., 2014; Vrieze et al., 2010; Vrieze & Sorensen, 2001; Waldman et al., 2008). After entering a river system, a sequence of odors and environmental cues mediate migration to a tributary for spawning (Binder et al., 2010; Sorensen & Vrieze, 2003; Teeter, 1980; Wagner et al., 2006b, 2009).

As a first step to the spawning migration, lamprey must orient and navigate to the shoreline. To achieve this orientation, Meckley and others postulate sea lamprey use barokinesis which involves a nightly, biphasic movement process to detect changing hydrostatic pressure (Meckley et al., 2017). The first phase consists of slow, sinuous movements along the bottom, across the local bathymetric gradient. The authors suggest this phase is to create a spatial gradient in absolute hydrostatic pressure to choose a heading towards shallower water. Once a heading was chosen, sea lamprey began relatively faster, directed swimming along the bathymetric gradient with vertical casting through the water column (phase two). This second phase included time spent at or near the surface presumably searching for surface-constrained odors that signal entry into the coastal zone where river-derived odors would be present. While repeated casting to the bottom ensured a heading toward shallower depths (Meckley et al., 2017; Vrieze & Sorensen, 2001).

Once they reach the coastal zone, sea lampreys begin the nocturnal search along the shoreline for an appropriate river. During transit between river plumes of extensive search period, lamprey remain remarkably parallel to the shoreline. Throughout this straight-line, relatively fast swimming period, lamprey continued the tactic of vertically casting (Meckley et al., 2014; Vrieze et al., 2011). Because visual land-marking to confirm position is unlikely for this species during this nocturnal migration this vertical casting likely ensured proximity to the shoreline and would allow for encountering both negatively and positively buoyant river plumes (Binder & McDonald, 2007; Keefer et al., 2013; Vrieze et al., 2011). When migrants encounter the river plume, they begin an intensive search with high turn rate and frequent stopping. This intensive search is postulated to increase the likelihood of encountering larval pheromones that label the river as appropriate spawning habitat (Meckley et al., 2014; Vrieze & Sorensen, 2001). Presumably to locate the river mouth, migrants traverse across the river plume and exhibit a coastal rebounding behavior typified by frequent approaches and retreats into very shallow water (Meckley, et al., 2014). Meckley et al. (2014) observed this coastal rebounding behavior to locate the river inlet occurred even if the animal did not enter the river.

As migrants enter the nearshore zone, they must make the critical decision of whether to enter the river or continue searching for another watershed. This decision hinges on the river plume containing larval pheromone, which is secreted from sea lamprey larvae buried in the sediment of upstream tributaries (Sorensen & Vrieze, 2003; Vrieze et al., 2011; Vrieze & Sorensen, 2001). Interestingly, the full larval pheromone is necessary to induce river entry, experimental application of partial components alone did not result in river entry (Meckley et al., 2014). As anadromous lampreys enter the estuarine environment, their physiology shifts to tolerate the new freshwater habitat (Ferreira-Martins et al., 2021). While little is known about the duration of this estuarine staging period, for anadromous and landlocked sea lamprey, the upstreaming spawning migration is influenced by increasing flow and temperature (Almeida et al., 2002; Andrade et al., 2007). To ensure efficient navigation by reducing the likelihood of becoming entrained in eddies and maintain contact with conditions that indicate upstream movement (consistent ability for rheotaxis), one tactic to navigating these intricate waterways is a bottom oriented, thalweg following behavior (Griffin et al., 2025; Holbrook et al., 2015).

In the estuarine and riverine environment, sea lampreys encounter a gauntlet of new predators, particularly shoreline birds and mammals (Cochran, 2009). Movement decisions must consider this increased vulnerability to predators. Continued migration associated with the river bottom could provide safety from shoreline predator detection (Griffin et al., 2025; Holbrook et al., 2015). Swimming along the bottom also provides energetic cost savings, as water velocity decreases near the substrate (Griffin et al., 2025). Upstream movement increases with discharge, likely to aid in passage over obstacles and increase accessibility to spawning tributaries (Binder et al., 2010), therefore bottom oriented movement could allow for more energetically efficient paths during periods of high flow. As migrants encounter confluence points in the river, they exhibit odor-mediated rheotaxis by following upstream tributaries that contain the larval pheromone (Meckley et al., 2012). As sea lamprey reach the spawning grounds, sexually mature males release a sex pheromone to attract mature females towards the spawning habitat and nests (Li et al., 2002).

This complex interplay of environmental factors and behavioral adaptations ensures that sea lampreys select a river system and tributary that maximizes the chances of successful reproduction and offspring survival (Docker & Potter, 2019). Once they reach the spawning habitat, sea lampreys must retain sufficient energy to successfully complete the spawning process (Larsen, 1980). As a semelparous species with a single reproductive opportunity in its lifetime, the sea lamprey is driven by a biological imperative that profoundly influences its behavior and physiology during the migration (Larsen, 1980). Once the process of sexual maturation begins, the lamprey is set on a trajectory towards death, regardless of spawning success.

The lamprey's internal state during this period is characterized by a myriad of physiological changes and energetic demands. The physiological transformations necessary for reproduction, such as sexual maturation and the production of pheromones, consume substantial energy reserves (Larsen, 1980). Simultaneously, the lamprey must navigate the challenging riverine environment, avoid predators, and locate suitable spawning sites (Boulêtreau et al., 2020; Johnson et al., 2015; Larsen, 1980; Moser et al., 2015). These competing demands necessitate a series of trade-offs.

The movement patterns of sea lamprey within river systems have far-reaching implications for both the management of their invasive populations and their conservation in native habitats. As an invasive species in the Laurentian Great Lakes, sea lampreys inflict significant economic and ecological damage by preying on native fish (Marsden & Siefkes, 2019; Siefkes et al., 2013). In their native European and North American Atlantic range, these migratory fish are valued component of aquatic ecosystems and hold cultural significance, serving as a traditional food source and playing a role in various ceremonies for some indigenous communities (Braga et al., 2019, 2020; Hanel et al., 2022). Understanding their movement ecology is crucial for developing more effective management strategies that align with both conservation and invasive species control goals, such as optimizing the design and placement of fishing devices, such as traps and fishways.

While trapping has shown promise in certain contexts, its overall impact on reducing lake-wide adult sea lamprey populations has not been consistently demonstrated, thus limiting its widespread adoption as a primary control method (Miehls et al., 2021). Bravener & McLaughlin (2013) describe low trap encounter rates leading to inefficient traps, while Rous et al. (2017) found a spatial mismatch between the trap entrance and sea lamprey preferred migratory routes. These traps are typically integrated into barriers, and by expanding our knowledge of sea lamprey movement tendencies, we might overcome this discrepancy to improve barrier integrated trap efficiency. Increasing our knowledge of sea lamprey movement in the open river channel could also provide the opportunity to increase the number of streams eligible for control or conservation intervention (Siefkes et al., 2021). Such streams may not have barriers or have barriers that are failing or are removed to improve river connectivity (Siefkes et al., 2021).

Integrating an understanding of sea lamprey movement with existing control strategies is pivotal for enhancing the cost-effectiveness of management programs for invasive populations (Miehls et al., 2021; Siefkes et al., 2021). When used as a supplemental control method, trapping can reduce the frequency and reliance on the chemical lampricide, 3-trifluoromethyl-4-nitrophenol (TFM) (Siefkes et al., 2021). Trapping strategies can particularly target rivers classified as "difficult-to-treat," where lampricide efficacy is often poor and repeated treatments are required (Miehls et al., 2021). These streams are typically characterized by complex habitats and hydrological conditions that hinder the effectiveness of lampricides. By incorporating trapping in these areas, managers can achieve effective control while reducing reliance on chemical treatments. Increasing trapping efficacy could also align with Tribal and First Nations goals to reduce chemical usage in aquatic systems (Mattes & Kitson, 2021). Climate change poses an additional challenge to sea lamprey control by allowing them to access to previously inaccessible spawning and larval grounds (Lennox et al., 2020). Areas that are currently too cold for offspring survival may become suitable for rearing, and raising water level could allow migrants to pass a previously impassable barrier (Lennox et al., 2020). Understanding how climate change will affect sea lamprey movement patterns is crucial for adapting control strategies and ensuring their long-term effectiveness. Trapping could provide a tool to combat this expanding range.

Trapping can also play a key role in improving population assessments of invasive sea lamprey (Marsden & Siefkes, 2019). By expanding trapping efforts to encompass more and larger rivers, researchers can gain a more accurate understanding of sea lamprey populations and distribution (Siefkes et al., 2013). This information can be used to refine control strategies and target resources more effectively.

Understanding sea lamprey movement is equally important for conservation in their native habitats. In the same way improved trapping efforts could improve invasive population assessment, populations in the native range could benefit (Moser et al., 2007). Additionally, trapping and translocating individuals around obstacles to optimal spawning grounds could improve recruitment (Ward et al., 2012). Knowledge of movement patterns could identify critical migratory corridors and movement strategies. Barriers negatively impact native sea lamprey populations by blocking access to critical spawning habitat (Docker, 2015; Nilsson et al., 2005). And rarely do migrants encounter a single obstruction on the spawning migration; Davies et al. (2021) revealed a cumulative effect of attempting to pass multiple weirs when travelling through the heavily fragmented River Severn basin, UK. In addition to the spatial and temporal impact of barrier passage, barriers can lead to reduced fitness condition and increased risk of predation (Davies et al., 2021; Newton et al., 2018; Nyqvist et al., 2017). Connectivity of migratory routes is thus crucial, and Moser et al. (2021) argue that restoring connectivity should be prioritized over improving habitat quality alone.

Fishways have been installed at many man-made barriers to provide passage around the barrier and alleviate habitat fragmentation (Larinier & Marmulla, 2004). These conventional fishways were often designed for passage of economically important species such as salmonids; the efficacy and suitability for other taxa have only recently been explored (Lucas et al., 1999). Foulds and Lucas (2013) showed European river lamprey (*Lampetra fluviatilis*), another anguilliform swimmer, had extremely poor passage at two technical fishways on a single English river. Individuals were recorded at the fishway entrances several times over the study period, but for animals that entered the fishway, only a single lamprey passed each fishway (Foulds & Lucas, 2013). Sea lamprey ascending four fishways on the Connecticut River, USA experiences substantial delays, if passage was successful at all (Castro-Santos et al., 2017). A more holistic understanding of lamprey migration and the migratory fish community should improve fishway design, while continuous evaluation and adaptive management of existing fishways are crucial to ensure they effectively serve a diverse group of target species (Castro-Santos et al., 2017; Foulds & Lucas, 2013; Lucas et al., 2009, 2020; A. T. Silva et al., 2018).

However, it is important to acknowledge that fishways, even those designed for multi-species passage, often fall short of their intended goals. A meta-analysis by Hershey (2021) revealed that fishway efficiency is highly variable and often surprisingly low, even for target species. This variability is influenced by numerous factors, including fishway type, species-specific swimming abilities, and environmental conditions. Notably, this meta-analysis revealed that no single fishway design consistently outperformed others, and even "nature-like" fishways, often touted for their ecological benefits, exhibited lower attraction efficiency than other types (Hershey, 2021). This underscores the need for careful consideration of fish behavior and riverine conditions when designing and implementing fish passage solutions (Hershey, 2021; Lucas et al., 2009; A. T. Silva et al., 2018).

An innovative approach for enhancing river connectivity while managing invasive species are selective fishways, structures designed to allow passage for desired species while blocking or deterring undesirable species. Incorporating knowledge of sea lamprey movement and behavior could help improve selective fish passage at current barriers, both with the aim to block invasive or allow natives (Pratt et al., 2009). Zielinski et al. (2020) proposed a novel design inspired by single-stream recycling processes, integrating multiple sorting mechanisms to target specific fish attributes. The design of these multiple sorting mechanisms requires vast knowledge of many attributes of the fish community (Benoit et al., 2023; Borowiec et al., 2021; Zielinski et al., 2019, 2020). To begin to address the need for a collection of biological attributes that influence passage, Benoit et al. (2023) have comprised a database of 220 Great Lakes species to assist in design and aid management actions. However, researchers highlight the lack of behavioral attributes in the literature for inclusion in this database (Benoit et al., 2023).

Whether the device is meant to block, trap or pass leveraging a species natural behavior and manipulating key stimuli can enhance capture efficiency. Fish naturally respond to environmental cues, such as water current, temperature gradients, and chemical signals, which can be strategically exploited to intercept movement or guide fishing timing and effort (Binder et al., 2010; Binder & McDonald, 2008; Meckley et al., 2017; Meckley et al., 2014). Manipulative strategies, such as using attractants like pheromones, food bait, or environmental cues, can further direct migrant movements (Johnson et al., 2012, 2015; Kirk et al., 2016). By combining these tactics, devices can be tailored to guide fish efficiently while minimizing non-target impact and maximizing capture or selective passage, depending on management goals.

DISSERTATION SUMMARY

This dissertation expands upon the foundational knowledge of sea lamprey migratory behavior by investigating specific mechanisms and strategies employed during their upstream spawning journey through rivers. The subsequent research chapters delve into the intricacies of navigation, energy management, and risk avoidance, leveraging fine-scale tracking technologies and hydrodynamic modeling to address critical gaps in our understanding.

Chapter 2 addresses the challenge of how a solitary, non-homing species like the sea lamprey navigates complex riverine and estuarine environments. Building on observations of bottom-oriented swimming (Holbrook et al., 2015), this chapter investigates the hypothesis that sea lampreys utilize hydro-geomorphological features, specifically river thalwegs (the deepest channel), as a 'highway' to achieve safe and energetically efficient navigation. We tracked migrating sea lamprey with fine-scale acoustic telemetry through a river reach exhibiting varied geomorphology, including areas of uniform and asymmetrical cross sections. Migrants had a close association with the river substrate (median 0.11 m above bottom) with a preference for the deepest portion of the river channel. This movement tactic resulted in a mean energy savings of 5.8% compared to swimming near the surface. We propose sea lampreys use hydrostatic pressure-guided rheotaxis to maintain course within the thalweg, achieving both efficient movement and enhanced safety during their upstream migration.

Chapter 3 focuses on how migrating sea lamprey balance energetic costs with ecological and environmental constraints; specifically, how sea lampreys adjust swimming tactics when encountering variable head water currents. This chapter addresses competing theories regarding optimal swim strategies proposed by Trump & Leggett (1980) and Brodersen et al. (2008). We used fine scale positions and computational fluid dynamics models to quantify the swim and ground speeds of constantly moving sea lampreys. This study provides field-based evidence that sea lampreys adjust their swimming effort in response to hydrodynamic conditions. We found swim speed increased with faster head currents, while ground speed remained relatively constant over the experienced water velocity range at a mean 0.92 body lengths s-1. This tactic aligns with predictions from the exponential cost-of-transport model (Trump & Leggett, 1980). We also found both swim and ground speeds showed a slight decrease in deeper water, suggesting a trade-off between movement efficiency and perceived safety.

Chapter 4 investigates how chemical cues such as alarm cue influence navigation decisions. We asked: (1) How do sea lampreys navigate around an area of high predation risk, and (2) Do they prioritize avoiding immediate danger or seeking safer routes when encountering a danger cue? We exposed migrating sea lamprey to midstream alarm cue and contrasted their fine scale movement paths to predicted patterns exhibited during the control (no alarm cue) condition. We found that, when exposed to alarm cue, sea lamprey paths were consistent with using odor-guided rheotaxis to localize and avoid the odor source. Alarm cue animals initiated an intensive search phase downstream of the odor source characterized by a 28% reduction in ground speed and 27% increase in path tortuosity, before resuming nominal upstream migration patterns after passing the odor source. When choosing routes around the odor source, sea lamprey in the alarm cue treatment did not preferentially select deeper, safer water. Instead, their paths split around the odor source, indicating a prioritization of immediate danger avoidance over seeking safety cues such as depth.

The work presented in this dissertation provides a more mechanistic understanding of sea lamprey migration in rivers, elucidating the behavioral tactics used to navigate, conserve energy, and mitigate predation risk. The consistent use of hydro-geomorphic features for navigation and the structured reactions to chemical cues reveal predictable patterns in movement. These predictable behaviors offer tangible opportunities for conservation and management, suggesting that interventions like fishing devices or fish passage structures can be more effectively sited and designed by considering preferred migration routes (e.g., thalwegs). These findings also underscore the critical importance of local environmental context, including flow conditions, channel morphology, and the sensory landscape, in shaping these behaviors, necessitating site-specific considerations for management applications. Future research should focus on explaining the specific sensory mechanisms underlying behaviors like pressure-guided rheotaxis, investigating how migratory strategies vary across a wider range of river morphologies and flow regimes (particularly flood conditions), and exploring the complex interplay when multiple chemical cues (attractants and repellents) are present simultaneously. Refining our understanding of behavioral thresholds and the potential fitness consequences of navigating complex landscapes will be crucial for developing robust, behaviorally-informed strategies for both invasive species control and the conservation of native lamprey populations.

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CHAPTER 2

NOT ALL WHO MEANDER ARE LOST: MIGRATING SEA LAMPREY FOLLOW RIVER THALWEGS TO FACILITATE SAFE AND EFFICIENT PASSAGE UPSTREAM

Griffin, K.R., Holbrook, C.M., Zielinski, D.P., Cahill, C.L., and Wagner, C.M. 2025. Not all who meander are lost: migrating sea lamprey follow river thalwegs to facilitate safe and efficient passage upstream. *Journal of Experimental Biology,* 228(4). doi:10.1242/jeb.249539.

ABSTRACT

Efficient navigation is crucial for the reproductive success of many migratory species, often driven by competing pressures to conserve energy and reduce predation risk. Little is known about how non-homing species achieve this balance. We show that sea lamprey (*Petromyzon marinus*), an ancient extant vertebrate, uses persistent patterns in hydro-geomorphology to quickly and efficiently navigate through complex ecosystems. Hydrodynamic flow models coupled with bathymetric mapping and fine scale acoustic telemetry revealed movement paths that tracked thalweg scour channels, which are often the deepest and fasted-glowing sections of a river. These paths allow rapid and efficient upstream migration, suggesting the existence of a bathymetric highway system. Near-substrate swimming along this path resulted in a median of 5.8% energy savings while also promoting improved safety from nocturnally active predators. We hypothesize sea lampreys use hydrostatic pressure-guided rheotaxis to achieve this navigation. It is likely this tactic relies on sensory information from the animal's primitive lateral line and perhaps the inner ear. Insights from this study can be used to redesign conservation practices to achieve improved control where the animal is invasive and improved fish passage within its native range.

INTRODUCTION

An animal that undertakes a long-distance reproductive migration must survive the journey and arrive with sufficient time and energy to reproduce. How efficiently individuals complete these tasks has important implications for several ecological and evolutionary processes that determine the success of populations (Dingle, 2014; Fudickar et al., 2021). Thus, it is widely held that natural selection should favor migration strategies that both minimize energy expenditure and reduce predation risk to improve fitness outcomes (Alerstam et al., 2003; Dingle & Drake, 2007; Lennox et al., 2016; Lima & Bednekoff, 1999). This optimization is challenging when the migratory route requires navigation through complex landscapes that exhibit varying energetic costs, uncertainty about the identity and location of predators, and multiple available routes (Bouchet et al., 2015; Crane et al., 2024; Sabal et al., 2021). Examining the environmental features that guide selection of safe and efficient routes can lead to a better understanding of the evolution of sensory-guided movement strategies (notably orientation and navigation). Furthermore, when the population of interest is invasive, elucidation of movement strategies can reveal opportunities to better manage impacts to native species and ecosystems.

With the advent of internal telemetry transmitters, fishes have emerged as accessible experimental systems for in situ mechanistic examinations of the orientation tactics used by migrants at fine spatial-temporal scales (Brönmark et al., 2014; Brownscombe et al., 2022; Cooke et al., 2008; Jacoby & Piper, 2023). Many fishes embark on annual spawning migrations that involve traversing estuaries and large rivers to reach distant spawning habitat (Morais & Daverat, 2016). The principal energetic costs are basal metabolism and the cost of swimming against a current (Claridge & Potter, 1975; Kinnison et al., 2001; McElroy et al., 2012). Consequently, there are evolutionary pressures to minimize both the total distance traveled and the rate at which energy is consumed along that route. The latter is hypothesized to involve selecting paths through complex flow fields that allow the fish to avoid swimming against high water velocities (Goodwin et al., 2014; Hintz et al., 2023; Nestler et al., 2012). In rivers, the slowest relative water velocities are most often found in the hydraulically rough flow near the substrate, particularly along riverbanks, where large fishes often migrate (e.g., sockeye salmon (*Oncorhynchus nerka*) (Hinch & Rand, 2000); pallid sturgeon (*Scaphirhynchus albus*) (McElroy et al., 2012)).

Theory also suggests migrating prey should opt to move in alignment with habitat features that promote safety, particularly when the immediacy of danger is difficult to ascertain (Åkesson et al., 2014; Gaynor et al., 2019; Luttbeg et al., 2020; Pfuhl et al., 2011). A common tactic to promote safe passage is to initiate movements during periods of low risk. Often this involves moving at night to avoid visual predators (J. W. Chapman et al., 2015; Gwinner, 1996; Reebs, 2002). In fact, most research directed toward understanding safe migration tactics has focused exclusively on movement timing. However, an important consequence of nocturnal movement is increased reliance on non-visual cues for predator detection and orientation, potentially complicating the selection of energetically efficient yet safe routes. This is particularly true for nocturnal species that do not exhibit natal homing and therefore cannot rely on an innate map-and-compass to navigate through the complex morphology of estuaries and river-wetland complexes (Åkesson et al., 2014). However, in rivers, moving nocturnally along shorelines may bring prey fishes into more frequent contact with shoreline predators.

The sea lamprey (*Petromyzon marinus*) is a non-homing (Bergstedt & Seelye, 1995; Waldman et al., 2008) Agnathan fish that is native to the northern Atlantic basin and invasive in the Laurentian Great Lakes. After 1-2 years at sea feeding parasitically on large-bodied fishes, sub-adults embark on a migration to the coastline and through complex estuarine and riverine habitats, relying entirely on stored energy to complete a journey that may be hundreds of kilometers in length and several months in duration (Moser et al., 2015). The sea lamprey is likely to be unaware of its geographic position at the start of the migration as its movements have been those of its host. Orientation toward shore is accomplished by undertaking large circular swims on the substate, ostensibly to sample the local gradient in hydrostatic pressure and align with shallowing water, after which the animal swims near the surface, periodically casting down to the bottom to confirm shallowing depth (Meckley et al., 2017). It selects rivers emitting the odor of conspecific larvae (Sorensen et al., 2005; Vrieze et al., 2010; Wagner et al., 2006a, 2009) and transitions to bottom swimming until arriving at the spawning habitat (Holbrook et al., 2015). Throughout this process it remains solitary, relying solely on recent sensory information to complete the migration (McCann et al., 2018).

The potential for considerable weight loss observed during the migration suggests sea lampreys should navigate efficient migration routes to preserve time and energy for spawning (Beamish et al., 1979). How this feat is accomplished is unknown. The animal’s apparent use of hydrostatic pressure sensing to orient to water depth during the early migration coupled with the transition to bottom swimming in rivers offers an intriguing possibility. Coastal rivers that drain to the Great Lakes and the Atlantic coast often contain a distinct fluvial thalweg (Albert et al., 2005; Herdendorf, 1990; Larson et al., 2013). In tidally dominated coastal marine systems this channel often merges into ebb and flood tidal scour channels found in estuaries (Dalrymple & Choi, 2007; Leuven et al., 2018), creating a bathymetric ‘highway’ system. Adopting a strategy of occupying the greatest relative depth while migrating upstream should ensure sea lamprey will efficiently migrate through the complex hydrology and morphology of coastal ecosystems without becoming entrained in small embayments or wetland channels whilst benefitting from the energy savings that accompany swimming near the substrate. Furthermore, after entering the shallowing riverine environment this tactic would allow migrants to occupy the deepest portion of the channel where relative safety from nocturnally active shoreline predators should be improved.

To test the hypothesis that sea lampreys use bathymetry to achieve safe and efficient upstream migration we examined fine scale movement paths of 56 sea lamprey migrating through a morphologically varied portion of the White River, MI, USA, with areas of distinct thalweg presence and more uniform channel cross-section. We coupled fine scale high-frequency positioning of the fish with a hydrodynamic flow model to test five predictions: (1) sea lamprey persistently swim near the substrate resulting in (2) a significant energetic cost savings vs. swimming higher in the water column; (3) sea lamprey tracks are non-uniformly distributed across the channel exhibiting (4) a preference to move through the deepest portion of the channel; and (5) as a consequence of these patterns, migrants would consistently choose the deeper, higher flow channel at an upstream confluence where two channels of similar width came together.

MATERIALS AND METHODS

Study Area

Fish tracking took place in the White River near Whitehall, Michigan, USA (43.42°N, 86.32°W) a tributary to Lake Michigan that flows for 134 km through Newaygo, Oceana, and Muskegon Counties with an average discharge of 12.7 m^3s^{-1}. The study site was situated in the lower watershed where the river cuts through a landscape dominated by wooded wetlands, emergent vegetation beds, and open water marshes (Fig. 2.1A); habitats similar to those of river-dominated estuaries where the sea lamprey migratory strategy evolved. The study consisted of two acoustic telemetry arrays (hereafter called main and upper arrays, Fig. 2.1B) placed into 0.55 river kilometer (rkm) reach that ranged in depth from 0.1 - 4.23 m and width from 31.7 – 58.5 m with a sandy substrate throughout. Discharge during the study period ranged from 10.59 – 19.54 m^3s^{-1}. The channel exhibited a mix of asymmetrical cross-sections that included a deep meandering thalweg (sinuosity = 1.24) embedded within the straighter channel (sinuosity = 1.06) and areas of more uniform cross-sectional depth (Fig. 2.2A). Shallow depositional areas were present opposite the distinct thalweg that became progressively occupied with submerged aquatic vegetation through late spring and into early summer. The main array was used to address the Predictions 1 - 4 through the stretch of asymmetrical and uniform river channel cross-sections. The upper array was placed 0.2 rkm upstream of the main array to investigate lamprey movement decisions at a confluence (Prediction 5). Both branches of the confluence rejoin upstream and contain larval odor from larval populations upstream of this point, but each branch exhibited different morphological and hydraulic features with the north branch containing the dominant flow and a distinct thalweg.

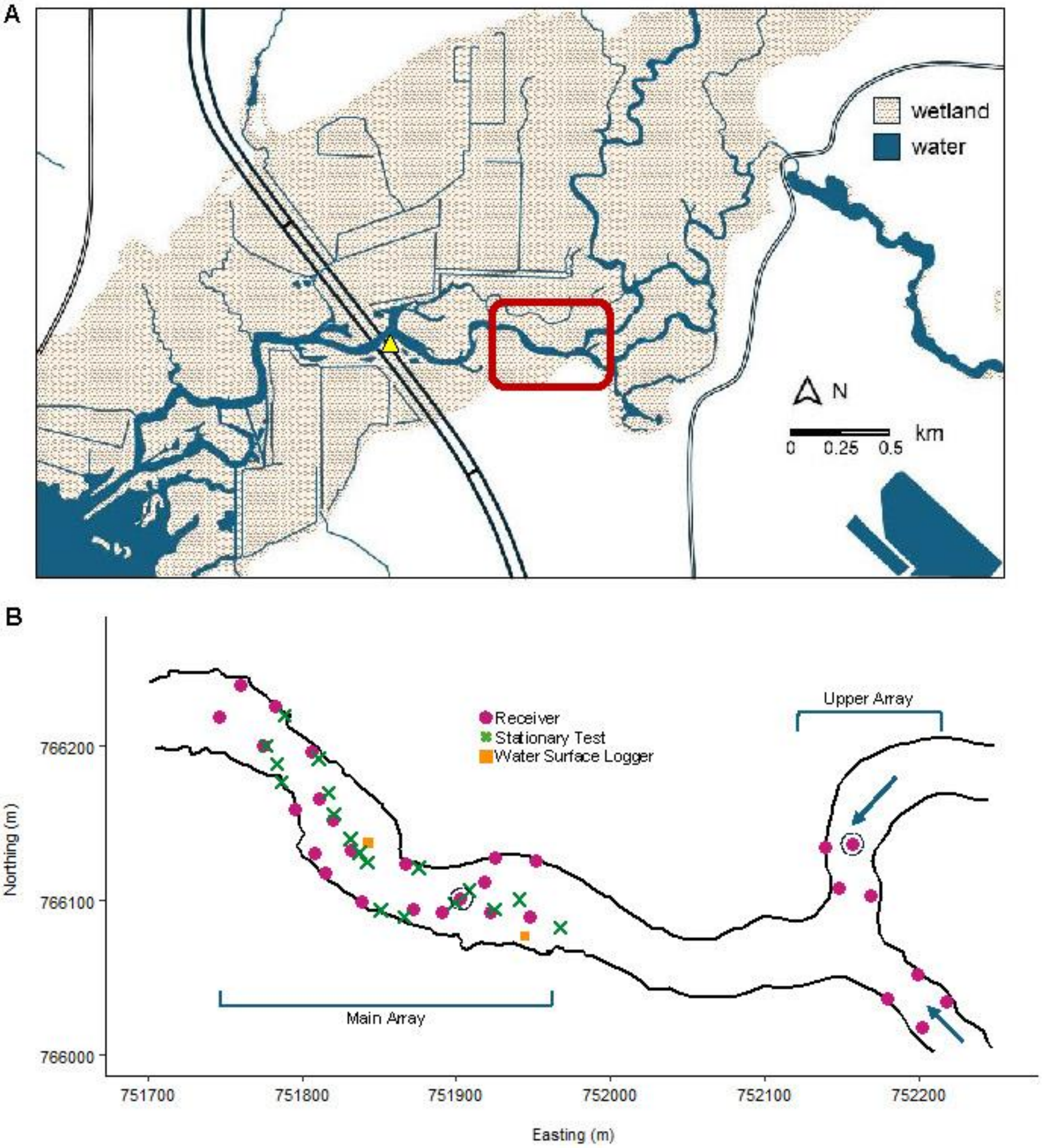

Figure 2.1. Location of the study site on the White River, Michigan. (A) Map of the study area. The study site is indicated by the red rectangle. Tagged sea lampreys were released upstream of US Highway 31 (yellow triangle). (B) Locations of the acoustic receivers with collocated or integrated synchronization tags (pink filled circles), stationary transmitters used in accuracy and precision tests (green crosses), and two water surface level data loggers (orange filled squares). Detections from the two receivers surrounded by dashed lines were not included in analysis (see text for details).

Telemetry array design and testing

Each array was designed by creating squares of equidistant sides constrained by river width to create the overlapping detection range required for fine scale positioning, adjusted to account for line-of-sight challenges due to channel morphology and natural obstacles (e.g., downed trees). Each receiver was attached to a 1.5 m piece of 13 mm diameter steel reinforcing bar using two hose clamps with the hydrophone positioned above the top of the metal rod. During deployment each rod was pressed into the substrate and a 2-m weighted grappling line was attached to aid recovery.

We conducted 6 diagnostic tests by drifting an acoustic transmitter (hereafter ‘tag’) through the initial main array design near the surface (n = 3) and near the substrate (n = 3) to identify potential gaps in detection and subsequent positioning. We identified a 0.4 km2 area with low detection efficiency (<47% during one drift near the substrate). We added one supplemental VR2W receiver to the array to increase coverage, improving detection efficiency of the area to 87%. The final main array consisted of acoustic telemetry data-logging receiver models HR2 (18) and VR2W (3) (Innovasea, Nova Scotia, Canada). The upper array included 8 VR2W receivers, four in each branch with detection range across the confluence. All receivers operated at 180 kHz and were capable of detecting signals encoded with pulse position modulation (PPM). Additionally, HR2 receivers were capable of detecting tags encoded with binary phase shift keying (HR), which transmitted each code over a much shorter interval (~1 ms) than a PPM signal (~ 1 s). To facilitate time synchronization among receivers, HR2 receivers contained integrated transmitters that emitted an HR-type code every 25–35 s and a PPM-type code every 270–330 s. VR2W receivers did not contain integrated transmitters, so an independent transmitter (Innovasea model V9-2x) was collocated with each VR2W. Final receiver positions were logged with a Trimble Geo XH with positional accuracy of ± 10 cm. Upon recovery, one HR2 receiver in the main array had water intrusion which corrupted detection data, and the collocated sync tag associated with one VR2W receiver in the upper array failed; detection data from these receivers were not included in positioning. The analysis included data from 17 HR2 and 3 VR2W receivers in the main array, and 7 VR2W receivers in the upper array (Fig. 2.1B).

Positioning performance of the main array was assessed by comparing the estimated positions to post-processed GPS measured positions (Trimble Geo XH) of collocated sync tags associated with each receiver, stationary tags with known location deployed throughout the study period, and mobile tag tests on 29 June. Stationary reference tests were performed by periodically moving two tags throughout the array during the study period (18 locations total, median test length = 26.76 hr, Fig. 2.1B). Mobile tests involved affixing a tag directly below the GPS antenna and drifting through the array (n = 2, mean test length = 781 s). Positional accuracy was measured as the Euclidean distance between array-determined location and the known GPS location for all positions taken from the stationary and mobile tests. Positional precision was estimated for the stationary tests only by calculating the distance between each unique estimated position and the median position for the tag during that test. Notably, tags used in the stationary reference test emitted only PPM code transmissions, whereas mobile tests used a tag transmitting both PPM and HR codes.

Bathymetric mapping

Bathymetry data were collected with a kayak mounted side- and bottom-scan sonar unit with internal GPS (Humminbird Helix 7 G3, Johnson Outdoors, AL, USA) on 02 June and 20 July 2021 following procedures described in Kaeser & Litts (2010). We recorded from transects paddled parallel to the shoreline approximately 2 m apart with the sonar frequency set to 455 kHz. Post-collection data processing using SonarTRX software (Leraand Engineering Inc., HI, USA) was performed to apply a slant-range correction and export XYZ (location and depth) files (Kaeser & Litts, 2010). Because water level fluctuated during the study, all depth measurements were standardized to a common vertical datum (NAVD 88) using a continuous water level time series (Fig. 2.2A). Water level data were recorded with two water surface data loggers (Solinst, Ontario, Canada) every 15 min for the duration of the study (Fig. 2.1B).

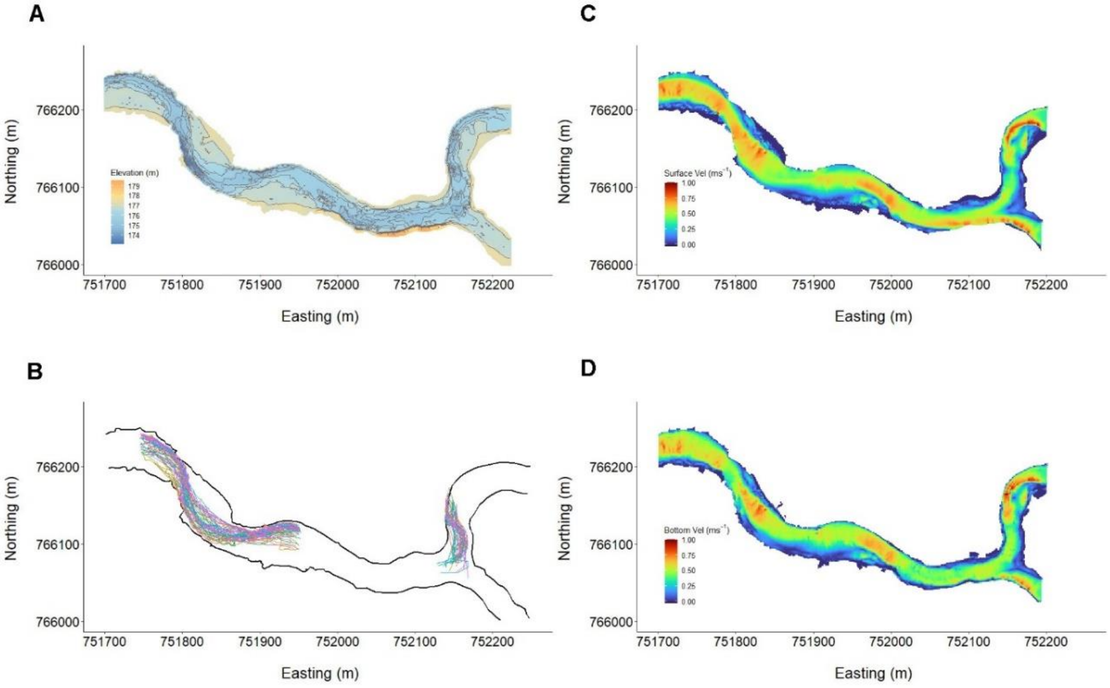

Figure 2.2. Sea lamprey tracks and study site bathymetry and water velocity. (A) Bathymetric map of the study site. (B) Observed fish tracks (*N* = 56) through the main and upper arrays after processing and

Figure 2.2 (cont'd)

filtering. Each track is colored differently. Map of water velocity (m s^{-1}) at standardized height from surface (C) and bottom (D) from the computational fluid dynamics (CFD) model for case 6 (modeled discharge = 19.54 $m^3 s^{-1}$).

CFD Modeling and validation

The flow field (water velocity and direction) in the White River was modeled using FLOW-3D HYDRO, version 23.1.0.12 (Flow-Science, New Mexico, USA) computational fluid dynamics (CFD) code. FLOW-3D solves the Reynolds-Averages Navier-Stokes equations governing motion for Newtonian incompressible flows using a finite volume method. A two-equation turbulence model, the Renormalization-Group k-ε model, was selected because it has wider applicability than the standard k-ε model (FLOW-3D User Manual, 2020; Pope, 2000) and better handles low Reynolds number and near-wall flows. A first-order upwind approximation scheme was employed for the momentum advection equations, and an implicit generalized minimum residual method solver was used to determine cell pressures and update the velocity field. The free water surface was tracked using the volume-of-fluid method (Hirt & Nichols, 1981). CFD models were run using a cluster node equipped with a 2.445 GHz AMD EPYC 7763 64-core processor and 32-GB memory.

The bathymetry data was converted to a three-dimensional triangular boundary mesh composed of elements with a side length of 0.5 m using MATLAB (Mathworks, Massachusetts, USA), stored as a stereolithography file (STL) and imported into FLOW-3D. Discretization of the geometry and mesh development were completed using fractional area – volume obstacle representation. A single structured mesh was used over the entire domain with rectangular prisms with a uniform cell size of between 2 to 0.5 m in both the horizontal and vertical plane. The upstream boundary condition was specified as a constant discharge, while the downstream boundary condition was specified as a constant water surface elevation. Water surface elevation values were obtained from water level loggers and discharge values were obtained from a combination of acoustic doppler current profiler (ADCP) surveys and a USGS gauge (041222000) located upstream (drainage area ratio of 1.29 between the site and gauge). The CFD model was qualitatively validated using ADCP surveys along four transects conducted on 16 June and 27 July 2021 with river discharge of 9.1 and 10.55 $m^3 s^{-1}$, respectively. For each of the validation discharges, the depth averaged velocity profile along each transect location was compared to ADCP data using a mesh cell size of 2 m, 1 m, and 0.5 m (see Fig. S2.1). The velocity profile matched the ADCP data well for both the 1.0 and 0.5 m mesh cell sizes. A mesh cell size of 0.5 m was used for all subsequent simulations, resulting in a mesh containing ~1.3 M elements.

A total of six flow scenarios were developed to simulate flow conditions that fully encompass the range of discharges experienced by sea lampreys in the White River when traveling through the acoustic receiver array (Table 1). To reduce simulation time, each CFD model was first run with a mesh with double resolution for 3000 s of flow time and then 1000 s of flow time were simulated at the finer scale (0.5 m cell size). After 1000 s, the models reached a quasi-steady state in which the total fluid volume within the computational domain reached a plateau and the model outputs were saved. Preliminary post-processing of CFD data was done using TecPlot 360 (TecPlot, Bellevue, Washington). Model output included all cell center coordinates, velocity vector, turbulent kinetic energy (TKE), turbulent intensity (TI), depth averaged velocity magnitude, and water surface elevation.

Table 1. Summary of water surface elevation (WSEL), total river discharge simulated, and number of subjects assigned to each flow scenario.

Scenario	WSEL (m)	Discharge range (m^3s^{-1})	*n* fish
1	177.27	10.59	22
2	177.28	11.68	12
3	177.30	12.42	7
4	177.31	14.98	8
5	177.33	16.99	2
6	177.34	19.54	5

Experimental subjects

Sixty adult sea lampreys were released between 21 May and 11 June 2021 (27 males and 33 females; mean ± SD, total length = 50.7 ± 2.9 cm, mass = 276.2 ± 38.7 g). Subjects were obtained from barrier traps operated by the U.S. Fish and Wildlife Service during the spawning migration from several rivers in Michigan. Experimental subjects were held in 1385 L round flow-through tanks that cycled Lake Huron water (100% water exchange every 4 h) with supplemental aeration at Hammond Bay Biological Station (Millersburg, Michigan, USA) until transport to Ludington Biological Station (Ludington, Michigan, USA) where subjects were held prior to tagging and release in a 900 L recirculating tank (100% water cycle every 1.5 min). Use of sea lampreys and all tagging procedures were approved by the Michigan State University Institutional Animal Use and Care Committee via animal use permit PROTO202100013.

Tagging and release procedures

Each lamprey was randomly selected and surgically implanted with one of two types of high residence (HR) acoustic transmitters. Each tag emitted two types of coded transmissions with varying pulse delay schedules: a PPM transmission every 13 – 27 s and a HR transmission every 1.8 – 2.2 s. Twenty subjects were implanted with V7P tags that transmitted horizontal position and depth via a pressure sensor with each coded transmission (Innovasea model V7P-2x, mass: 1.4 g in air, 0.7 g in water; 7 mm D x 19 mm L; power output: 143 dB re 1 µPa at 1 m). We tested each pressure sensing tag in a pressurized PVC pipe to five levels (0, 3, 6, 9, and 14 PSI) equivalent to 0 – 10 m. Calibrated slope and intercept values were calculated for each tag. These calibrated values were later used to calculate depth from transmitted sensor values (pressure sensor accuracy: ±0.5 m; resolution: 0.075 m). The remaining 40 animals received V5 tags transmitting two-dimensional positions only (Innovasea model V5-2x, mass: 0.74 g in air, 0.45 g in water; 5.7 x 5.66 mm D x 12.7 mm L; power output: 141 dB re 1 µPa at 1 m).

Subjects were anesthetized by immersion in 0.9 mL L^{-1} AQUI-S 20 E solution (AQUI-S, New Zealand) for final concentration of 100 mg L^{-1} eugenol. Lampreys were removed from the anesthetic bath after reaching stage IV of anesthesia, when individuals lost muscle tone but retained gill movement (mean time to stage ± SD, 1200 ± 164 s). After length and weight measurements, individuals were placed in a wet splint foam cradle with fresh water flowing through the mouth and gills maintaining constant gill irrigation. A 10 mm incision was made approximately 10 mm off the ventral midline that ended in line with the anterior insertion of the first dorsal fin to insert the tag in the peritoneal cavity. The incision was closed with two independent interrupted surgeon knots (4-0 Unify sterile PDO monofilament). After each surgical tagging procedure was complete (surgery time, mean ± SD, 185 ± 47 s) animals were monitored in individual postoperative holding tanks until regaining equilibrium, resuming natural swimming and/or attaching to the tank via oral disc (recovery time, mean ± SD, 1262 ± 731 s), and then returned to the post-tagging section of the holding tank. The following day, tagged lampreys were transported to the release site in aerated coolers and acclimated to river water by half volume water exchange until transport tank temperature was within 2^{o}C of river temperature (acclimation time, mean ± SD, 1115 ± 234 s). Lampreys were released into the river 0.9 rkm downstream of the acoustic array between 09:00 and 10:00 local time (Fig.2.1B). Tagging surgeries were performed between 21 May and 10 June, and releases took place between 21 May and 11 June with five or six individuals per release.

Telemetry data processing

Acoustic telemetry data were processed using Fathom Position software (Innovasea, v1.8.2) to synchronize time and estimate fish positions. Each receiver’s internal clock was corrected to remove clock drift. After time-correction, detection records of collocated tags throughout the array were aligned to time synchronize each receiver to the remaining receivers. Fine scale positions were calculated within the Fathom Position software by time-difference-of-arrival of acoustic detections arriving at three or more receivers based on hyperbolic principles (MacAulay, 2023; Smith, 2013).

Position error and filtering

Animal positions were filtered using a three-stage approach (see supplementary material for more details): (1) only segments of tracks exhibiting upstream movement through the array were included; (2) positions from outside of the array grid were removed; and (3) fish exhibiting sudden implausibly high-speed swimming with an immediate return to the prior track were identified by ground speed and removed (Almeida et al., 2002; Hardisty, 1979; Quintella et al., 2009). Because we were interested in characterizing the migratory route taken during upstream movement and the environmental factors that guide the selection of the route, only positions from upstream movement were included in the analysis. Each estimated position was assigned a measure of error sensitivity, HPEs, unitless. Previous studies have used the relationship between HPEs and measured error to remove positions that exceed a threshold (Meckley, Holbrook, et al., 2014). In the present study, this relationship did not reveal a meaningful threshold for filtering erroneous positions. However, there was clear evidence suggesting positional accuracy degraded considerably as a transmitter moved outside of the array boundary. Thus, we made the decision to exclude positions outside the array boundary. After this exclusion, stationary tests revealed an overall median accuracy (difference in the Euclidean distance from estimated and known position) of 0.41 m, and the two mobile tests had median accuracies of 1.28 m and 1.34 m (Table S1).

After censoring fish positions, visual inspection of fish tracks revealed outliers, e.g. positions on land or a track that exhibited a sudden large lateral movement with an immediate return to the previous trajectory. To identify and remove these errant positions, we applied a filter based on movement speed (per movement speeds reported in Almeida et al., 2002; Hardisty, 1979; Quintella et al., 2009). First, we calculated forward- and backward-looking ground speeds (gs) for each step of the track. Positions exceeding 2.5 body lengths·s-1 in both directions were removed and gs was recalculated. At this stage, no errant positions were identified in both directions; however, some positions exceeded 2.5 body lengths·s-1 in one direction. Next, we calculated gs resulting from the positions before and after this flagged position. If the resulting gs was less than 2.5 body lengths·s-1, the flagged position was removed. After this stage, all forward- and backward-looking gs were considered valid. Tracks were again visually inspected to ensure filtered positions did not compromise the track integrity (Fig. S2.4).

Prior to analysis, 7,765 of 12,218 animal positions were censored from the main array (6,610 from stationary fish or fish persistently moving downstream and exiting the array in the downstream direction, 834 from outside the array and 321 from movement speed) and 23 of 393 animal positions were censored from the upper array (22 stopped or downstream movement positions and 1 from movement speed).

Data analysis

Prediction 1: sea lampreys were closely associated with the river bottom

Sea lamprey vertical distribution was described as height in meters from river bottom for the pressure tagged individuals (n = 18; two fish failed to move upstream during the study period).

Prediction 2: the cost of swimming near the bottom was less than swimming higher in the water column

To ascertain the cost savings of swimming near the river bottom, we compared the cost (= work performed) for each discrete step of each movement path when closely associated with the river bottom vs. the cost of the same path artificially elevated to near the water surface. To achieve this, each fish position was assigned two elevations to create two identical 2D paths: one at the median height observed from fish with depth sensor tags (0.108 m above the bottom) and another at the same offset from the surface (i.e., 0.108 m below the water surface). For each combination of fish position and elevation, water velocities were extracted from the CFD scenario model that most closely resembled the experienced discharge at time of movement.

The work performed for each lamprey movement track (near-bottom and near-surface) was calculated with equations modified from McElroy et al. (2012), where the environmental conditions encountered over the chosen course influence physical cost (Eqn.1). Notably, this equation assumes drag is the prominent force and other turbulent coherent structures only minorly influence energy requirement which likely does not hold in all conditions. A work value was calculated for each discrete step of the path with the following equation, where ρ is the fluid density (kg m^{-3}), C_D is a dimensionless drag coefficient (Webb, 1975), S is the surface area of each fish (m^2), U_r is the relative velocity (m s^{-1}), and t is time (s).

$$W = \frac{1}{2}\rho C_D S U_r^3 t \qquad (1)$$

As no drag coefficient has been reported for land-locked sea lamprey, we used the value estimated from the relationship between drag force and water velocity interacting with body surface area for Pacific lamprey (*Entosphenus tridentatus*) which resemble Great Lakes sea lamprey in size and shape, where $C_D = 0.01$ (estimated from Fig. 4 in Zobott et al., 2020). The relative velocity, U_r was calculated over each step, where d is the distance (m), t is the time (s), and U_s is the average water velocity magnitude (m s^{-1}) between measured locations along a path (Eqn. 2):

$$U_r = \frac{d_s}{t_s} + U_S \qquad (2)$$

Step lengths had a median value of 2.46 m; therefore, the mean water velocity between adjacent positions on a path is representative of the velocity experienced over that step. We assumed the lamprey body to be oriented to water flow (Binder et al., 2010), rather than the path direction, thus velocity magnitude was used. This might lead to overestimation of W in some areas near the surface that exhibit flow reversal (e.g., eddies). Work performed over each step for bottom and surface paths was compared using a one-sided paired Wilcoxon signed-rank test to address the hypothesis that bottom paths had lower cost than surface paths, and we set the significance level for this test at $\alpha = 0.05$.

Prediction 3: Sea lampreys are non-uniformly distributed across the channel cross-section

To test whether sea lampreys were not uniformly distributed across the river channel, we established transects perpendicular to the river centerline. We then estimated the crossing point for each lamprey path at each transect using linear interpolation from the closest positions upstream and downstream of the transect. We retained transects that were crossed by a minimum of 50 fish (89 transects, mean ± 1 se distance apart 2.50 ± 0.07 m). To determine if sea lamprey were nonrandomly distributed across the river channel at each transect, we applied the randomization test described in Holbrook et al. (2015). Each transect was divided into ten equal-width segments, and sea lamprey crossing points were assigned to one segment in each transect. We then compared the difference between observed frequencies of crossing for each segment to expected frequencies drawn from a multinomial distribution of equal probabilities for all ten segments in the transect to calculate a test statistic, X^2_{obs}. Next, we simulated 10,000 draws from a multinomial distribution representing the 10 intervals of equal probability to compile a distribution of test statistics, X^2_{null}. To determine a p-value, we calculated the proportion of X^2_{null} that were more extreme than X^2_{obs}. The p-value was used as a measure of strength of evidence against the null hypothesis of uniform lateral distribution across the river channel, where $p < 0.01$, $p < 0.05$, $p < 0.10$, and $p > 0.10$ indicated strong, moderate, weak, and no evidence, respectively.

Prediction 4: Sea lampreys prefer to migrate through the deepest portion of the channel

We used an independent t-test to compare the relative water depth usage at each transect for observed and simulated fish to assess relative depth use. Simulated fish positions were randomly drawn from the 10,000 replicates described above at each transect. Relative water depth was calculated by dividing the water depth at each simulated and observed fish position (from the bathymetric mapping) by the maximum water depth of the transect. Consistent significant differences with greater use of deeper segments would indicate a preference for selecting the thalweg.

Prediction 5: sea lampreys consistently choose the deeper channel at upstream confluence

Lamprey positions were visually inspected for channel choice and assigned to the north or south channel. To test preference for either channel we performed a one-sample binomial test with the expected proportion of 0.5 for each channel (equal probability of selection).

All analyses were conducted in R version 4.2.3 with the following packages: cmgo, raster, sf (Golly & Turowski, 2017; Pebesma & Bivand, 2023; R Core Team, 2022a).

RESULTS

The acoustic telemetry array detected 57 of the 60 tagged individuals at least once. After censoring, positions from 56 animals (31 females, 25 males) were included in the dataset (Fig. 2.2B). Analysis for Predictions 1 – 4 included 4,453 positions in the main array, of which 3,108 were 2D and 1,345 were 3D positions. The upper array inspection (Prediction 5) included 370 positions. Positions per individual ranged from 34 to 189 (median 81).

Three-dimension positions revealed close association with the river bottom regardless of lateral position (Prediction 1). At the 89 transects crossed by at least 50 fish, the median distance from the bottom for the 18 animals transmitting 3D positions ranged from -0.02 to 0.49 m (mean = 0.25 m) (Fig. 2.3). Consistent with Prediction 3, sea lampreys were non-uniformly distributed laterally across the channel at each of the 89 transects (X^2 range = 27.93 – 126.14, all $p < 0.001$, indicating strong evidence for rejecting the null hypothesis of a uniform use of the channel cross-section, Fig. 2.3). Lamprey positions on the transects were consistent with a preference for moving through the deeper portions of the channel (Prediction 4, Figs. 2, 4). For 82 of 89 transects, *t*-tests revealed a preference for movement through the deeper portion of the river (t = 2.07 – 9.10, all $p < 0.04$). Lamprey positions were in water 23% deeper than predictions from modeled fish paths (observed mean (± 1 se) relative depth, 0.68 ± .004 m; predicted mean relative depth with uniform distribution, 0.45 ± 0.004 m). Twenty-six individuals consistently chose the deepest quarter of the river, with median relative water depths greater than 0.75 m (median relative water depth per individual range = 0.38 – 0.90 m). Lampreys did not exhibit a preference for moving through the deepest part of the channel at 7 transects (transects 23, 24, 50-54 labeled with green crosses in Fig. 2.3 and Fig. 2.5). These transects aligned with portions of the river channel exhibiting a more uniform cross-section (i.e., the ratios of median depth to maximum depth in Fig. 2.3 were approaching 1). Consistent with Prediction 2, swimming at the surface (median cost per step = 52.43 J; mean cost per m = 22.64 J/m) was on average 5.8% more costly than swimming near the bottom (median cost per step = 49.76 J; mean cost per m = 21.67 J/m) of the river (Z = -9.48; *df* = 4396, $p < 0.0001$; r = 0.14). All 56 individuals chose the deeper north channel that also had greater discharge (Prediction 5, $z = 7.35$, $p < 0.0001$; Fig. 2.2C).

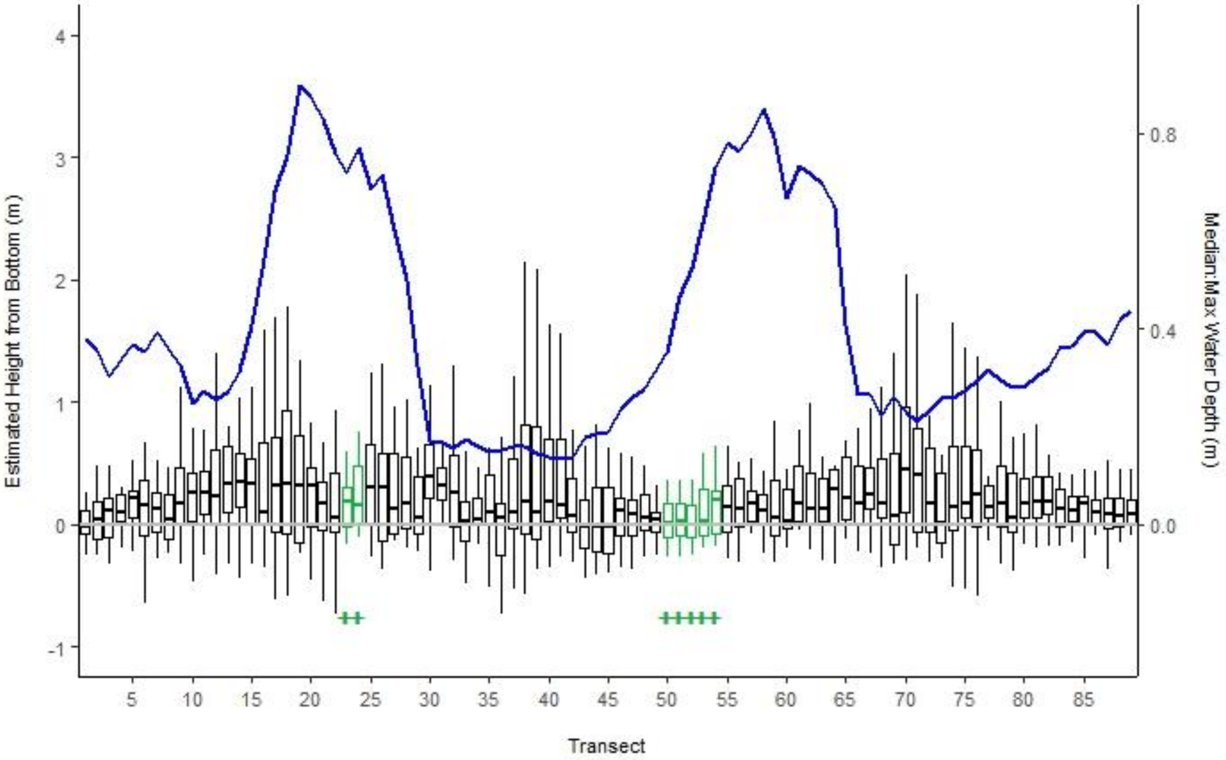

Figure 2.3. The vertical distribution of pressure-sensory tagged sea lampreys (n = 18) moving through the main array at 89 transects. The ratio of median to maximum water depth at each transect is represented by the solid blue line. High values of this ratio are associated with areas of the stream with a more uniform cross-section. Vertical distributions are described as estimated height from bottom (m). Boxes indicate interquartile range (IQR), solid line between corresponds to median height, and whiskers represent the highest and lowest value within 1.5 x IQR. Solid horizontal grey line indicates the river bottom. Distributions in green and indicated with + refer to transects where lampreys did not reveal a preference for the deepest portion of the transect, where observed fish (*N* = 56) relative depth usage did not differ significantly from simulated fish relative depth.

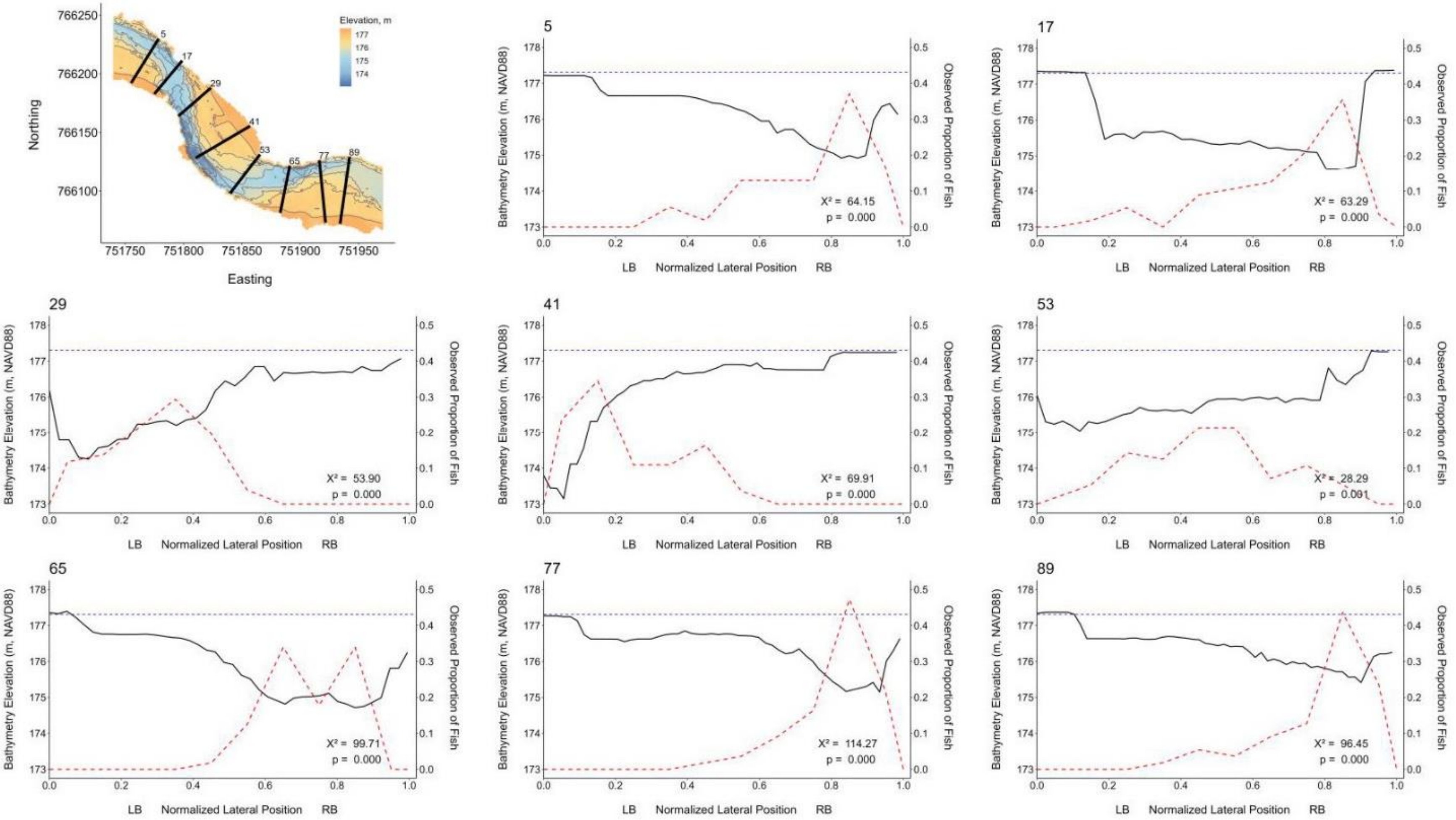

Figure 2.4. Normalized lateral distribution of fish and water depth at eight representative transects. Subplots for the individual transects show the depth profile (solid black line) relative to the average water surface elevation (blue dotted line) and the observed proportion of fish in each of 10 bins representing 10% of the normalized width (red dashed line). X^2 and *p* values indicate significant difference from a uniform fish distribution for the transect. LB, left bank. RB, right bank.

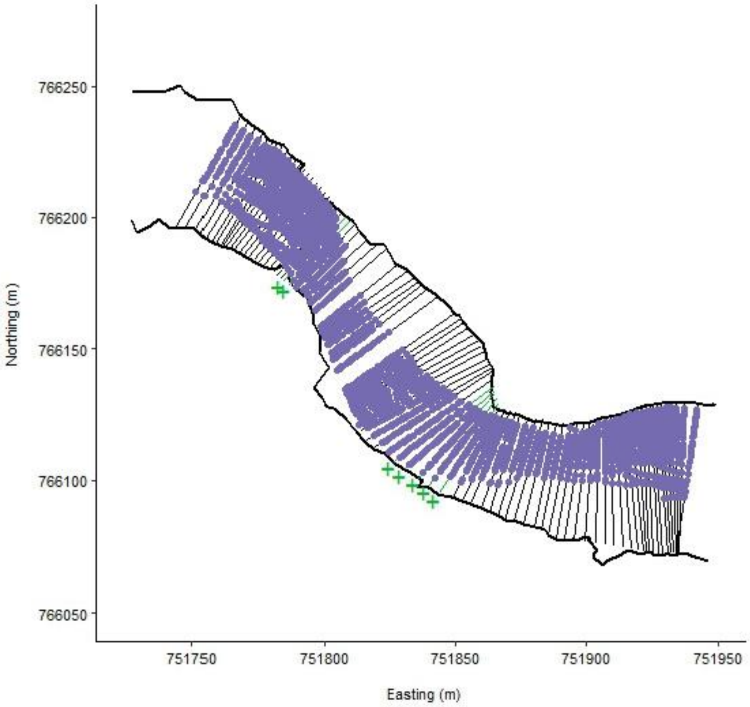

Figure 2.5. Observed fish positions (*N* = 50 – 56) on each of the 89 transects. Transects marked with green + indicate non-significant difference between observed and simulated fish relative depth usage.

DISCUSSION

This study demonstrated that sea lampreys on the spawning migration moved in close association with the river bottom achieving a significant energetic savings relative to moving higher in the water column. Additionally, we observed a distinct pattern of thalweg tracking in shallow river systems, with migrants adjusting their lateral position to remain in the deepest areas. When encountering a confluence, all lampreys chose the deeper channel with greater flow despite both channels exhibiting areas of relatively high water velocity (Fig. 2.2C-D). These insights have important implications for both the management and conservation of sea lamprey populations, providing opportunities to improve trapping efficiency and design more effective fish passage systems.

Fishes that undertake long or costly migrations are more likely to engage in energy saving swim tactics than those that move short distances (Bernatchez & Dodson, 1987). Swimming in close association with the river substrate is consistent with minimizing the rate of energy expenditure by swimming against slower velocity water. In the White River, sea lamprey maintained a median height above bottom of 0.108 m, comparable but slightly lower than the 0.16 m median height observed in the deeper Mississagi River (Ontario, Canada; Holbrook et al., 2015). This resulted in a mean energy savings of 5.8% relative to the modeled cost of swimming identical paths higher in the water column. Notably, our study took place during an unusually dry spring. Sea lamprey often time upstream movement to coincide with freshets (Almeida et al., 2002; Morman et al., 1980). During floods the relative cost savings associated with bottom swimming should be greater. The practical effect of this behavior is to allow the animal to maintain a desired ground speed at a slower tail beat frequency preventing exhaustion over long periods of sustained swimming (Beamish, 1974; Hoover & Murphy, 2018). We anticipate that efficient navigation upstream may require lampreys to move out of boundary layer flow nearest the substrate (lower mean velocities but higher relative turbulence) and into the lower layers of the bulk flow (higher mean velocity with lower relative turbulence) to maintain rheotactic alignment with the bulk flow. The distance above channel bottom lamprey must reach to encounter bulk flow is likely to be variable owing to changes in channel topography, substrate material, and discharge which influence the boundary layer thickness. This tactic should lead to preservation of energy for predator avoidance, mate search and assessment, gamete development, nest building, and spawning activity (Alerstam et al., 2003; Johnson et al., 2015; Lennox et al., 2016).

Swimming in close association with the bottom should also allow sea lampreys to determine the depth of the water column by sensing hydrostatic pressure (Burt de Perera et al., 2005; Davis et al., 2021). There is evidence that sea lampreys use hydrostatic pressure to orient and navigate towards coastlines early in the spawning migration (Meckley et al., 2017). The sea lamprey's ability to sense hydrostatic pressure may involve the vestibular hairs of the inner ear (Maklad et al., 2014) and/or superior neuromasts on the epidermis. Other fishes have been shown to detect hydrostatic pressure using the lateral line, inner ear, and swim bladder (Bleckmann & Zelick, 2009; Fraser et al., 2008). Given that sea lamprey lack a swim bladder and have a primitive lateral line, and that the sea lamprey inner ear exhibits structural similarity with other pressure-sensitive fishes, the inner ear may house the ability to detect changing water depth, although the lateral line cannot be excluded (Fraser et al., 2008; Hammond & Whitfield, 2006; Khorevin, 2008; Maklad et al., 2014).

When swimming near the bottom, the perception of reducing hydrostatic pressure may indicate the ecosystem is shallowing or the animal has moved close to the riverbank. Either circumstance should increase the risk of encountering nocturnal shoreline and submerged predators that feed on migrating lampreys (Boulêtreau et al., 2020; Cochran, 2009; Harvey & White, 2017). In a study of European river lampreys (Lampetra fluviatilis) migrating through a shallow river reach of uniform cross-section, migrants were observed avoiding river edges (Kerr et al., 2023). We hypothesize the sea lamprey has evolved to avoid areas deemed too shallow to be safe, and to avoid near-surface swimming. These tactics would also assist in avoiding entrainment into fringing wetlands or coves when moving through estuaries and river-wetland complexes. Sea lampreys are also known to increase ground speed when exposed to a danger cue in small shallow rivers (Luhring et al., 2016). Whether they show similar acceleration when moving through a shallow reach of a river or during low flows is currently unknown. Additionally, there may be a water depth that labels a location as sufficiently safe. In these 'safe enough' portions of the river (i.e. sufficiently deep), a tactic of movement through areas of highest cost savings such as near the bottom and closer to the riverbanks where water velocity is lower than the main channel may be favored, as observed by Holbrook et al. (2015).

We hypothesize that sea lampreys use a novel behavior to navigate through shallow river and estuarine systems by principally aligning opposed to water direction and using hydrostatic pressure to make lateral course corrections to stay in the deepest part of the channel. In the relatively shallow White River migrating sea lamprey movement paths exhibited a non-uniform distribution across the channel with a distinct preference for moving through the deepest areas. Wherever a distinct thalweg was present movement paths converged in alignment with the thalweg. When the channel transitioned to a more uniform cross-section, movement paths diverged and spread across the channel while continuing to avoid the shallow margins, reconverging when the thalweg reemerged. This pattern of thalweg tracking is consistent with navigation in response to changing hydrostatic pressure via pressure guided rheotaxis. Lampreys have a lateral line system comprising superficial neuromasts capable of detecting changes in water velocity and direction that allows migrants to orient upstream (Gelman et al., 2007, 2008; Johnson et al., 2012; Katori et al., 1994; Yamada, 1973). If the direction of movement becomes misaligned with the thalweg, we anticipate the animal detects a lessening hydrostatic pressure and can execute a contralateral movement to remain in the deeper parts of the channel. This tactic would naturally result in the animals becoming more dispersed in uniform cross-section reaches of the stream as the animal would not perceive a change in hydrostatic pressure with lateral drift and would continue to orient into the bulk flow. This pattern was observed by Kerr et al. (2023) when observing river lamprey migrating through a river with a uniform cross-section.

Migration through estuaries, drowned river mouths, and river-wetland complexes involves selecting movement pathways through complex channel bedforms and hydraulic fields that shift over time and space (Nestler et al., 2012). Because scour channels are persistent morphological features of estuarine and river bottoms that predictably lead to the upper watershed, a migration strategy that includes movement through these features should reduce the time needed to arrive at the spawning habitat. For example, in tidally dominated estuaries it is typical to find single or dual channels cut into the bed by ebb and flood tidal scour that eventually link into the fluvial thalweg (Dalrymple & Choi, 2007). This hydro-geomorphological pattern is common to many estuaries and rivers that currently or historically recruited large migrations of sea lamprey from the Atlantic Ocean (e.g., Ouse-Humber estuary (Karunarathna et al., 2008; S. Silva et al., 2017), Scheldt River estuary (Leuven et al., 2018)). Because the Great Lakes do not experience tides, only the fluvial thalweg is present in shallow coastal river-wetland complexes, often extending to the river mouth and slightly offshore (Herdendorf, 1990; Larson et al., 2013). Use of pressure-guided rheotaxis would allow migrants to navigate upstream within the scour channels and thereby swim a relatively short path through the riverscape by avoiding diversion into minor side channels associated with wetlands, marshes and tributaries. In effect, following a 'bathymetric highway' system. Moreover, because the relationship between channel shape and hydrodynamic forces that structure estuarine and riverine bedforms are persistent over geological time, allegiance to relative depth and flow values would allow successive generations to successfully navigate as channels shift position in response to variation in river discharge, sediment loads, and tides. How then do they choose in places where multiple erosional channels diverge? Superimposed on the hydro-geomorphological 'roadmap' is larval odor, a conspecific cue that labels habitat as suitable for reproduction and guides migrants into spawning streams (Sorensen et al., 2005). The odor is carried downstream and migrating sea lampreys avoid swimming through waters that do not contain the odor, preventing entry into tributaries that lack larval populations (Wagner et al., 2006a, 2009). Similar reinforcement may occur when moving through estuaries and freshwater river-wetland complexes; however, given the extensive mixing that occurs in estuarine systems, hydrogeomorphology may provide a more consistent and distinct orientation cue.

Upstream movement through the thalweg should also result in increased safety. Remaining on the bottom in the deepest portion of the river likely decreases detection by nocturnal shoreline predators, particularly when the thalweg meanders into close proximity to the riverbank (Boulêtreau et al., 2020; Imre et al., 2014). In shallow rivers, remaining in the deepest portion reduces the chance of breaking the water surface, thus minimizing the risk of detection by aerial or surface-dwelling predators. Sea lampreys exhibit a dark dorsal surface and counter shading that should also reduce predator detection by visually hunting predators. Although thalweg tracking optimizes the physical position within the river to reduce encounters with predators, countershading ensures that any potential sightings are less likely to result in detection or predation. Moving through areas with higher water velocity near the surface, which are less desirable hunting grounds for many predators, further aids in avoiding grappling and ambush tactics commonly employed by predatory species (Hart & Finelli, 1999; Peckarsky et al., 1990). Additionally, by reducing the total migration time (increased navigational efficiency) thalweg tracking also reduces the time exposed to predators (Pinti et al., 2020).

We expect the navigational tactics observed in the White River to arise in similar systems. That is, relatively shallow rivers (≤5 m deep) embedded in wetland complexes or estuaries that contain distinct scour channels in the bed. We are aware of two other studies of fine scale lamprey navigation in rivers during the spawning migration. Kerr et al. (2023) evaluated movement paths of migrating adult European river lamprey in a shallow river with uniform cross-section. They observed patterns similar to those in the portion of our study reach that also had a uniform cross-section: upstream oriented paths widely distributed across the channel with avoidance of the shallow margins. They (and we) conclude that eschewing movement through shallow river margins would result in avoiding slow moving waters where rheotaxis would be difficult to maintain. We further posit that avoidance of shallow areas will help migrants avoid entering tributary channels leading into surrounding wetlands. In our study, sea lampreys approached a confluence of roughly equal-width channels from a uniform cross-section reach, with all individuals selecting the deeper route associated with the mainstem of the river. The alternative route led to a shallow and heavily vegetated channel that eventually reconnected with the main river. Consequently, the choice was not affected by larval odor, as the populations of larvae were upstream of where the two channels reconnected. This selection may have been reinforced by the higher discharge in the mainstem.

In the other fine scale lamprey spawning migration study, Holbrook et al. (2015) investigated sea lamprey movement paths in the Mississagi River, a tributary to Lake Huron, in a 1.22 km reach that was 3-6 m deep in the main channel descending to >15 m in a river bend. Here, sea lampreys moved along the bottom and in the straight sections of the study area were more likely to move between the river's edges and the thalweg. The findings of the three studies can be reconciled through the lens of optimization of the two dominant and competing selective pressures: minimizing energy expenditure while also maximizing avoidance of predators. In most northern temperate zone rivers occupied by sea lampreys, the least expensive path will coincide with the riskiest path, movement along the river margin, when predation pressure is coming from nocturnal shoreline mammals (Cochran, 2009; McElroy et al., 2012). If the animal relies on hydrostatic pressure to avoid shorelines, it is functionally avoiding shallow areas regardless of their location. We can imagine this as a lens of water at the surface with a thickness equal to the depth the animal deems safe. Near the shoreline this lens of unsafe water would intersect with the substrate rendering the full water column unsafe. Likewise, the zone of energetic savings is associated with swimming near the substrate, with the greatest energetic savings near the riverbank where flow is slowest, and the least savings under the fastest flow, typically in the thalweg. In shallow systems with a distinct thalweg, much or all the river margins may be unacceptably shallow (i.e., unsafe), causing animals to move through the thalweg. Where the channel becomes more uniform, all but the shallow margins represent the deepest area, leading to dispersion of movement paths consistent with our study and that of Kerr et al. (2023). In a deeper river with steeper banks, as in Holbrook et al. (2015), migrants could move closer to the riverbanks to benefit from greater energetic savings while remaining sufficiently deep to promote safety. We would expect a pattern similar to that observed in deeper rivers to occur in shallow rivers during spring high flow events, a time of high migration (Moser et al., 2015). During spates water depths would increase, as would water velocities near the thalweg. However, when the river passes through wetland-dominated landscapes, as in our study site, thalweg tracking may persist during floods. The wetland surface surrounding the White River site was typically 20-30 cm above the water surface at base flow. Floods greatly increased flow, but not surface elevation, as the water spilled onto the wetland surface.

The ability to anticipate where and when an animal will move presents opportunities to improve conservation and management actions. In the Great Lakes basin there is a considerable desire to develop methods for invasive sea lamprey control that do not rely on the application of pesticides (Burkett et al., 2021; Lewandoski et al., 2021; Siefkes et al., 2021), including the development of effective means to fish migrating sea lampreys prior to spawning (McLaughlin et al., 2007; Miehls et al., 2020). Current and historical approaches to fishing sea lamprey for control invariably focus on unbaited traps placed in association with dams (Miehls et al., 2021). Many of these traps experience low and variable success because of low and inconsistent encounter rates with migrants (Bravener & McLaughlin, 2013) especially when trap entrances are placed well above the substrate amidst high velocity turbulent flow (Rous et al., 2017). Our findings suggest evaluation of channel morphology and hydrology lampreys experience as they approach the barrier and the fishing device location could be useful in diagnosing why certain barrier-integrated traps fail (e.g., their position is misaligned with preferred movement paths) and might also be modified to improve trap encounter rates. Moreover, the patterns we observed suggest fishing sea lamprey in open river channels away from dams is viable. Fishing practices should involve placement of fishing devices in meandering thalwegs where they run adjacent to the riverbank, targeting reaches that flow through flat landscapes that experience relatively small changes in depth during floods. Within their native ranges, there is also a strong desire to create opportunities to pass several migrating lamprey species around dams (Moser et al., 2021). Because fish passage devices are placed in association with dams, typically at the riverbank, an examination of the hydro-geomorphological features that guide movement downstream of the dam may also help to diagnose unsatisfactory performance. For example, a study conducted in the River Mondego (Portugal) revealed anadromous sea lamprey were more likely to attempt passage of a dam during low flow, focusing their attempts near the center of channel (deeper, faster flow), well away from the fish passage device (Pereira et al., 2017). Because dams are often sited in places with uniform and geologically stable cross-sections, improving success of failing fish passage devices may involve reengineering the approach via dredging or other modifications to the channel geometry. Whether trapping for control or attempting fish passage, our findings reinforce those of other workers who suggest device entrances should be placed near the river bottom (Holbrook et al., 2015; Rous et al., 2017).

Conclusion

Scientists have long been fascinated by the movement strategies animals use to complete long-distance reproductive migrations. These efforts have focused on homing animals that utilize geomagnetic information and map-and-compass navigation. Notably, many migrating animals neither home nor use this mechanism (B. B. Chapman et al., 2014). Our study has revealed a novel navigational tactic utilized by non-homing sea lampreys that involves optimization of competing selective pressures to minimize energy expenditure predation risk by relying on physical features of river morphology and hydrology that persist over geological time. Remarkably, this tactic likely requires inputs from only two sensory systems: the lateral line for detecting water velocity and direction, and an unknown mechanism for sensing hydrostatic pressure changes (possibly superior neuromasts and/or the inner ear). Insights from this and similar studies offer significant opportunities to improve the performance of conservation actions related to invasive species control and population enhancement. We suggest the coupling of fine scale, high frequency recording of animal positions with carefully constructed mechanistic hypotheses of movement strategies will prove a powerful approach to designing, reconfiguring, and operating infrastructure (fishing devices and dams) to achieve improved outcomes.

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APPENDIX

Validating CFD with ADCP surveys

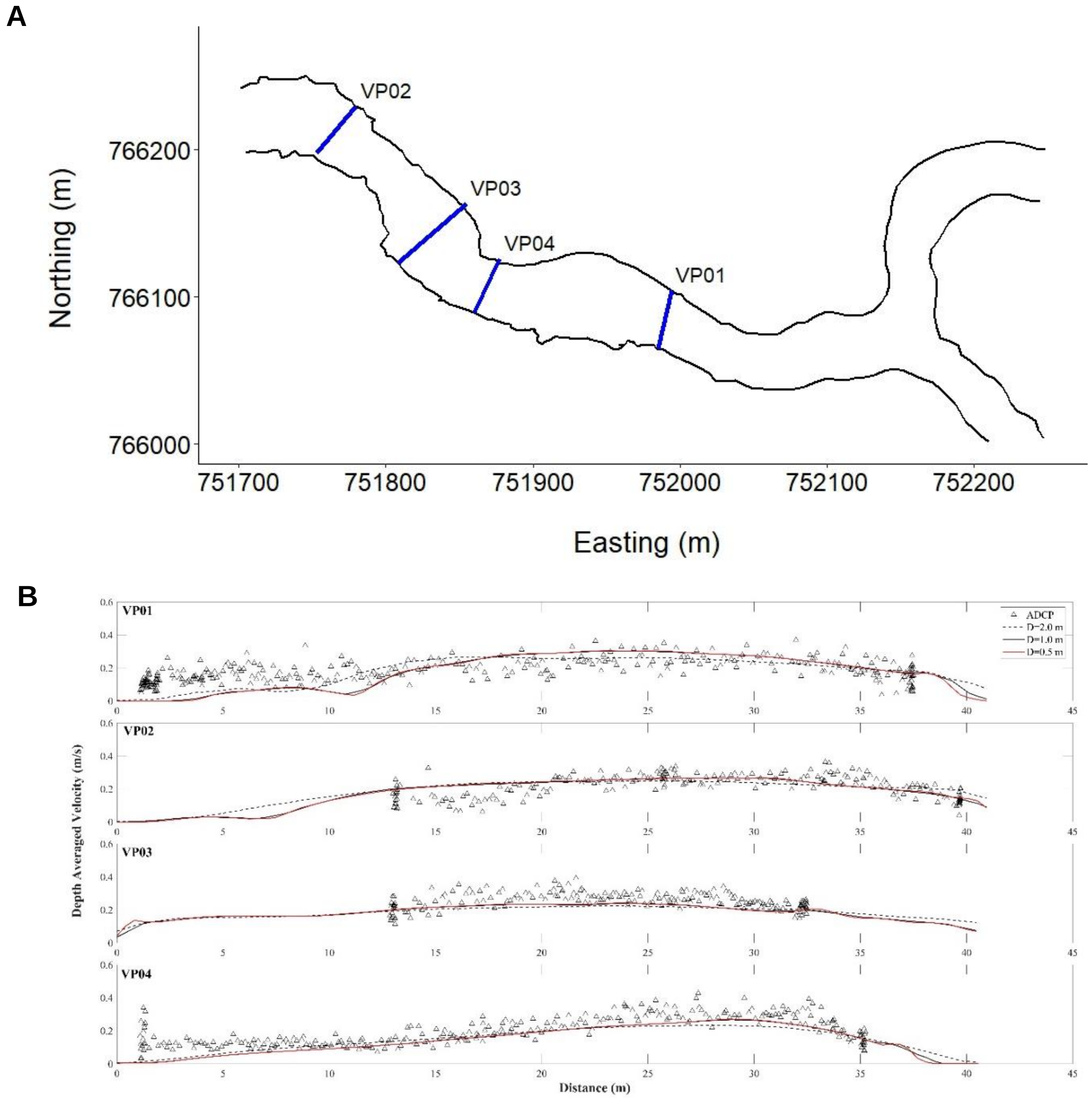


Figure S2.1. Comparison of depth averaged velocity measurements at four ADCP survey transects taken along the White River on 16 June 2021. (A) Map indicating acoustic doppler current profiler (ADCP) survey transects with solid blue lines. (B) The ADCP velocity measurements are indicated by black triangles and CFD values are indicated by the red, black, and black-dashed lines.

Fish position error estimation and data filtering

Each estimated fish position was assigned an estimate of horizontal position error sensitivity (HPE_s, unitless) and transmitters with known locations (collocated with receivers) were also assigned measurements of horizontal position error (HPE_m, m) where measured GPS location was known. We calculated the relationship between Fathom-provided HPE_m and HPE_s for the collocated receiver positions to apply to fish position HPE_s values to estimate absolute position error (HPE_m^*, m). To limit the influence of positions with high uncertainty on the calculated relationship, we excluded positions with HPE_s values in the 95th percentile (Smith, 2013). Although this exclusion resulted in 104,536 sync positions, the range of HPE_s values was limited to 0.47 – 4.74. We calculated the twice distance root mean squared (2DRMS) as twice the square root of the combined variance in the X (easting) and Y (northing) direction for each 1-m bin averaged over all receivers (Fig. S2.2). Next, to estimate HPE_m^* we applied the slope and intercept of the linear regression of HPE_s and 2DRMS to HPE_s values (Meckley et al., 2014; Smith, 2013).

To validate this approach, we calculated HPE_m^* using the same slope and intercept for the 11,047 stationary and 379 mobile tests positions and compared that value to measured positional error (i.e., the Euclidean distance between known GPS location and estimated position). This comparison did not result in the expected 1:1 relationship between HPE_m^* and measured error (regression equation: HPE_m^* = 0.821 + 7.14 * measured error; R^2 = 0.08). Instead, high HPE_m^* values were assigned to positions with low measured positional error therefore overestimating the positional error. For example, applying the HPE_m^* filter of 5 m to the mobile test positions identified 49% of positions (n = 185) as erroneous, but the median accuracy of those positions was 1.82 m (mean = 5.49 m) (Fig. S2.3).

HPE_m^* did not offer a useful threshold for filtering erroneous positions within the array. However, there was clear evidence from both known positional error and HPE_m values suggesting positional accuracy degraded considerably as a transmitter moved outside of the array boundary. After censoring stationary and mobile tests to exclude positions outside of the upstream-most and downstream-most receivers, the 17 resulting stationary tests (Table S1) revealed an overall mean accuracy (± 1 SE) of 1.03 ± 0.04 m (median 0.41 m; mean range of each test 0.39 – 3.39 m), and the 2 tag drags had a mean accuracy (± 1 SE) of 1.70 ± 0.15 m (median = 1.28 m) and 2.37 ± 0.41 m (median = 1.34 m).

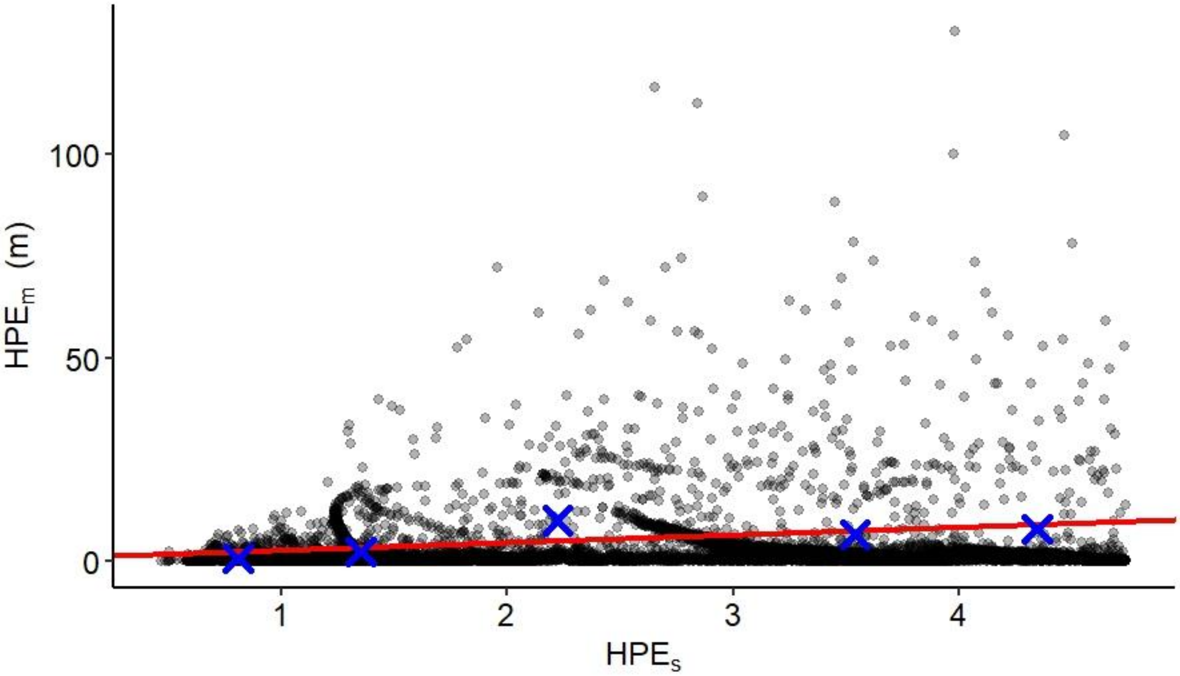
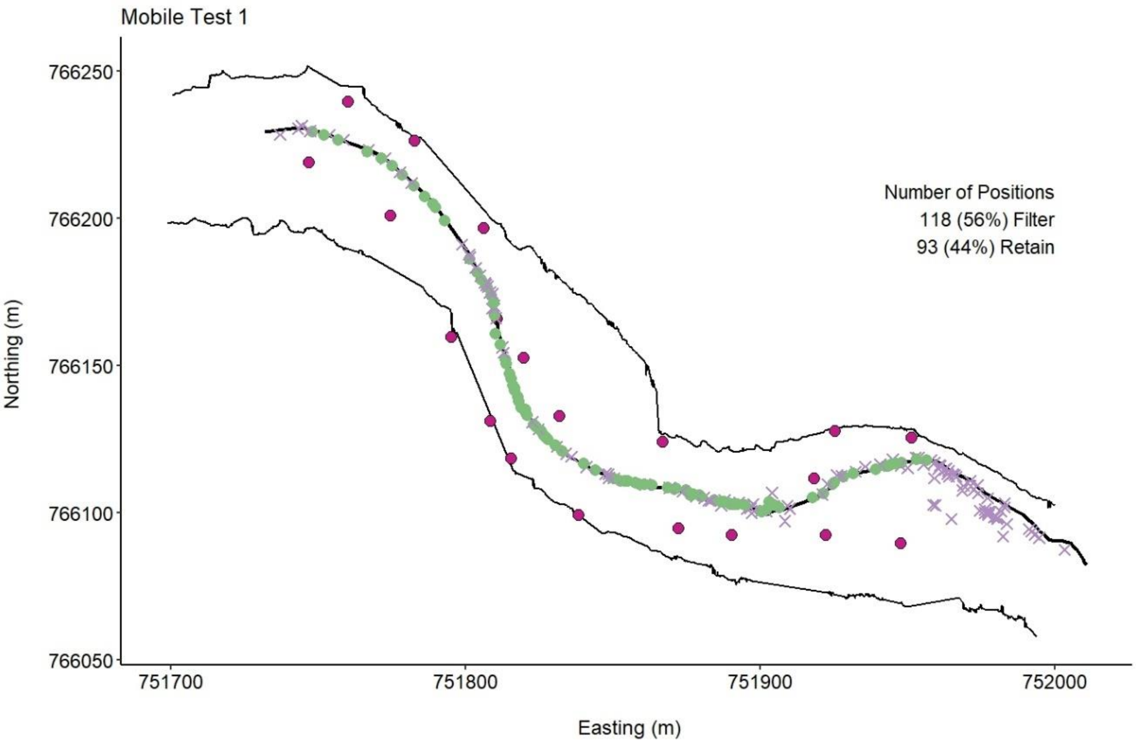


Figure S2.2. Fathom-provided horizontal position error (HPE$_m$) versus horizontal position error sensitivity (HPE$_s$) values for each estimated collocated sync tag position. The blue x represents twice the distance root mean square error of X and Y components of error within an HPE$_s$ bin of one; 2DRMS is represented by the solid red line running between these points.



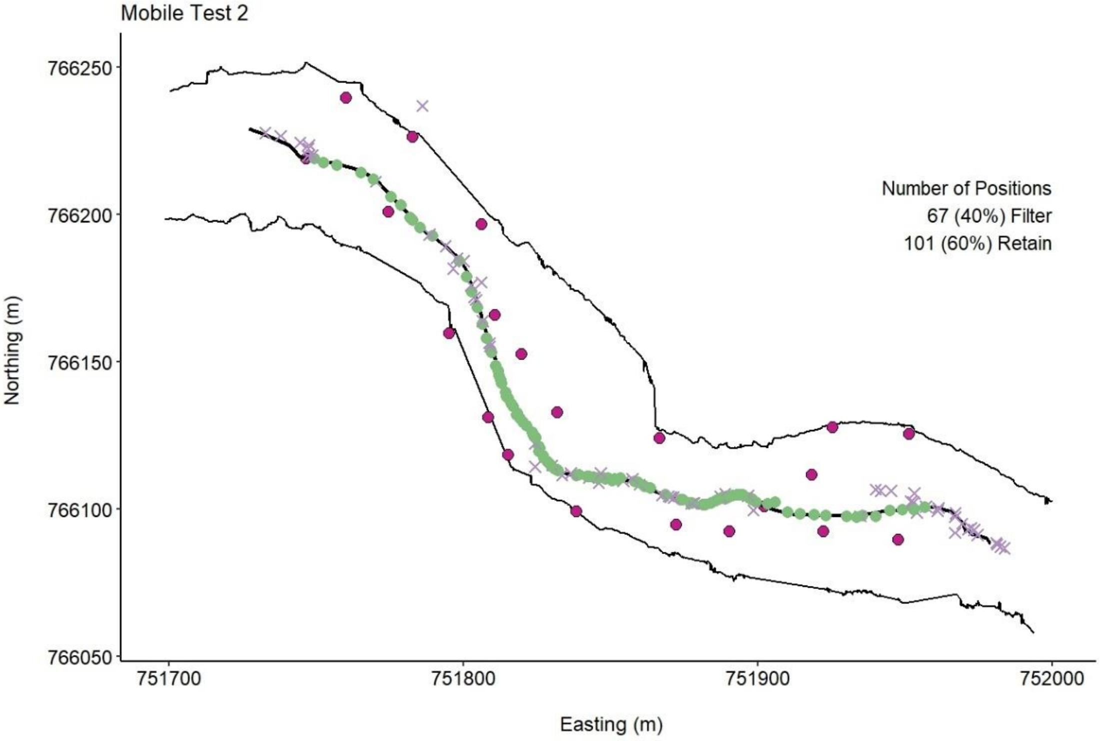


Figure S2.3. Estimated positions and known GPS track from mobile tests. Positions retained (green circle) and filtered (purple crosses) from mobile tests when applying HPE_m^* filter of 5 m. Acoustic receivers are indicated by pink circles. The solid black line indicates the known GPS track.

Table S2.1. Accuracy and precision of stationary tests (*N* = 17) after censoring positions outside the receiver array.

Test	n Positions	Accuracy (m)				Precision (m)				Test Length (hr)	Fix Rate
		Mean	SD	SE	Median	Mean	SD	SE	Median		
1	1280	0.49	2.69	0.08	0.18	0.40	2.70	0.08	0.07	120.59	88.90
2	989	1.07	6.06	0.19	0.34	0.87	6.11	0.19	0.11	90.75	91.27
3	419	0.97	4.66	0.23	0.30	0.77	4.69	0.23	0.07	39.17	89.59
4	294	0.71	4.15	0.24	0.20	0.61	4.16	0.24	0.09	27.72	88.83
5	244	0.39	0.99	0.06	0.25	0.25	0.99	0.06	0.10	22.49	90.85
6	205	0.62	0.73	0.05	0.55	0.22	0.72	0.05	0.11	20.32	84.50
7	219	0.45	0.38	0.03	0.40	0.18	0.38	0.03	0.08	20.32	90.25
8	567	0.66	3.32	0.14	0.40	0.43	3.36	0.14	0.14	53.59	88.61
9	554	0.85	2.14	0.09	0.41	0.68	2.13	0.09	0.25	53.64	86.51
10	1795	1.10	2.36	0.06	0.75	0.59	2.37	0.06	0.25	166.85	90.10
11	1777	1.24	3.19	0.08	0.55	1.12	3.15	0.07	0.51	166.60	89.33
12	234	0.87	3.80	0.25	0.40	0.76	3.82	0.25	0.17	21.68	90.38
13	214	0.54	1.36	0.09	0.40	0.41	1.36	0.09	0.23	21.78	82.31
14	235	2.33	9.04	0.59	0.66	1.95	9.01	0.59	0.20	22.11	89.00
15	241	1.02	2.80	0.18	0.42	0.86	2.77	0.18	0.28	22.15	91.12
16	271	3.37	9.31	0.57	0.63	3.33	9.23	0.56	0.71	25.76	88.11
17	273	1.52	3.25	0.20	0.64	1.22	3.17	0.19	0.43	25.79	88.64

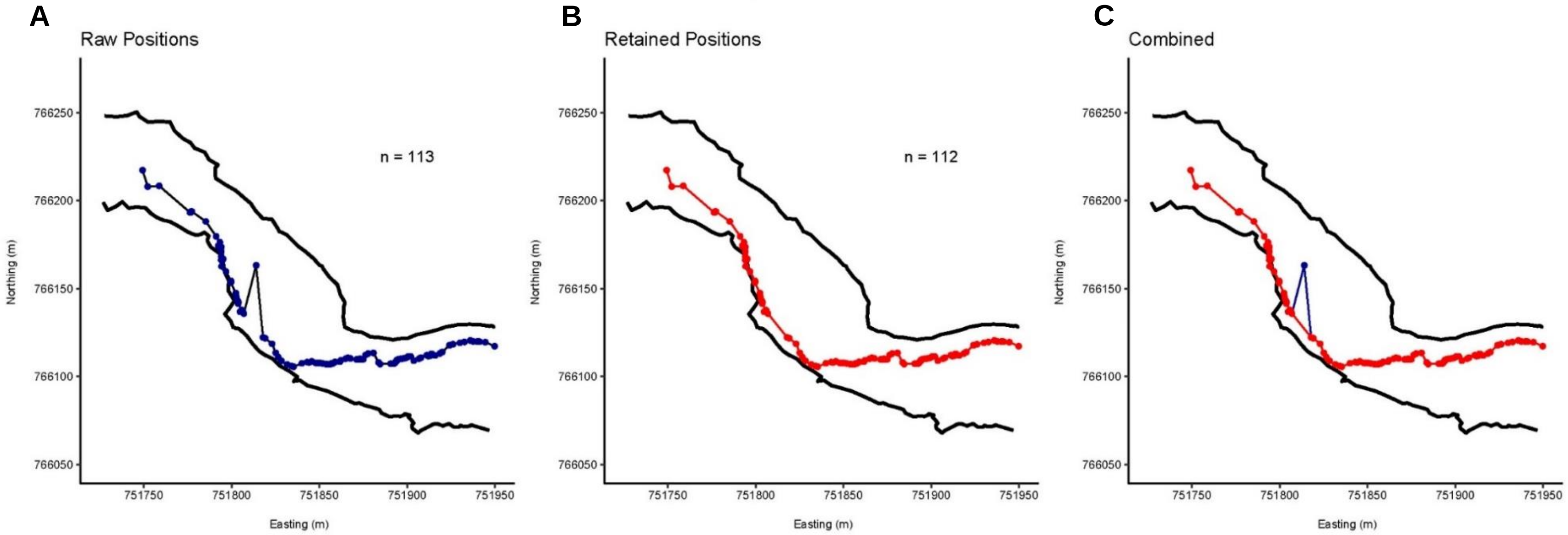


Figure S2.4. Estimated sea lamprey positions and interpolated track before and after applying movement filters. Exemplary animal track made from (A) unfiltered and (B) movement speed filtered positions. (C) Filtered track overlay unfiltered track.

CHAPTER 3

KEEPING PACE: MIGRATING SEA LAMPREYS ADJUST SWIM SPEED IN RESPONSE TO SHIFTING HEAD CURRENTS TO MAINTAIN GROUNDSPEED

ABSTRACT

Migrating fish must balance energetic costs with environmental and ecological constraints during upstream movement. While theoretical models predict that fish can conserve energy by adjusting swim speed in response to head currents, field-based tests of these predictions are limited. We used fine-scale acoustic telemetry and computational fluid dynamics (CFD) modeling to track adult sea lamprey (*Petromyzon marinus*) migrating through a shallow coastal river and evaluated how movement speeds varied with environmental conditions and individual traits. Swim speed increased with head current velocity, while ground speed remained constant, supporting the hypothesis that lampreys regulate swim effort to maintain a fixed migration pace. The average ground speed closely aligned with the predicted optimal of ~1 body length per second. Additionally, both swim and ground speeds declined slightly in deeper water, potentially reflecting a trade-off between movement efficiency and predator avoidance. These findings provide field-based support for theoretical models of energy optimization and underscore how migratory fish adaptively adjust behavior to local hydrodynamic conditions. Our results highlight the value of high-resolution tracking and modeling in revealing the behavioral strategies that underlie efficient migration.

INTRODUCTION

Natural selection will favor animals that move efficiently. Accordingly, energy-saving tactics are a prominent feature of fish migration strategies, shaping behavior, physiology, and biomechanics (Alerstam et al., 2003; Dingle & Drake, 2007). When fish migrate upstream through rivers to spawn, the persistent downstream flow of water imposes a substantial energetic cost (Goodwin et al., 2014; Hintz et al., 2023; Nestler et al., 2012). In coastal rivers, this journey involves navigating through complex and dynamic energy landscapes typified by shifting water velocities and flow directions while attempting to conserve energy reserves for gamete production and reproductive behaviors (Lennox et al., 2016; Shepard et al., 2013). Thus, efficient navigation strategies are theorized to include tactics that minimize the cost of swimming against variable head currents.

Two related but competing theories predict how a migrating fish might minimize energy expenditure in the face of variable head currents by altering swim speed. Trump & Leggett (1980) offer a mathematical model that predicts minimum energy expenditure when a fish modulates its swim speed to maintain a constant ground speed across most water velocities, slowing and accelerating in concert with the current. The model relies on the assumption that energy expenditure is an exponential function of swim speed, implying the cost of transport increases rapidly at higher current speeds. Notably, the model predicts an optimal ground speed of ~1 body length per second (BL s^{-1}) in most conditions. More recently, Brodersen et al. (2008) used findings from swim tunnel respirometry to derive a model with a power function relationship between energy cost and swim speed. They too predict increasing swim speed in faster currents; however, the optimal strategy involves also increasing ground speed to move quickly through velocity challenges. These models are often used to explain observed ground speeds in field studies where measurements are averaged over large distances (e.g., Brodersen et al., 2008; Zelalem et al., 2024) or to estimate optimal ground speeds in high current systems (Castro-Santos, 2006). With recent improvements in the accuracy and precision of acoustic telemetry systems, there is the potential to link fine-scale fish movements to environmental features that vary over seconds and minutes, yielding insights into short-term movement decisions during migration (Elings et al., 2024; Orrell et al., 2023). Nevertheless, we are aware of no explicit tests of these theories involving direct observation of fish migrating through shifting currents in open river channels.

In addition to moving efficiently, migrants also need to avoid predators, locate potential mates and spawning habitats, and sometimes feed, leading to migration strategies that incorporate trade-offs among multiple factors (Sabal et al., 2021). Consequently, route selection in rivers is not solely a function of minimizing the cost of swimming. For example, the sea lamprey (*Petromyzon marinus*) begins its spawning migration after 1-2 years of parasitic feeding on large-bodied fishes in the open-waters of large lakes or the ocean. This migration involves passage through coastal, estuarine, and riverine habitats, potentially spans hundreds of kilometers, lasts several months, and is fueled entirely by energy reserves (Moser et al., 2015). River selection is mediated by olfactory cues; specifically, attraction toward odorants (bile acids) released by conspecific larvae (Sorensen et al., 2005; Vrieze et al., 2010; Wagner et al., 2006a, 2009). Upon entering the riverine environment, they transition to swimming in the relatively slower velocities near the substrate until reaching suitable spawning grounds (Griffin et al., 2025; Holbrook et al., 2015). Recently, Griffin et al. (2025) observed sea lampreys following the thalweg scour channel in a relatively shallow reach (≤ 5 m deep) of a coastal river that passed through a wetland landscape. They hypothesized that migrants selected migratory paths along the greatest relative depth to ensure efficient navigation through complex multi-channel landscapes while simultaneously remaining in the deepest areas to avoid contact with nocturnal shoreline predators. However, this precludes movement through the lowest water velocities associated with the shallow river margins, and which are routes preferred by other fishes (e.g., sockeye salmon *Oncorhynchus nerka*, Hinch & Rand (2000); pallid sturgeon *Scaphirhynchus albus*, McElroy et al. (2012)). If sea lampreys in shallow rivers must rely on this navigational strategy that subjects them to the inherently faster flow of the thalweg, theory suggests they would evolve energetically conservative swim tactics to minimize the cost of transport (Alerstam et al., 2003).

The objective of this study was to quantify the swim and ground speeds of constantly swimming sea lampreys moving through a shallow coastal river and explicitly relate changes in movement speed to estimates of head currents encountered. To that end we coupled fine-scale acoustic telemetry tracking with a computational fluid dynamics model of the river that estimated the head current encountered for each step of the observed movement paths. Our goal was to ascertain whether the exponential model (Trump & Leggett, 1980) or the power function model (Brodersen et al., 2008) better predicted the changes in movement speeds observed in sea lamprey. Specifically, we tested the following hypotheses using linear mixed-effects models: (1) swim speed would increase when facing accelerating head currents (predicted by both models); and (2) ground speeds would either remain fixed (exponential model) or increase (power function model) when facing faster head currents. We also investigated whether ground speeds would average one body length per second as predicted by Trump & Leggett (1980). Finally, we explored the effects of within-individual traits (sex, size) and additional environmental variables (water temperature and depth) on the observed swim and ground speeds. These findings complement and extend the extensive movement analysis of these data provided by Griffin et al. (2025) focused on the sea lamprey navigational strategy and path selection.

MATERIALS AND METHODS

Study area

This study was conducted in the lower White River near Whitehall, Michigan, USA (43.42°N, 86.32°W), a 134-km tributary to Lake Michigan, from 21 May – 11 June 2021 (Fig. 3.1A). The study reach flowed through a wetland landscape dotted with trees and shrubs, and the channel exhibited a mostly sandy substrate with a relatively deep thalweg that meandered through shallow depositional areas where submerged aquatic vegetation emerged through late spring into early summer. Both channel depth (0.1 - 4.23 m) and width (31.7-58.5 m) were typical of medium-sized Great Lakes rivers. During the study discharge at the site varied from 10.59 – 19.54 m^3s^{-1}.

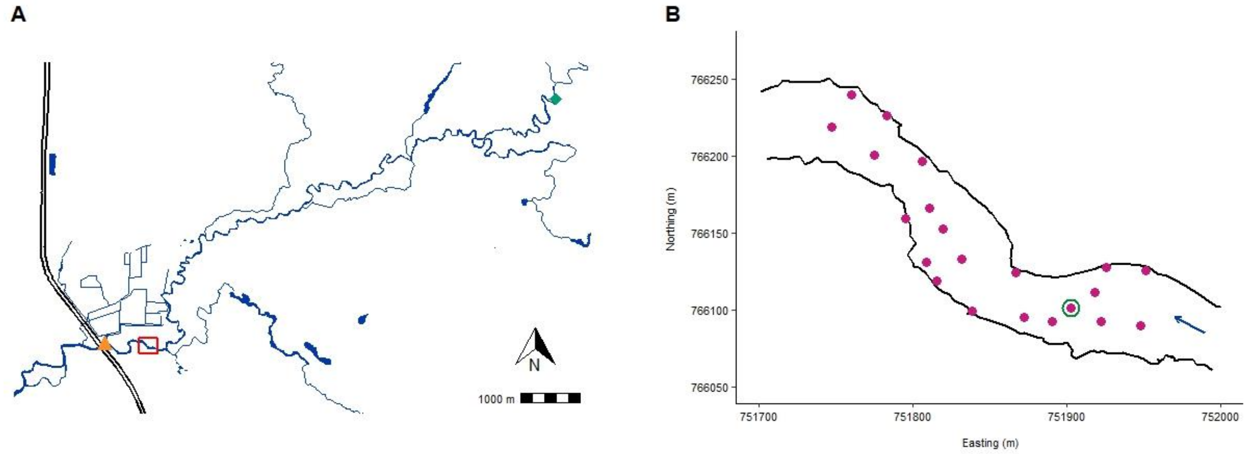


Figure 3.1. Study area and study site located on the White River, Michigan. (A) Map of the study area. The red rectangle indicates the study site. The orange triangle indicates the sea lamprey release point upstream of US Highway 31. The green diamond indicates the upstream receiver. (B) Acoustic receiver locations (pink circles) in the study site. Detections from the receiver surrounded in the solid green line were not included to estimate fish positions (see text for details). Water flow direction is indicated by the blue arrow.

Telemetry array

Sea lampreys were tracked with an acoustic telemetry array that covered a 0.5 river kilometer (rkm) reach comprising 18 HR2-180 kHz and 3 VR2W-180 kHz acoustic telemetry data-logging receivers (Innovasea, Nova Scotia, Canada) (Fig. 3.1B). HR2 receivers were capable of detecting pulse position modulation (PPM) and binary phase shift keying (HR) encoded signals, while VR2W receivers could detect only PPM signals. To enable time synchronization among receivers, HR2 units were equipped with integrated transmitters capable of emitting both HR and PPM signals at intervals of 25-35 s and 270-330 s, respectively. VR2W receivers, lacking integrated transmitters, were collocated with external transmitters (Innovasea model V9-2x). Each receiver was mounted to a 1.5 m length of 13 mm-diameter reinforcing bar with hose clamps ensuring the hydrophone was positioned above the metal bar. At deployment, a weighted grappling line was attached to the bar to aid in recovery, then the bar was pressed into the substrate. Receiver locations were recorded with a Trimble Geo XH with positional accuracy ± 10 cm.

Prior to data collection, the detection efficiency and positioning accuracy of the array was evaluated in a two-step process. First, a single acoustic transmitter (hereafter called tag) was drifted through the array both near the surface (n = 3) and the substrate (n = 3) to identify areas of low detection efficiency. A single location exhibited a detection efficiency of <47% which was improved to 87% by the addition of a supplemental VR2W receiver in the area. Second, we compared estimated positions from collocated sync tags associated with each receiver, stationary reference tags and mobile tag tests to post-processed GPS measured positions (Trimble Geo XH). Stationary reference tests consisted of periodically moving two PPM-encoded tags throughout the array during the study period (18 locations total, median test duration = 26.76 hr, Fig. S3.1). We conducted two further mobile tests, each involved drifting through the array with a dual HR and PPM-encoded tag affixed directly below the GPS antenna (mean test length = 781 s). Positional accuracy was calculated as the Euclidean distance between the array-estimated position and the known GPS location for all positions obtained from the stationary and mobile tests. Positional precision was determined by calculating the Euclidean distance between each unique estimated position and the median location.

Bathymetric mapping

River bathymetry was mapped with a kayak mounted side- and bottom-scan sonar unit with internal GPS (Humminbird Helix 7 G3, Johnson Outdoors, AL, USA) on 02 June and 20 July 2021 per methods described by (Kaeser & Litts, 2010). We paddled transects parallel to the shoreline approximately 2 m apart while recording at 455 kHz. Post-collection processing, including a slant-range correction, were performed with SonarTRX software (Leraand Engineering Inc., HI, USA) and XYZ (location and depth) files were exported. To address fluctuations in water level, we created a common vertical datum (NAVD 88) from bathymetry data and a continuous water level time series recordings from two water surface data loggers (Solinst, Ontario, Canada) recording water level every 15 minutes during the study period (Fig. 3.2A).

Flow model

Water velocity and direction at fish positions were derived from a FLOW-3D HYDRO (version 23.1.0.12; Flow-Science, New Mexico, USA) computational fluid dynamics (CFD) model of the White River. For turbulence modeling, we used the Renormalization-Group k – ε model due to its broader applicability relative to the standard k – ε model (FLOW-3D User Manual, 2020; Pope, 2000), particularly for low Reynolds number conditions and near-wall flows. The model utilized a first-order upwind approximation for the momentum advection equations. Cell pressures and the velocity field were updated with an implicit generalized minimum residual method solver.

Bathymetric data were transformed into a three-dimensional triangular boundary mesh using MATLAB (MathWorks, Massachusetts, USA), with a 0.5 m element side length, saved as an STL file and imported into FLOW-3D. Geometry discretization and mesh development employed fractional area-volume obstacle representation. The model domain was represented by a structured mesh, with uniform rectangular prisms ranging from 2 m to 0.5 m in size in both horizontal and vertical dimensions. Constant discharge was applied as the upstream boundary condition, while the downstream boundary condition was set to a fixed water surface elevation. Water surface elevation data were obtained from water level data loggers (see above), and discharge values were derived from acoustic doppler current profiler (ADCP) measurements and an upstream USGS gauge (041222000), which accounts for a drainage area ratio of 1.29 between the gauge site and study location. To validate the CFD model, ADCP surveys were conducted along four transects on 16 June and 27 July 2021 with river discharge of 9.1 and 10.55 m^3s^{-1}, respectively. For each validation discharge, depth averaged velocity profiles across each transect were compared to the ADCP data using mesh cell sizes of 2 m, 1 m, and 0.5 m. Velocity profiles from mesh cell sizes of 1.0 and 0.5 m matched ADCP data well, with all further simulations using the 0.5 m mesh resolution, resulting in a domain consisting of ~ 1.3 M elements.

To capture the discharges experienced by sea lamprey while migrating through the White River, six flow scenarios were developed that covered the range of observed discharges during the study (10.59, 11.68, 12.42, 14.98, 16.99, and 19.54 m^3s^{-1}). To optimize computational time, each model initially ran with a coarser mesh for 3000 s of flow time followed by simulation at the finer 0.5 m cell resolution for 1000 s until a quasi-steady state was reached as indicated by stabilization of total fluid volume within the domain. Preliminary post-processing of model outputs was conducted using TecPlot 360 (TecPlot, Bellevue, Washington). Model output included all cell center coordinates, velocity vector, and water surface elevation.

Lamprey capture and tagging

Sea lamprey were obtained from U.S. Fish and Wildlife Service operated traps located on several Michigan rivers during the spawning migration. After capture, subjects were held in 1385 L round flow-through tanks with supplemental aeration recycling Lake Huron water (100% water exchange every 4 h) at the Hammond Bay Biological Station (Millersburg, Michigan, USA). Subjects were transported to Ludington Biological Station (Ludington, Michigan, USA) and held prior to tagging and release in a 900 L recirculating tank (100% water cycle every 1.5 min). Use of sea lampreys and all tagging procedures were approved by the Michigan State University Institutional Animal Use and Care Committee via animal use permit PROTO202100013.

Subjects were surgically implanted with one of two types of high residence (HR) acoustic transmitters: depth and horizontal positioning V7P (Innovasea model V7P-2x, n = 20, mass: 1.4 g in air, 0.7 g in water; 7 mm D x 19 mm L; power output: 143 dB re 1 µPa at 1 m; pressure sensor accuracy: ±0.5 m; resolution: 0.075 m) or horizontal positioning only V5 (Innovasea model V5-2x, n = 40, mass: 0.74 g in air, 0.45 g in water; 5.7 x 5.66 mm D x 12.7 mm L; power output: 141 dB re 1 µPa at 1 m). Each tag was programmed to emit two varying pulse delay coded transmissions: PPM transmission (13 – 27 s) and HR transmission (1.8 – 2.2 s). Prior to tagging, pressure sensing V7P tags were calibrated in a pressurized PVC pipe to five levels (0, 3, 6, 9, and 14 PSI) equivalent to 0 – 10 m.

Sixty adult sea lamprey were tagged and released between 21 May and 11 June 2021 (mean ± SD; males: n = 27, total length = 49.8 ± 2.5 cm, mass = 260.0 ± 32.4 g; females: n = 33, total length = 51.4 ± 3.1 cm, mass = 290.0 ± 38.7 g). Tagging included first anesthetizing an individual by immersion in 0.9 ml L^{-1} AQUI-S 20 E solution (AQUI-S, New Zealand; final eugenol concentration: 100 mg L^{-1}). When the subject lost muscle tone but retained gill movement (anesthesia stage IV), it was removed from the anesthetic bath (mean time to stage ± SD, 1200 ± 164 s). Length and weight were recorded before placing the lamprey into a wet splint foam cradle. A tube placed into the buccal cavity maintained constant gill irrigation. The tag was inserted into the peritoneal cavity through a 10 mm incision approximately 10 mm off the ventral midline, and the incision was closed with two independent interrupted surgeon knots (4-0 Unify sterile PDO monofilament). The subject was then monitored in a holding tank after surgery (mean surgery duration ± SD, 185 ± 47 s). Once the individual regained equilibrium, resumed natural swimming and/or attached to the tank via oral disc, it was returned to the post-tagging section of the holding tank (mean recovery time ± SD, 1262 ± 731 s). Animal release involved transporting tagged lamprey in aerated coolers to the release site the following day, then acclimating to river water by half volume water exchange until the transport tank water temperature was within 2^{o}C of river temperature (mean acclimation time ± SD, 1115 ± 234 s). Fish were released at a road crossing 0.9 rkm downstream of the acoustic array between 09:00 and 10:00 local time (Fig. 3.1A).

Telemetry data processing

Lamprey positions were estimated with Fathom Position software (Innovasea, v1.8.2). After correcting each receiver's internal clock for time drift, each receiver was time synchronized to a single receiver via detection records of collocated tags. Time-difference-of-arrival of acoustic detections based on hyperbolic principles were used within the Fathom Position software to calculate positions (MacAulay, 2023; Smith, 2013). Raw positions were filtered using a three-stage approach: (1) removed positions where overall movement was consistently in the downstream direction (i.e., brief reversals and tortuous movement remained); (2) removal of positions outside the array grid; and (3) removal of positions that exhibited sudden, implausibly high-speed swimming with an immediate return to the prior trajectory (Almeida et al., 2002; Hardisty, 1979; Quintella et al., 2009). Fathom Position assigned each estimated position a unitless measure of error sensitivity, HPEs. HPEs rapidly degraded for positions outside of the array geometry leading us to exclude those positions. After removing those positions, median accuracy (calculated as the Euclidean distance between estimated and known positions) of stationary tests were 0.41 m and the two mobile tests were 1.28 and 1.34 m, respectively. Visual inspection of fish tracks within the array grid revealed outliers, e.g. positions on land or exhibiting quick large lateral movement with a return to the previous track. We used a filter based on movement speed to identify and remove these errant positions (per movement speeds reported in Almeida et al., 2002; Hardisty, 1979; Quintella et al., 2009). For each forward- and backward-looking step of the track, we calculated ground speed (GS). Positions exceeding 2.5 body lengths s-1 (BL s^{-1}) as calculated from both methods were removed and GS was recalculated. After this recalculation, no erroneous positions were identified, but some steps did exceed 2.5 BL s^{-1} with either forward- or backward-looking calculations. Next, we calculated the GS of the step when removing this flagged position and censored the position if the resulting GS was less than 2.5 BL s^{-1}. Again, forward- and backward-looking GS was calculated, and all were considered valid. Finally, tracks were visually inspected to ensure track integrity remained after filtering positions. The three-stage approach censored 7,765 of 12,218 animal positions: (1) 6,610 from stationary or persistent downstream movement; (2) 834 from outside the array boundary; and (3) 321 from movement speed.

Data analysis

Each fish position was assigned a standardized height from bottom, 0.108 m, equal to the median height observed from fish with depth sensing tags. Variables were extracted from the CFD model scenario that most closely resembled the discharge experienced during movement at each 3D position (e.g., Fig. 3.2B). For each step along the path, we calculated forward-looking ground speed and swim speed. We accounted for fish alignment to flow by decomposing water velocity and swimming trajectories into x and y vectors. Ground speed was calculated in the x and y direction, indicated by GSx and GSy, respectively. Swim speed in each direction was calculated by:

$$SS_x = GS_x – U; SS_y = GS_y – V$$

Where U and V are the components of water velocity in the x and y direction. Swim speed was calculated as:

$$\mathrm{SS_{step}} = \sqrt{\mathrm{SS_x^2} + \mathrm{SS_y^2}}$$

Water depth over the step was calculated as the mean water depth at the two measured positions. We removed steps where the mean water depth was < 0.3 m (n = 40 steps; < 1%). Bathymetry data in this area were identified a priori as unreliable during data collection (i.e., debris and obstructions preventing adequate sampling). Data used in the analysis included 4,357 steps from 56 individuals (Fig 3.2C).

Swim speed (BL s^{-1}) and ground speed (BL s^{-1}) were examined by fitting multiple linear mixed effects models (LMM) with the `nlme` package (Pinheiro & Bates, 2025). Fixed effects included water velocity 2D magnitude (BL s^{-1}), water depth (m), water temperature (^{o}C), and individual sex and total length (cm). Interactions between water velocity x depth and sex x total length were also included as fixed effects. Prior to model fitting, multicollinearity among predictors was assessed using variance inflation factors (VIF) and pairwise correlations. VIF values were below 1.5 for all predictors, both when all fixed effects were included and when the model was limited to water depth and velocity magnitude, indicating minimal multicollinearity (Table S1). Specifically, the VIFs for velocity and depth in the reduced model were 1.11 each. The correlation between velocity magnitude and depth was moderate (Pearson’s r = –0.32), further supporting the inclusion of their interaction in candidate models without raising concerns of redundancy or collinearity. All models used individual as a random intercept, and temporal autocorrelation between fish positions was modelled with a continuous autoregressive correlation structure of order 1. Model fits were compared with Akaike’s information criterion (AIC) (Burnham & Anderson, 2002). We used the `bbmle` package to calculate AIC and difference in AIC (ΔAIC) values (Bolker & R Development Core Team, 2023), with substantial support indicated by ΔAIC values < 2 (Burnham & Anderson, 2002). Model estimates for each effect and marginal and conditional R2 values were calculated with the ‘sjPlot’ package (Lüdecke 2024). Models with substantial support were validated with visual inspection of residual plots. All statistical analyses were conducted with R 4.2.2 (R Core Team, 2022b).

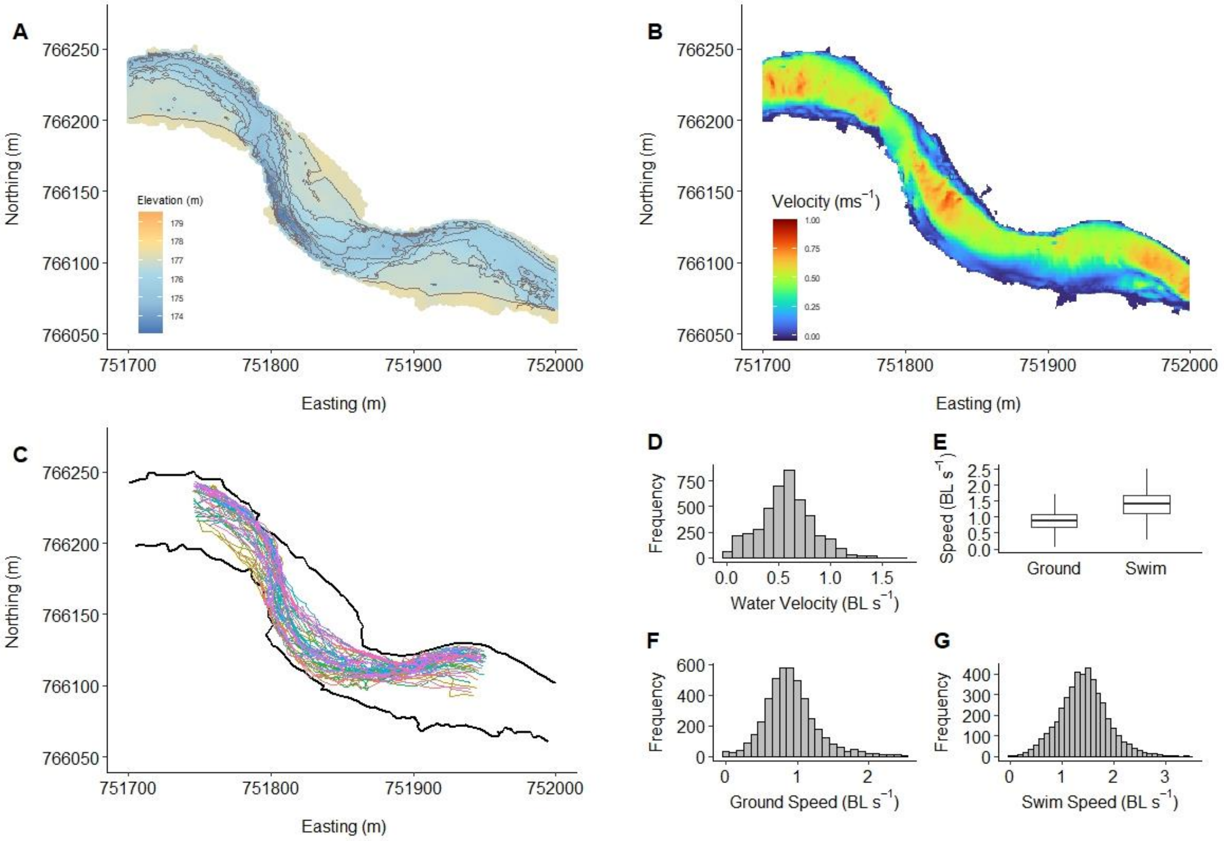


Figure 3.2. Study site bathymetry and water velocity, and sea lamprey tracks and swim speed and ground speed exhibited. (A). Study site bathymetric map. (B) Map of water velocity (m s^{-1}) at standardized height from bottom assigned to fish positions from 19.54 m^{3}s^{-1} discharge case. (C) Observed sea lamprey tracks (*N = 56)* after processing and filtering. Each color represents a distinct track (D) Frequency of water velocity (BL s^{-1}) subjects experienced. (E) Distribution of ground and swim speeds (BL s^{-1}); box indicates interquartile range (IQR), solid line corresponds to median; whiskers represent the highest and lowest value within 1.5×IQR. Frequency of (F) ground speeds (BL s^{-1}) and (G) swim speeds (BL s^{-1}) sea lamprey exhibited.

RESULTS

Swim Speed

All combinations of fixed effects resulted in 50 candidate models for swim speed. Model comparison based on ΔAIC revealed one candidate model with substantial support (ΔAIC for next top model = 4.50). The most supported model suggested a positive relationship between swim speed and head current water velocity (Prediction 1). In this model, swim speed was significantly related to the interaction between water velocity and water depth (Table 3.1; Fig. 3.3A, 3.3B). This top model explained a considerable proportion of the variation in swim speeds (marginal $R^2 = 0.30$). Swim speed was significantly and positively related to water velocity ($\beta = 1.05$, SE = 0.06, $p < 0.001$, Table 3.1; Fig. 3.3A). Increasing water depth was associated with slower swim speeds ($\beta = -0.04$, SE = 0.02, $p < 0.05$; Table 3.1; Fig. 3.3B). Additionally, the interaction between water velocity and water depth was also significant and negative ($\beta = -0.10$, SE = 0.03, $p < 0.001$, Fig. 3.4), suggesting that the positive effect of water velocity on swim speed was attenuated in deeper water. Mean sea lamprey swim speed was 1.43 BL s^{-1} (range 0.03 – 3.49 BL s^{-1}; Fig. 3.2E, 3.2G) which varied only slightly across individuals (sd = 0.15; Fig. S2A).

Table 3.1. Statistical outputs from the most supported linear mixed effects models for swim speed and ground speed. Parameter estimates with standard error in parentheses are shown for fixed effects only. * significant $p < 0.05$; *** significant $p < 0.001$

	Dependent variables:	
	Swim Speed	Ground Speed
Intercept	1.02*** (0.04)	1.05*** (0.03)
Depth	-0.04* (0.02)	-0.06*** (0.01)
Velocity	1.05*** (0.06)	
Velocity x Depth	-0.10*** (0.03)	
Observations	4357	4357
Marginal R^2	0.30	0.01
Conditional R^2	0.41	0.16

Ground Speed

Ground speed models from combination of all fixed effects produced 50 candidate models. One top model showed substantial support (ΔAIC for next top model = 5.91). This best candidate model revealed no relationship between head current water velocity and ground speed consistent with Prediction 2 for the exponential model. Mean sea lamprey ground speed was 0.92 BL s^{-1} (range: 0.01 – 2.48 BL s^{-1}; Fig. 3.2E, 3.2F). The most supported model included only the main effect for water depth ($\beta = -0.06$, SE = 0.01, $p < 0.001$, Fig. 3.3D), where each 0.1 m increase in water depth sea lamprey ground speeds slowed by 0.006 ± 0.002 BL s^{-1}. The top model did not include water velocity (Fig. 3.3C). Marginal R^2 value (0.01) suggested water depth had a small effect on ground speed. Conditional R^2 (0.16) revealed individual variation captured more variance in swim speed than water depth alone. Although individuals showed slight variation in mean ground speed (sd = 0.15, Fig S3.2B).

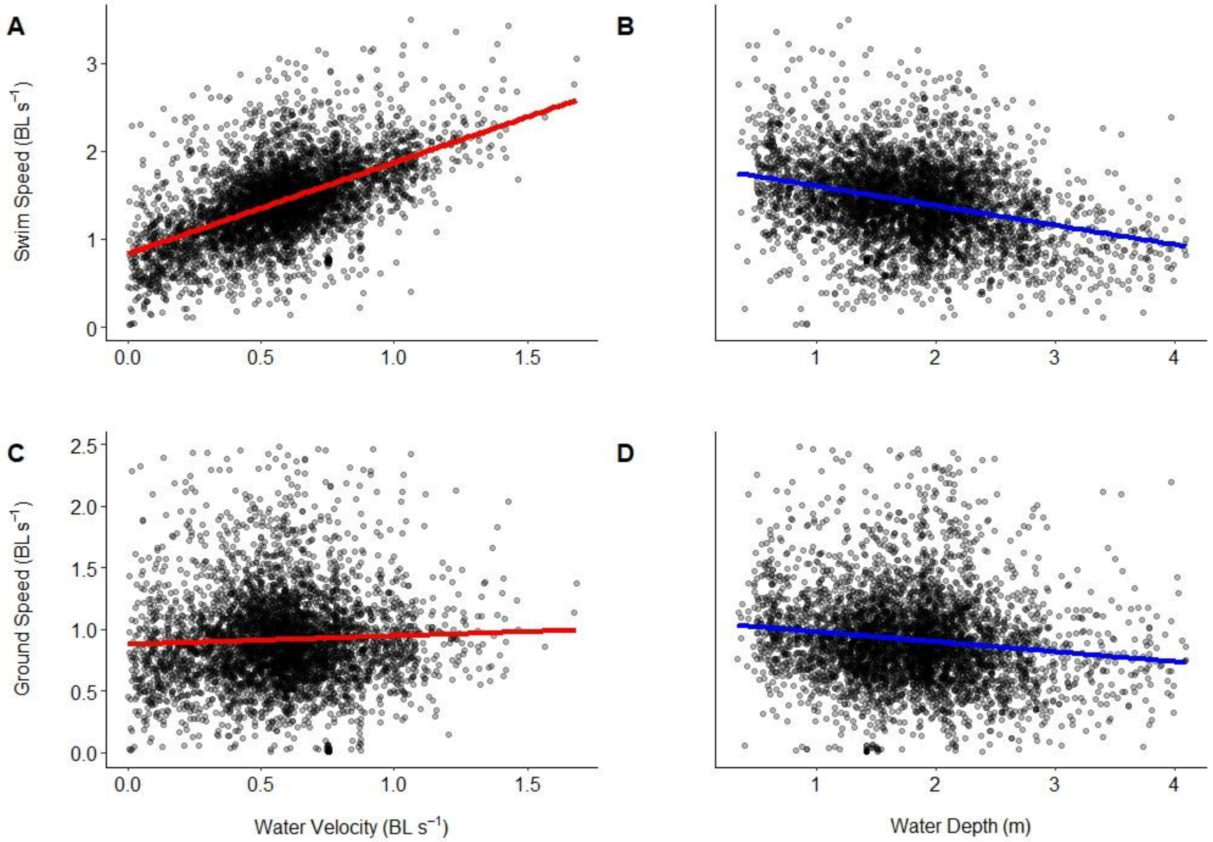


Figure 3.3. Relationships between sea lamprey swim and ground speeds (BL s^{-1}) and environmental variables. (A) Water velocity (BL s^{-1}) was significantly related to swim speed ($p < 0.001$). (B) Water depth (m) had a negative relationship with swim speed ($p < 0.05$). (C) Water velocity (BL s^{-1}) had no influence on ground speed ($p > 0.05$). (D) Water depth (m) had a slight negative relationship with ground speed ($p < 0.05$). Solid lines represent linear regression fits for each relationship.

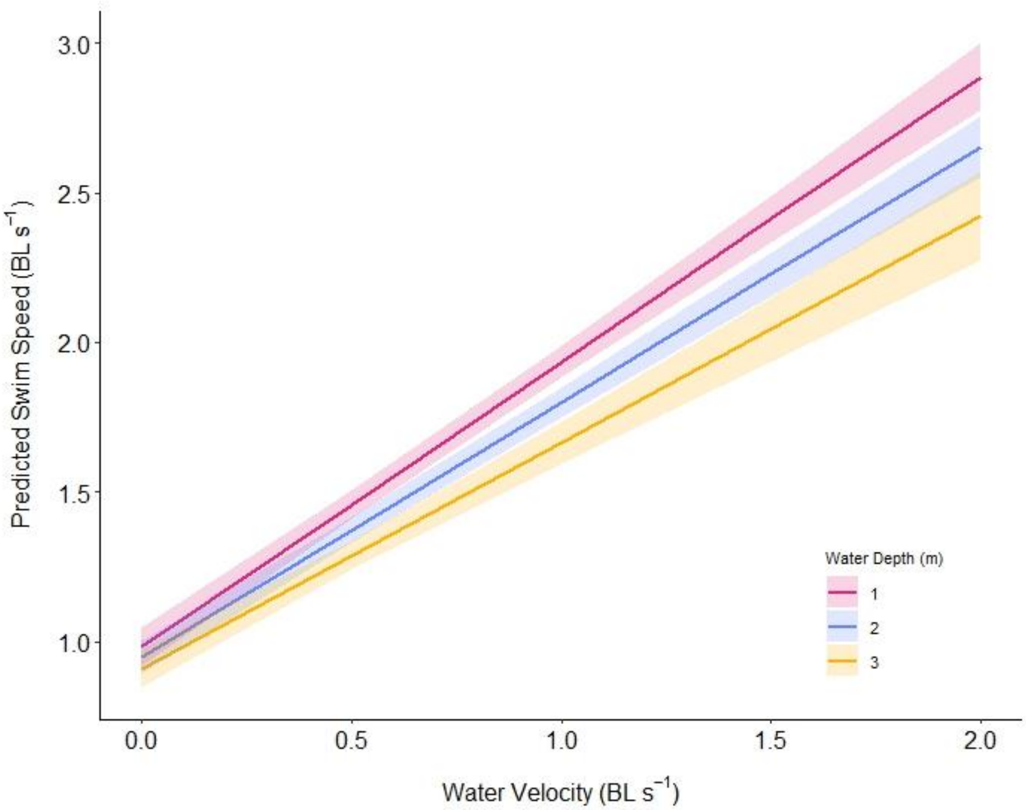


Figure 3.4. Predicted swim speed (BL s^{-1}) of migrating sea lamprey in response to water velocity (BL s^{-1}) at three representative water depths (minimum, mean, and maximum observed values). Predictions and 95% confidence intervals were estimated from top linear mixed effects model for swim speed.

DISCUSSION

Sea lamprey swim speeds increased as head current velocity increased, consistent with both power (Brodersen et al., 2008) and exponential (Trump & Leggett, 1980) relationships between cost of transport and swim speed (Prediction 1). The mean swim speed of 1.43 BL s^{-1} appeared sustainable during the period of observation (i.e., fish did not stop when moving through the study reach), though the observation period was relatively short. Transit time through the site ranged from 6.7-25.5 min, averaging 11.6 min. Observed maximum swim speeds ranged from 2-3 BL s^{-1}. Swim performance is commonly assessed in controlled conditions using swim tunnels and following a standardized incremental velocity test to establish the critical swim speed (Brett, 1964). Swimming below the U_{crit} is considered sustainable for long periods, as during migration. There currently are no published U_{crit} estimates for landlocked sea lamprey. U_{crit} estimates are available from forced swim tunnel tests with tagged anadromous sea lamprey (1.14 BL s^{-1}; Almeida et al., 2007) and Pacific lamprey (Mesa et al., 2003), each of which were lower than the observed sustained swim speeds for landlocked sea lamprey in this study. Swim tests in small tunnels can create stressful conditions that increase metabolic costs and lead to underestimation of U_{crit} (Hvas & Oppedal, 2019; Kern et al., 2018) and maximum swim performance (Kraskura et al., 2024) relative to behavior observed in the field. Our field data suggest the sustainable swim speed for migrating sea lamprey exceeded the U_{crit} from closely related species.

Our field data demonstrate that sea lampreys adjusted swim speed in response to changing head currents to maintain a steady ground speed during the spawning migration. This finding is consistent with the exponential relationship between cost of transport and water velocity for sea lamprey (Prediction 2 per Trump & Leggett, 1980). Notably, the observed mean ground speed was 0.92 BL s^{-1}, very near the optimum value predicted by Trump & Leggett's (1980) model of ~1 BL s^{-1}. Several previous studies report slower ground speeds for migrating anadromous sea lamprey: 0.76 BL s^{-1} (Quintella et al., 2009); 0.63 BL s^{-1} (Castro-Santos et al., 2017); 0.56 BL s^{-1} (Almeida et al., 2002); 0.43 BL s^{-1} (Andrade et al., 2007). These point-to-point values covered long distances between detections, assumed minimum distance routes, and likely included undetected rest periods (Almeida et al., 2002), each of which would contribute to underestimation of the true ground speed when swimming. An additional acoustic receiver placed 15.1 rkm upstream of our field site detected 24 of our fish on the night after movement through our main array. In the Great Lakes migrating sea lamprey are typically active between nautical twilight and nautical dawn (Haas et al., 2024; Meckley et al., 2017; Meckley, et al., 2014). If we assume that our sea lampreys were inactive from nautical dawn until nautical twilight, the estimated ground speed for animals that were detected on the upstream receiver averaged 0.82 BL s^{-1} (range: 0.50 – 1.13 BL s^{-1}), in keeping with the previous reports. We anticipate our animals made stops along the route or slowed to negotiate paths around natural obstacles common to the river (e.g., submerged fallen trees).

How might sea lampreys, solitary and nocturnal, perceive and react to shifting head currents without the ability to visually landmark? Sea lampreys possess a functional mechanosensitive lateral line comprising numerous neuromasts in solitary pits arrayed in lines along the head and trunk (Gelman et al., 2007). The trunk lateral line exhibits two neuronal populations that respond to opposing flow direction, with the magnitude of signal from the neuromast increasing as water velocity increases (Gelman et al., 2008). Functionally, this allows the animal to detect the direction and speed of water flowing along the trunk. If the animal maintains a steady tailbeat frequency as the head current increases, ground speed is reduced while the speed of the water (stimulus) along the body increases. An increasing signal from the neuromast may then elicit an increase in motor output to compensate, producing a steady ground speed (Daghfous et al., 2016). Ostensibly there would be an upper swim speed threshold beyond which the animal would begin to exhaust. The head currents experienced by the migrating sea lampreys in our study were not particularly rapid, ranging from 0.01 to 1.68 BL s^{-1} (mean: 0.58 BL s^{-1}). When faced with high water velocities or obstacles, sea lamprey switch from constant swimming to saltatory swimming characterized by alternating burst movements with resting by attaching to structures with the oral disc (Quintella et al., 2009).

Maintaining a steady ground speed suggests the distance moved per unit time during migration will be a function of the amount of time spent swimming. Thus, the timing of arrival to the spawning ground is regulated by activity schedule. Migration timing in sea lamprey is strongly influenced by water temperature trends. While migration has been described at 10 - 22^{o}C (Applegate, 1950; Hogg et al., 2013; Pereira et al., 2019; Stier & Kynard, 1986), peak migration was observed at approximately 15^{o}C in the Great Lakes basin (Binder et al., 2010). Further, consecutive days of increasing water temperature, rather than absolute temperature, was related to increased migratory behavior, while decreased activity was associated with decreasing daily water temperature (Binder et al., 2010). Maintaining a fixed ground speed could also have implications for the consequences of encountering barriers to upstream movement, both natural and anthropogenic. When migrating sea lampreys encounter an obstacle, many experience delay, but few reverse downstream or abandon the river (Almeida et al., 2002; Castro-Santos et al., 2017; Davies et al., 2021). The time delay experienced while attempting to pass barriers would not be recuperated by increasing ground speed, potentially reducing the time available to find mates and spawn (Johnson et al., 2015). In the Great Lakes, home to the sole invasive population of sea lamprey, barriers erected low in watersheds are used to block upstream movement. Encountering a barrier low in the river system suggests less energy expended on swimming, thereby increasing time and energy to invest in gametes and reproduction (Beamish et al., 1979; Johnson et al., 2015; Moser et al., 2015; William & Beamish, 1979).

Swim speed was reduced in the deeper parts of the river, accompanied by a small decrease in ground speed. The top swim speed model revealed a significant interaction between water velocity and depth, where swim speeds increased more steeply with rising water velocity in shallow areas compared to deeper areas. In deeper zones, sea lampreys exhibited less pronounced increases in swim speed. This pattern likely reflects a behavioral strategy to minimize energy expenditure while maintaining an effective migration pace.

In a prior analysis, Griffin et al. (2025) observed migrating sea lamprey in relatively shallow coastal rivers utilizing thalweg scour channels to safely and efficiently navigate through hydraulically and geomorphologically complex environments. In addition to providing a navigational ‘roadmap’, they proposed moving in the deepest areas of the channel may also be safer, reducing exposure to nocturnal predators whenever the thalweg meanders close to the shore (Cochran, 2009 Gallagher et al., 2017; Gaynor et al., 2019; Harvey & White, 2017). Luhring et al. (2016) observed migrating sea lamprey accelerating in a shallow river when exposed to conspecific chemical alarm cue, an odor that is released from damaged tissue when sea lampreys are wounded by predators (Bals & Wagner, 2012; Wagner et al., 2023). If acceleration is a response to a perceived increase in risk, here, deceleration may have been associated with a perceived increase in safety when the animal moved into deeper areas. This would lead to the expectation of slower average ground speeds in deeper rivers, if the animal continued to transit through the deepest parts of the channel. However, Holbrook et al. (2015) monitored Great Lakes sea lamprey movement paths in a deeper river did not observe a preference for movement in the deepest areas. Rather, they observed more movement nearer the sides of the channel where the depths were similar to the deeper areas of the White River. It is possible there is a threshold depth that represents safety, and if deep enough, the animal transitions to moving in areas with lessor head currents to reduce the energetic cost of migration.

Sea lamprey upstream migration tends to coincide with high discharge events (Almeida et al., 2002; Morman et al., 1980; Moser et al., 2015). During these flood events, adjusting swim speed to maintain an optimal ground speed through high velocity flows could deplete energy stores more quickly. More frequent resting events during floods could allow for recovery and maintain upstream movement (Quintella et al., 2009). Alternatively, avoiding areas of relatively higher water velocity could reduce cost of transport during high discharge. Movement paths during flood events may shift toward the riverbanks to move through relatively lower water velocities, similar to movement paths chosen in a deep river (> 5 m) (Holbrook et al., (2015)). An important caveat to our findings is the fact that our study took place during an unusually dry spring. Discharge during the nights data were collected ranged from 10.59 – 19.54 m^3s^{-1}. Typical peak spring discharges in the White River that we may anticipate elicit more upstream movement by sea lamprey are 23.78 - 28.60 m^3s^{-1}.

An integral component of this study was the utilization of continuous fine-scale fish tracking, which allowed us to capture high-resolution movement data that exclusively reflects active swimming behavior. By focusing solely on continuously swimming sea lamprey and excluding periods of rest, our approach provides a more ecologically relevant assessment of migratory performance compared to traditional point-to-point and mark-recapture methods and allows for the direct observation of unconstrained and volitional movement. The integration of readily available computational fluid dynamics models to estimate localized water velocities and depths further enhanced our understanding of how environmental factors influence swimming behavior rather than relying on mean head current values. This methodological framework enabled us to directly compare environmental conditions with behavioral adjustments, thereby shedding light on the varied strategies sea lamprey use to optimize energy conservation. New approaches are emerging that suggest fine-scale acoustic telemetry data can be used to estimate swim performance metrics (e.g., U_{crit}) in nature (e.g., Hassan et al., 2022). We anticipate these approaches may lead to a more accurate understanding of natural swim behavior.

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APPENDIX

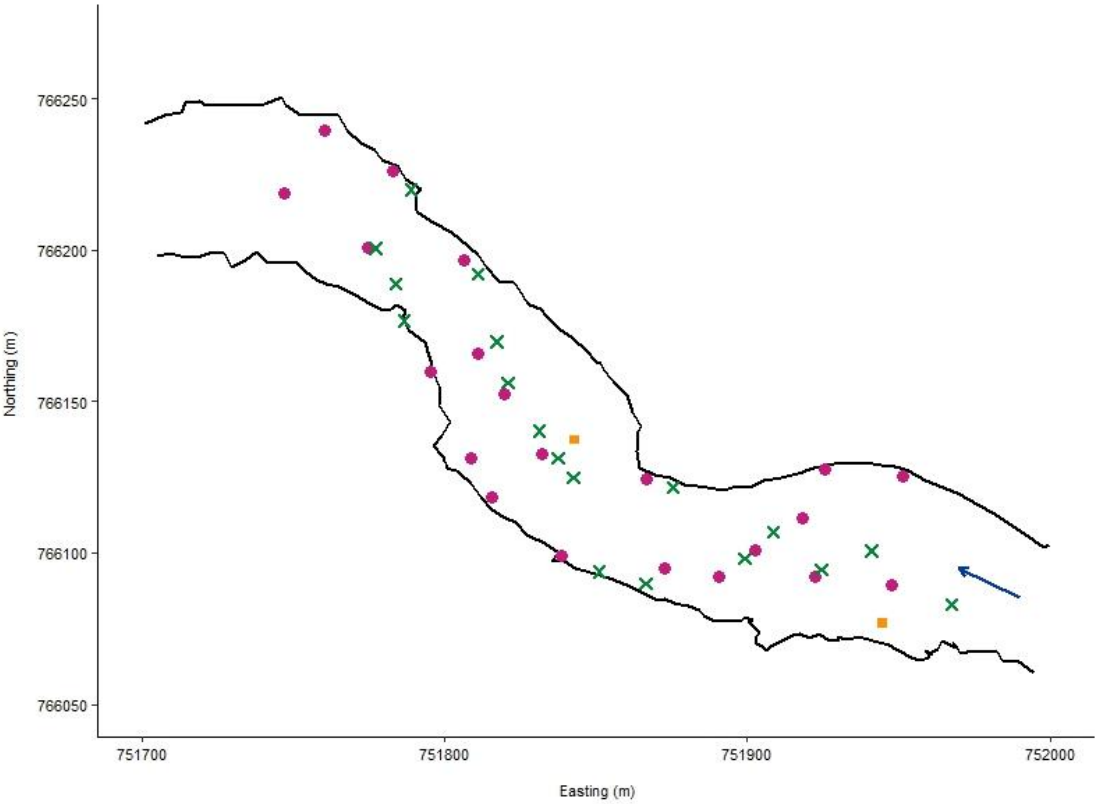

Figure S3.1. Location of acoustic receivers, reference tests and water surface data loggers in the study site. Acoustic receivers are indicated by pink circles. Stationary transmitters used to evaluate array accuracy and precision are indicated by green crosses. Two water surface level data loggers are shown as orange squares. Water flow direction is indicated by the blue arrow.

Table S3.1. Variance inflation factors (VIF) for predictors in ground speed and swim speed models.

Full model		Reduced model	
Main Effect	**VIF**	**Main Effect**	**VIF**
Depth	1.127544	Depth	1.113803
Velocity 2D mag	1.405886	Velocity 2D mag	1.113803
Sex	1.155677		
Length	1.201706		
temperature	1.297679		

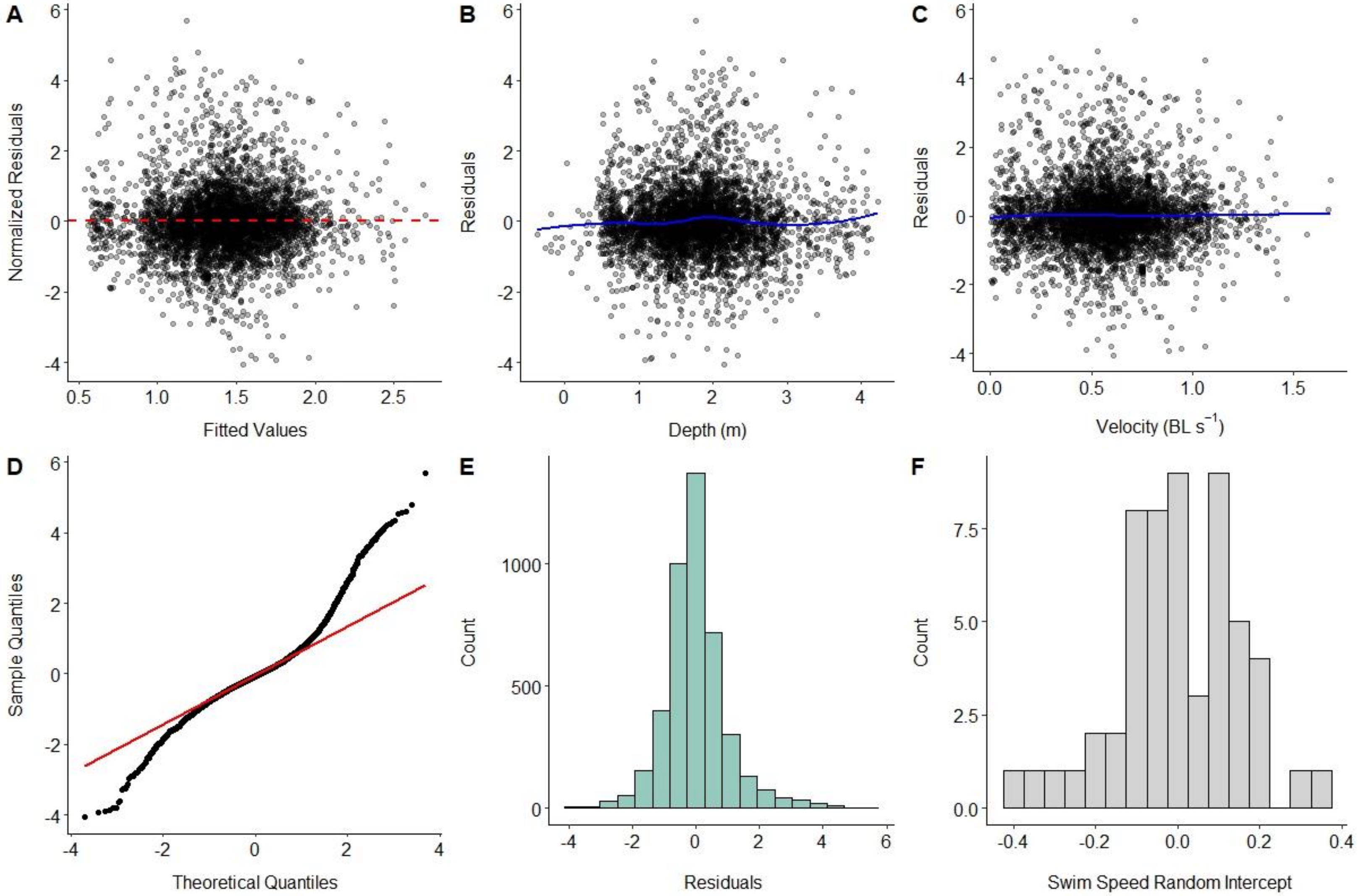

Figure S3.2. Diagnostic plots used to validate the most supported swim speed model. (A) Normalized residuals plotted against fitted values. (B) Residuals plotted against depth (m). (C) Residuals plotted against velocity (BL s^{-1}). (D) Quantile-Quantile plot of sample quantiles versus theoretical quantiles. (E) Histogram of the residuals. (F) Histogram of the random intercept values.

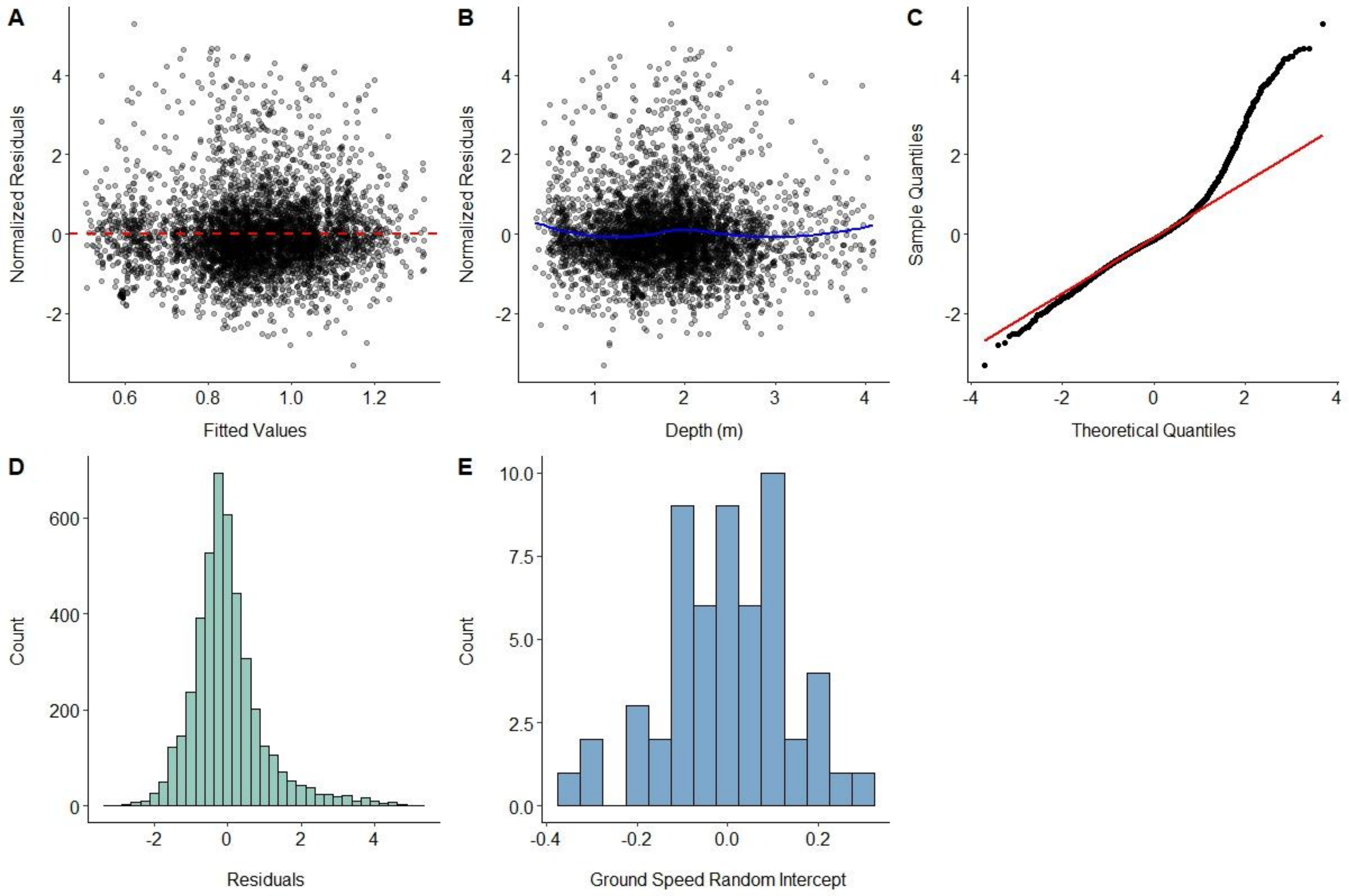

Figure S3.3. Diagnostic plots used to validate the most supported ground speed model. (A) Normalized residuals plotted against fitted values. (B) Residuals plotted against depth (m). (C) Quantile-Quantile plot of sample quantiles versus theoretical quantiles. (D) Histogram of the residuals. (E) Histogram of the random intercept values.

CHAPTER 4

SEA LAMPREY AVOID RISK OVER PRIORITIZING SAFETY WHEN USING ODOR-GUIDED RHEOTAXIS TO AVOID PREDATION RISK WHILE MIGRATING IN RIVERS

ABSTRACT

Migratory animals often face increased predation risk, especially where physical constraints funnel movement through predictable locations where predators gather. For riverine fishes, these constraints simultaneously shape the spatial structure of chemical cues that can inform predator avoidance. We investigated how migrating sea lamprey (*Petromyzon marinus*) respond to spatially localized risk by analyzing fine-scale movement paths in the presence and absence of conspecific alarm cues. Exposure to alarm cues produced structured and reversible changes in movement consistent with odor-guided rheotaxis: sea lampreys initiated an intensive search phase characterized by reduced ground speed and increased turning, then resumed typical migratory behavior after passing the odor source. When selecting routes around the alarm cue source, lampreys did not prefer deeper, potentially safer paths; rather, they made contralateral turns relative to plume position, suggesting immediate avoidance of danger over prioritization of habitat features that indicate greater safety. These findings highlight the importance of structured chemical information in aquatic environments, enabling migrants to effectively navigate predation risks without abandoning migration. This behavioral flexibility underscores the potential for leveraging chemical cues in conservation and invasive species management, but the environmental context should be carefully considered.

INTRODUCTION

Migration enables animals to exploit seasonally available resources for feeding and reproduction that are separated by large distance (Alerstam et al., 2003; Dingle, 2014; Fudickar et al., 2021). The risks of migration revolve around energetic costs (either cost of transport or total energy expended) and exposure to heightened predation (Crane et al., 2024; Goodwin et al., 2014; Hintz et al., 2023; Lennox et al., 2016; Lima & Bednekoff, 1999; Nestler et al., 2012). Migrants often must traverse environments where the types, densities, and hunting strategies of predators are uncertain, complicating risk assessment (Sabal et al., 2021). Predation risk becomes acute where migration pathways are geographically or biologically constrained, such as within river confluences or routes dictated by homing behavior (Bouchet et al., 2015; Cohen & Satterfield, 2020). Many predators time their movements to arrive in these places where migrants are funneled into relatively small spaces (Bouchet et al., 2015; Cohen & Satterfield, 2020; Furey et al., 2018). For example, brown bears (*Ursus arctos*) travel many kilometers to intercept migrating salmon (*Oncorhynchus spp*) (Glenn & Miller, 1980), even visiting multiple spawning sites to exploit various spawning populations (Deacy et al., 2016). Grey wolves (*Canis lupus*) began their movement before caribou (*Rangifer tarandus*) to intercept the caribou prior to reaching the calving grounds, then tracked the caribou on their outmigration to wintering grounds (Michelot et al., 2024). Natural selection should therefore favor migration strategies that incorporate effective tactics to detect, assess, and respond to predation risk in the places where predators gather.

Fishes that migrate through rivers and estuaries often do so under significant spatial limitations—narrow channels, high flows, and persistent obstacles – all act to constrain where fishes may move (Fullerton et al., 2010). Predators, both aquatic and terrestrial, exploit these constraints (Bouchet et al., 2015; Kennedy et al., 2016; Kiffney et al., 2006). Kennedy et al. (2016) found the piscivorous striped bass (*Morone saxatilis*) was consistently associated with physical discontinuities such as a sandbar and confluence. Migrating Atlantic salmon (*Salmo salar*) smolt predation rates increased 4.8-fold and 9.0-fold through impoundments and the estuary, respectively, compared to free-flowing reaches, and 88% of estuarine predation events were attributed to mammals (Mensinger et al., 2024). Within these often turbid or structurally complex aquatic environments, non-visual sensory modalities, especially olfaction, become paramount for risk assessment (Ferrari et al., 2010). Fishes rely heavily on chemical cues, including alarm cues released from injured conspecifics and kairomones passively released by predators, to detect and avoid areas of heightened risk (Ferrari et al., 2010; Wisenden et al., 2004). These cues elicit innate anti-predator responses such as avoidance, reduced activity, or increased vigilance at first detection of the odor (Ferrari et al., 2010).

In rivers and estuaries, the physical dynamics of flowing water impose a useful structure on chemical information. Cues are carried downstream from their source via advection, forming turbulent plumes with a discernible spatial structure (Vickers, 2000; Weissburg, 2000). This structure transforms chemical presence into spatially explicit information contained in odor concentration, plume shape, and flow direction that fish can exploit for navigation using odor-guided (aka odor-gated) rheotaxis (Coombs et al., 2020; Weissburg, 2000). This behaviour involves orienting relative to two sources of information: turning into the head current (rheotaxis) which contains directional information as to the location of odor source, augmented by lateral movements guided by odor detection within the plume. This process often involves two phases. Initial odor detection, which may be sporadic in turbulent flow subject to large eddies, elicits extensive movement in the upstream direction (e.g., lobsters orienting to food odor (Moore et al., 1991), larval horseshoe crabs orienting to habitat odor (Butler & Tankersley, 2020)). As the animal nears the source of the odor, it engages in intensive search characterized by slower speeds and increased turning, allowing localization of the odor source (Moore et al., 1991; Svensson et al., 2014). The strategy is most effective when the animal continuously attends to the directional cue first (water flow) rather than turbulence-induced changes in odor concentration (Vasey et al., 2015). Thus, the very physical constraints and flow dynamics of riverine environments that concentrate migrants and elevate predation risk simultaneously provide the structured chemical information landscape necessary for migrants to navigate around localized threats without abandoning their migratory goal.

The sea lamprey (*Petromyzon marinus*), a non-homing vertebrate (Bergstedt & Seelye, 1995; Waldman et al., 2008) possessing a well-developed olfactory system crucial for mediating key life history events (Buchinger et al., 2015), offers a compelling model for investigating olfactory navigation under predation risk during migration. Following a parasitic phase in marine or large lake environments, sub-adult sea lampreys migrate into rivers to spawn, a solitary journey fueled entirely by stored energy reserves (McCann et al., 2018; Moser et al., 2015). Their predominantly nocturnal and near-substrate swimming behaviour during migration likely minimizes exposure to diurnal, visually oriented predators (Almeida et al., 2002; Binder & McDonald, 2007; Griffin et al., 2025; Holbrook et al., 2015) but necessitates reliance on non-visual senses and potentially increases vulnerability to epibenthic predators (Boulêtreau et al., 2020). When exposed to conspecific alarm cue in rivers, sea lamprey exhibit context-dependent responses. When the odor is avoidable (a plume emitting from a single location), migrants show spatial avoidance, moving laterally to bypass the source (Hume et al., 2015; Imre et al., 2010; Wagner et al., 2011, 2023). However, if the cue represents an unavoidable threat (e.g., bank-to-bank activation), they accelerate upstream movement through the risky area (Luhring et al., 2016). Notably, when encountering the alarm cue under either context, migrants did not reverse direction nor abandon the river system. Rather, they continued upstream movement (Hume et al., 2015; Luhring et al., 2016; Wagner et al., 2011). Sea lampreys demonstrate odor-guided rheotaxis to navigate towards attractant cues (Johnson et al., 2012). Larval odors guide migrants to suitable spawning grounds (Sorensen et al., 2005; Vrieze et al., 2010; Wagner et al., 2006a, 2009), and adult male pheromones attract females to nests (Johnson et al., 2009, 2012). This capability for precise olfactory navigation towards attractants, combined with the strong, threat-sensitive avoidance of alarm cue suggests the capacity to avoid alarm cue plumes via odor-guided rheotaxis (Wagner et al., 2023).

When presented with multiple routes around the localized threat, which path should the migrant take? Alternative routes often differ in environmental context that can influence the outcome of a predator-prey interaction. The landscape of fear theory posits that spatial variation in perceived predation risk shapes prey behaviour, a trade-off between reducing vulnerability and other fitness-enhancing tasks (Gaynor et al., 2019; Laundré et al., 2010; Palmer et al., 2022). Superimposed is the landscape of safety, where areas of refuge or reduced detection probability varies in space. Theory predicts prey navigational decisions should involve integrating information from both perceived risk and perceived safety (Jordan & Ryan, 2015). MacKay et al. (2021) found crayfish (*Faxonius rusticus*) used both safety and fear cues in habitat selection when exposed to alarm cue. Theoretical work on cue prioritization suggests that the reliability and information content of available cues are key determinants of behavior. While cues indicating safety may often be more valuable during periods of low risk, fitness maybe in improved when using cues that indicate immediate, precise danger when risk is high (Luttbeg et al., 2020). Under nominal conditions, sea lamprey choose routes that balance safety with energetic efficiency, migrating along the bottom of the deepest portion of a shallow (<5 m) river (Griffin et al., 2025). Thus, if sea lampreys prioritize safety cues, we would expect a preference for deeper routes around the alarm cue source; if they react to danger cues first, we might observe route choice based on plume avoidance, regardless of depth.

In the present study, we examined fine scale movement paths of migrating sea lamprey exposed to midstream alarm cue (n = 33) or control (n = 39) treatments in the White River, MI, USA to address two main questions. First, how do sea lampreys navigate around an area of high predation risk when migrating in rivers? We hypothesize that sea lampreys use odor-guided rheotaxis in response to alarm cue plumes, including an intensive search period when detecting the alarm cue, characterized by: (1) extensive movement paths aligned with the river's thalweg (per Griffin et al. 2025) at distance from the odor source (P1); (2) a reduction in ground speed (P2) and greater rates of turning (i.e., more tortuous paths) as it approaches the alarm cue source (P3), followed by a return to extensive movement after passing the head of the alarm cue plume (P4). We contrasted the predicted patterns of movement with the control condition (no alarm cue) where we expected continuous swimming at a fixed rate of speed while following the river thalweg, per the observations of Griffin et al. (2025). Second, when they encounter alarm cue, do they select paths around the risky area that prioritize attraction toward safety or simple avoidance of danger? We propose two competing hypotheses. If sea lamprey continue to prioritize safety in the face of apparent immediate danger, they should choose the deeper route around the alarm cue source. Alternatively, if they switch priorities to simply avoiding the danger through the most expedient route, we expect them to turn counter to the increasing odor concentration in line with the alarm cue source, resulting in paths that split around the odor source (i.e., fish on the left and ride sides of the cue source turn toward the banks as they swim past) and exhibit no preference for the deeper route.

MATERIALS AND METHODS

Study Area

The study took place in the White River near Whitehall, Michigan, USA (43.42°N, 86.32°W), a tributary to Lake Michigan, with an average discharge of 12.5 m^3s^{-1} (Fig. 4.1A). Fish were tracked through two acoustic telemetry arrays (hereafter called the main and upper arrays, Fig.4. 1C) covering a 0.58 rkm reach of the lower watershed that ranged 0.1 – 4.78 m in water depth and 31.7 – 58.5 m in width. The channel included sandy substrate with areas of uniform cross-sections and asymmetrical cross-sections, exhibiting a meandering thalweg within the straighter channel with depositional areas opposite the thalweg that increased in submerged aquatic vegetation density into the summer (Fig. 4.1B). The main array was placed through the reach with the mix of asymmetrical and uniform cross-sections while the upper array was deployed 0.15 rkm upstream of the main array where two river branches meet. The diverging branches rejoin the main river several km upstream, but the north branch contained the dominant flow and distinct thalweg, and the south branch was shallow and lower flow (Fig. 4.1B). Two acoustic receivers were placed upstream of the study site to monitor progress without disturbing the fine-scale telemetry arrays (Fig. 4.1A).

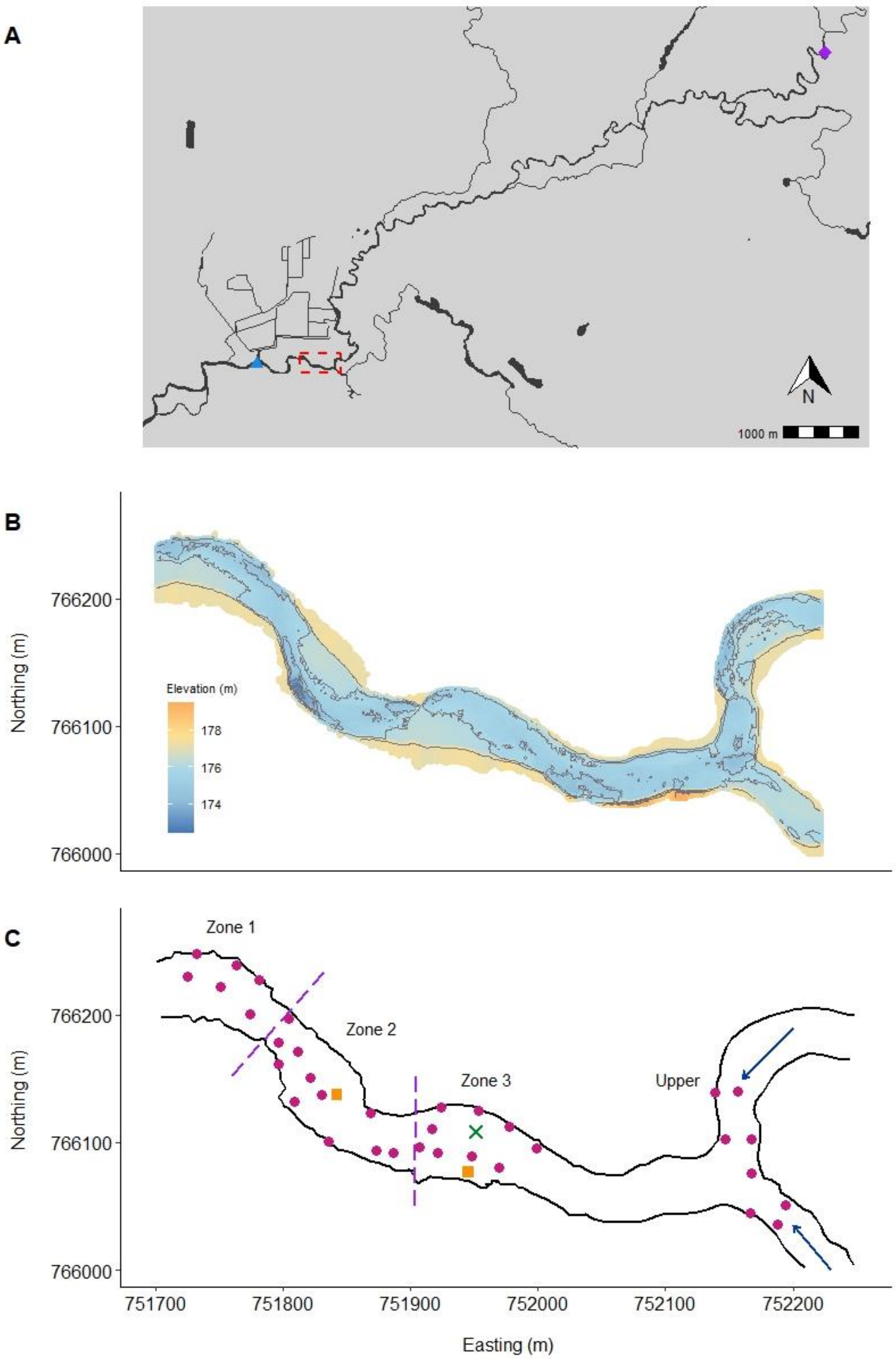

Figure 4.1. White River, Michigan study area and study site. (A) Map of the study area with the study site outlined in red dashed rectangle. Sea lamprey were released 0.9 river kilometers downstream of the

Figure 4.1 (cont'd)

acoustic array (blue triangle). Upstream receiver located at a canoe livery (purple diamond). (B) Bathymetric map of the study site. (C) Location of acoustic telemetry receivers (pink circles), odorant application site (green cross), and water surface level data loggers (orange squares). Flow direction is indicated by blue arrows. The main array was divided into three zones indicated by the dashed purple lines.

Telemetry array design and testing

Using two hose clamps, each receiver was affixed to a 1.5 m piece of 13 mm diameter steel reinforcing bar with threaded bolt welded to the top, ensuring the hydrophone was above the top of the bolt. During deployment, a 2 m weighted grappling line was attached to the rod and a t-bar device with female-thread was screwed onto the rod to press the rod into the substrate. The array was designed to create overlapping detection range necessary for fine scale positioning, with receiver placement adjusted for line-of-sight difficulties from channel morphology or natural obstructions (e.g., debris).

The initial array design was tested by drifting an acoustic transmitter (hereafter referred to as tag) through the array near the surface (n = 4) and near the substrate (n = 2). One receiver was repositioned to improve line-of-sight after diagnostic tests. Final receiver positions were recorded with a Trimble Geo XH (positional accuracy ± 10 cm). All receivers used in this study operated at 180 kHz. The main array included acoustic telemetry data-logging receiver models HR2 (18) and VR2W (8) (Innovasea, Nova Scotia, Canada). The upper array was comprised of 8 VR2W receivers spanning across the confluence and into each branch. All receiver models were capable of detecting pulse position modulation (PPM) signals, while HR2 receivers could also detect binary phase shift keying (HR) encoded signals. To aid in time synchronization, each receiver was associated with a collocated sync tag. HR2 receivers had self-contained sync tags that emitted an HR-type code every 25–35 s and a PPM-type code every 270–330 s, while VR2W receivers were deployed with an independent collocated tag (Innovasea model V9-2x), that emitted a PPM-type code every 270–330 s. Prior to animal release, one HR2 receiver was discovered partially detached from the steel bar. We recovered the receiver, confirmed operation, and redeployed to the array. Thus, all detection records and array performance metrics were limited to after this receiver was returned to the array.

We assessed the positioning performance by comparing the array estimated positions to pos-process GPS measured positions (Trimble Geo XH) of collocated sync tags, stationary tags, and mobile tags. Stationary reference tests involved periodically moving two tags in the main array (21 total locations, Fig. S4.1A; median test length = 91.92 hr, Table S1). Mobile tests were performed by drifting through both arrays with a tag affixed directly below the GPS antenna (n = 3, mean test length = 17.55 min, Fig1B). We calculated the Euclidean distance between array-estimated location and known GPS location to represent positional accuracy for all three types of tests. For stationary and sync tags, we calculated positional precision as the Euclidean distance between each unique estimated position and the median estimated position.

Bathymetric mapping

We recorded bathymetry data by slowly maneuvering a side- and bottom-scan sonar unit with internal GPS (Lowrance HDS Live-9, Navico, OK, USA) in transects parallel to the shoreline following protocol described in Kaeser & Litts (2010). Several transects were recorded on 14, 18, 20 and 26 July 2022. Bathymetry data were processed with BioBase software (BioBase, MN, USA) to output XYZ (location and depth) files. A continuous water level time series, collected with water surface data logger (Solinst, Ontario, Canada) every 15 min, was applied to all depth measurements to create a standardized vertical datum (NAVD 88, Fig. 4.1B).

Experimental subjects

We released 90 adult sea lamprey between 24 May and 16 June 2022 (45 males, 45 females; mean ± SD, total length = 50.8 ± 2.8 cm, mass = 278.9 ± 39.0 g). Experimental animals were captured during the spawning migration at barrier integrated traps on several Michigan rivers. Upon capture, lamprey were held at Hammond Bay Biological Station (Millersburg, Michigan, USA) in 1385 L round flow-through tanks that cycled Lake Huron water (100% water exchange every 4 h) with supplemental aeration. Subjects were haphazardly chosen from all captured individuals for transport to Ludington Biological Station (Ludington, Michigan, USA) where subjects were held prior to tagging and release in a 900 L recirculating tank (100% water cycle every 1.5 min). Use of sea lampreys was approved by the Michigan State University Institutional Animal Use and Care Committee via animal use permit PROTO202100013.

Tagging and release

Experimental subjects were randomly selected and surgically implanted with one high residence (HR) acoustic transmitter. Each tag was programmed with a variable delay for both code-types: PPM 13 – 27 s and HR 1.8 – 2.2 s. Sixty individuals were implanted with V5 tags which transmit horizontal position (Innovasea model V5-2x, mass: 0.74 g in air, 0.45 g in water; 5.7 x 5.66 mm D x 12.7 mm L; power output: 141 dB re 1 µPa at 1 m). Thirty lamprey received V7P tags which transmit depth via pressure in addition to horizontal position (Innovasea model V7P-2x, mass: 1.4 g in air, 0.7 g in water; 7 mm D x 19 mm L; power output: 143 dB re 1 µPa at 1 m). Each V7P tag was tested in a pressurized PVC chamber at 0, 3, 6 and 9 PSI (depths equivalent to 0 – 7 m). These values were used to create calibrated slope and intercept values for each tag to calculate depth from each raw transmitted value (pressure sensor accuracy: ±0.5 m; resolution: 0.075 m).

Tagging surgeries began by immersing subjects in a 0.9 ml L^{-1} AQUI-S 20 E solution (AQUI-S, New Zealand; final concentration 100 mg L^{-1} eugenol) until reaching stage IV anesthesia typified by loss of muscle tone but retaining gill movement (mean time to stage ± SD, 925 ± 190 s). We recorded length and weight, then placed the lamprey in a wet splint foam cradle with constant freshwater gill irrigation. Approximately 10 mm off the ventral midline and in line with the anterior insertion of the first dorsal fin, a 10 mm incision was made to insert the tag into the peritoneal cavity (mean surgery time ± SD, 129 ± 30 s) and closed with two independent interrupted surgeon knots (4-0 Unify sterile PDO monofilament). After tagging, animals were placed in a post-operative tank and monitored until regaining equilibrium and resuming normal activity such as natural swimming and/or attachment to the tank via oral disc (mean recovery time ± SD, 689 ± 250 s), then returned to the post-surgical area of the holding tank. Lamprey were transported to the release site the following day in aerated coolers. Fish were acclimated to river water by half volume water exchange (mean acclimation time ± SD, 26.8 ± 5.2 min) then placed into an in-river holding tank 0.9 rkm downstream of the acoustic array around 10 am local time (Fig. 4.1A). The holding tank was opened at 21:10 local time to allow animals to volitionally exit and migrate.

Alarm cue preparation

The alarm cue was extracted following procedures detailed in Bals & Wagner (2012). Briefly, we used Soxhlet extraction with adult male and female lamprey whole carcasses to derive the odorant. The main chamber of each Soxhlet extractor (2.08 m, Ace Glass Inc., NJ, USA) was loaded with 9 or 10 lamprey (mean mass per batch = 1943 g) and attached to a six-bulb water-cooled Allihn condensers. A 50:50 solution of 200 proof ethanol and deionized water was added to a 12 L solvent reservoir and headed to 75 – 80°C with a hemispherical mantle for a minimum of three cycles to produce ~ 10.2 L of alarm cue extract. After cooling overnight, each extract was stored at -20°C until use. To avoid cross-contamination, control and alarm cue treatments used separate carboys and tubing for storage and application in the river.

Field experiment

We used the most recent discharge record (m3 s-1) from an upstream USGS gauge (041222000) to calculate the pump rate required to activate 20% of the stream discharge to 0.5 PPM concentration by volume (mean pump rate = 65 mL min-1). Visual rhodamine dye test was used to confirm the targeted 20% of the stream channel would be activated downstream of application point. Control treatments pumped 50:50 DI H2O:ethanol, while alarm cue treatments pumped 50:50 alarm cue extract:ethanol. Trials were conducted from 24 May to 16 June 2022, with alarm cue (n = 5) and control (n = 5) treatments alternating nights to capture similar environmental conditions. For each trial, the in-river animal holding cage was opened at 2120 hours local to allow lamprey (n = 9 per trial) to exit of their own volition. Each odorant was pumped into the stream from four sources near the substrate for 4 h (2100 – 0100 hours) by two laboratory-grade peristaltic pumps (Masterflex model 7533–20, Cole Palmer) powered by a 12 V battery from a boat situated mid-channel near the upstream end of the main array (Fig. 4.1C).

Telemetry data processing and filtering

We used Fathom Position software (Innovasea, v2.4.1) to synchronize receiver time and estimate positions. We corrected the time drift of each receiver's internal clock and synchronized the detection records of each collocated sync tag to a single receiver to estimate fine scale positions based on time-difference-of-arrival (MacAulay, 2023; Smith, 2013). We used a three-stage approach to filter raw positions: (1) restricted to movement initiated downstream of the array on the night of release; (2) removed positions outside the river boundary; and (3) removed positions resulting from sudden, implausibly high-speed swimming followed by immediate return to prior trajectory (Almeida et al., 2002; Hardisty, 1979; Quintella et al., 2009).

After restricting positions to movement on the night of release and inside the river, visual inspection of fish tracks showed large lateral movement with return to prior path. We identified and removed these errant positions based on movement speed (per movement speeds reported in Almeida et al., 2002; Hardisty, 1979; Quintella et al., 2009). Positions resulting from forward- and backward-looking ground speed (GS) exceeding 2.5 body lengths s^{-1} (BL s^{-1}) were removed. We then recalculated forward- and backward-looking GS, but no positions exceeded the 2.5 BL s^{-1} from both calculations. However, some positions exceeded the threshold from calculations in either direction. Next, we calculated the GS of the step resulting from removing the flagged positions. If the GS of the resulting step was valid, the flagged position was removed. After 2 iterations, we recalculated forward- and backward-looking GS and all steps were considered valid. Track integrity was confirmed by visually inspecting the track after filtering positions. This three-stage approach removed 7,123 of 10,717 position: (1) 6,995 positions from holding station in the array (typically during daylight) or movement outside the night of release; (2) 12 from outside the river; and (3) 116 from movement speed.

Data analysis

Visual inspection of the tracks revealed three zones in the main array with different patterns between and within treatments. We assigned fish positions into one of these three zones or the upper array to investigate how movement metrics differed between treatments for each zone. The beginning of Zone 2 was defined as 200 m downstream of the odor source, and the beginning of Zone 3 was 60 m downstream of the odor source.

RQ1: how do sea lampreys navigate through an area of high predation risk when migrating in rivers?

We used separate linear mixed effects models (LMM) with the `nlme` package to determine how movement metrics differed between alarm cue and control treatments (Pinheiro & Bates, 2025). Dependent variables for each model were height above bottom (m), ground speed (BL s^{-1}) and tortuosity, where tortuosity is the ratio of the observed path length to straight line distance between start and end points. Fixed effects included treatment, zone and their interaction, and each model included a continuous autoregressive correlation structure of order 1 and random effect for individual. To investigate differences between zones within each treatment and between zones, we conducted pairwise comparisons on the estimated marginal means (EMM) for each zone with Tukey's adjustment for family-wise error rate and for each treatment with the `emmeans` package (Lenth, 2017). Models for vertical distribution were limited to pressure tagged individuals (alarm cue n = 13; control n = 11). Ground speed and tortuosity models included the whole dataset after filtering (alarm cue n = 33; control n = 39).

RQ2: when sea lamprey encounter predation risk, do they select paths that prioritize safety or danger cues?

To test for differences in lateral distribution between treatments, we estimated the point where each lamprey path crossed 117 transects using linear interpolation between the closest upstream and downstream position to the transect. Transects were created perpendicular to the river centerline (mean ± s.e.m. distance apart, 2.55 ± 0.06 m) with the `cmgo` package (Golly & Turowski, 2017), and each transect was crossed by a minimum of 60 fish. We first determined if sea lamprey were non-uniformly distributed across the river channel at each transect with randomization tests on each treatment condition described in Holbrook et al. (2015). Each transect was binned into ten segments of equal width, and sea lamprey was assigned to one of these bins for each transect. To assess whether the observed lateral distribution deviated from a uniform distribution, we performed a chi-squared goodness-of-fit test. The observed frequencies (χ^2obs) within each bin were compared to expected frequencies derived from a multinomial distribution assuming equal probability for each of the ten bins.

To evaluate significance, we generated 10,000 independent random samples from a multinomial distribution with ten intervals of equal probabilities to create a distribution of test statistics, χ^2null. We interpreted the p-value as the strength of evidence against the null hypothesis of a uniform lateral distribution across the river channel, with the following thresholds: $p < 0.01$ indicating strong evidence, $0.01 \leq p < 0.05$ indicating moderate evidence, $0.05 \leq p < 0.10$ indicating weak evidence, and $p \geq 0.10$ indicating no evidence.

To assess whether the lateral distribution differed between alarm cue and control treatments, we used Fisher's Exact test given the many bins with observed frequencies of 0. For each transect, we constructed a 2 × 10 contingency table, where the rows represented treatment and the columns represented the ten lateral bins. Observed fish counts in the alarm cue treatment were compared against expected fish counts from the control group, assuming no difference in lateral distribution between treatments. Fisher's Exact Test was performed separately for each transect, generating a p-value for each comparison.

To identify the transect at which lateral distribution significantly diverged between treatments, we modeled the probability of significance using a binomial regression. The dependent variable was whether Fisher's Exact Test for a given transect resulted in a significant difference (1 = significant, 0 = non-significant), and the independent variable was transect ID. This approach allowed us to estimate the transect where treatment effects became evident along the river channel.

To determine if sea lamprey chose a single path or split around the odorant, we calculated the normalized lateral distribution for each transect identified with the binomial regression. We used Hartigan's Dip Test (`diptest` package) to assess whether lateral distribution of each treatment exhibited multimodality with the null hypothesis of unimodality (Maechler, 2024).

We used single-tailed binomial tests to determine if sea lamprey consistently chose paths to the left, right or split around the odorant application point. Paths were labeled based on relative location at the application point (either closer to the north bank or south bank). A prior tracking study in the area revealed a close association with the north bank in this area (Griffin et al., 2025), therefore we chose a null proportion of 50/50 and an alternative hypothesis of bias towards the north bank.

All statistical analyses were performed in R (version 4.2.2). The significance level for all statistical tests was set at $\alpha = 0.05$.

RESULTS

After censoring to upstream directed movement on the night of release, positions from 72 individuals ($n_{AC} = 33$, $n_{CON} = 39$) were included in the dataset (Fig. 4.2). Positions from the main array included 3,005 total positions (n_{3D} = 882, $n2_{D}$ = 2,123). The upper array produced 577 fish positions (n_{3D} = 181, n_{2D} = 396).

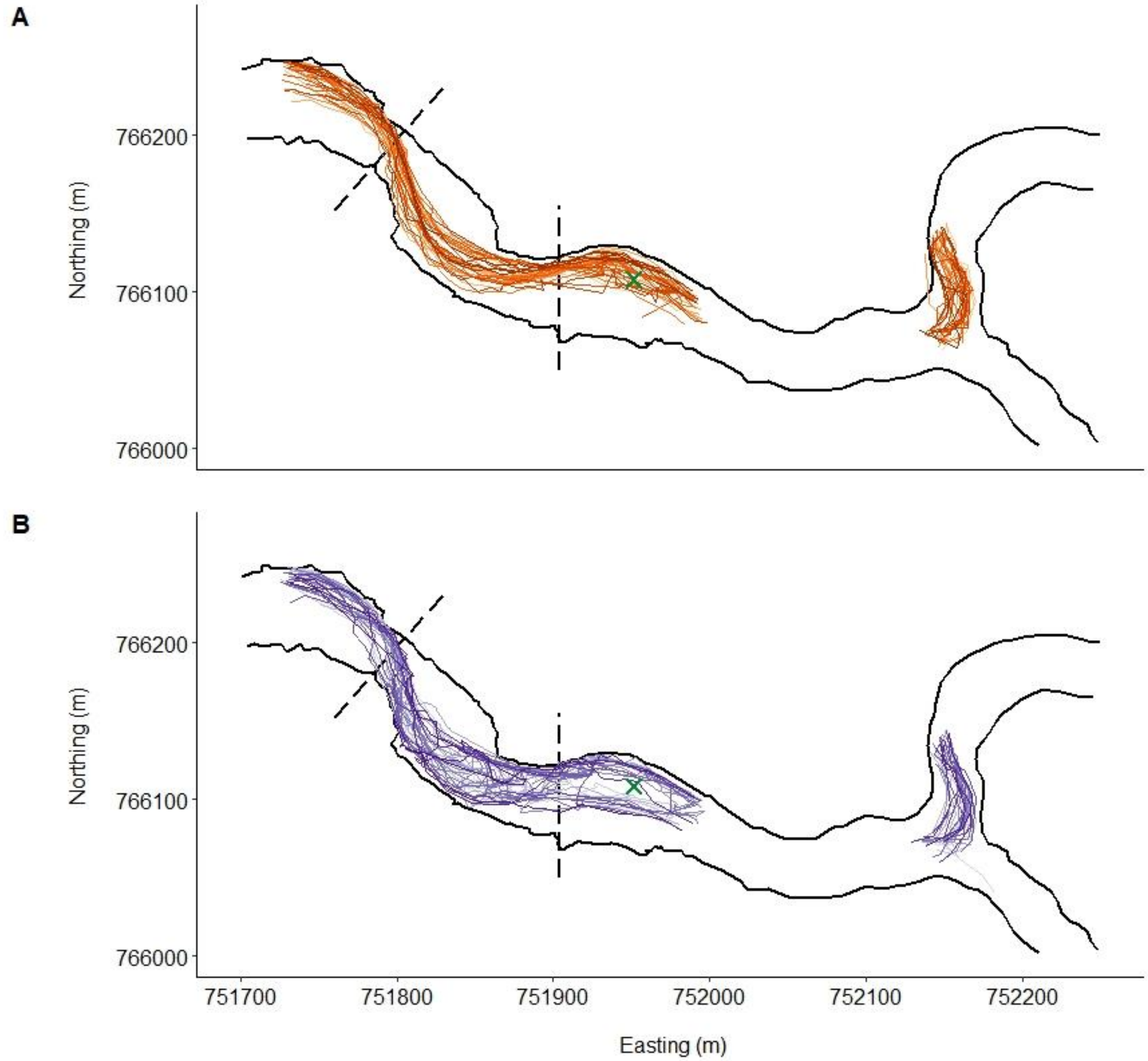

Figure 4.2. Sea lamprey tracks under two treatment conditions: (A) alarm cue and (B) control. Green x indicates the location of odorant application.

RQ1: how do sea lampreys navigate through an area of high predation risk when migrating in rivers?

Vertical distribution linear mixed effects model (LMM) had a significant effect for Zone 3 (Table 4.1). EMM showed sea lamprey in both treatments had a close association with the substrate across all zones (EMM range ± se: control = 0.03 – 0.34 m, alarm cue = 0.07 – 0.40 m, Table 4.2, Fig. 4.3A). There was no difference in height from bottom between treatments across all zones (all $p > 0.1$, Table. 4.3, Fig. 4.3A), but fish in both treatments were significantly closer to the bottom in Zone 3 than Zone 1 (β = -

0.21, $p < 0.05$, Fig. 4.3A). Pairwise comparisons between zones within treatments revealed sea lamprey in the control group were more closely associated with substrate in Zone 3 than the Upper array (mean difference = -0.31, $p < 0.01$, Table 4.4), with a trend towards lower height in Zone 3 relative to Zones 1 and 2 ($p = 0.15$ and 0.088 m, respectively, Table 4.4). Animals in the alarm cue group were also significantly lower in Zone 3 compared to Zone 2 and Upper array (mean differences = -0.29 and 0.33 m; both $p < 0.001$, Table 4.4). The LMM explained a modest portion of the variance (marginal $R^2 = 0.057$; conditional $R^2 = 0.137$), indicating that individual differences and autocorrelation accounted for more variability than height from bottom.

LMM for ground speed revealed a significant interaction between treatment and zone (Table 4.1). EMM showed that sea lamprey in the control condition maintained consistent ground speeds across Zones 1 - 3 (EMM range ± se: 1.07 – 1.09 ± 0.03 BL s^{-1}, $p > 0.05$, Table 4.2, 4.4, Fig. 4.2C), but slowed in the upper array (EMM ± se: 0.84 ± 0.03 BL s^{-1}, $p < 0.001$, Table 4.2, 4.4, Fig. 4.2C). Sea lamprey exposed to alarm cue had ground speeds 0.27 and 0.16 BL s^{-1} slower ($p < 0.001$) than control migrants in Zones 2 and 3 respectively (Table 4.3, Fig. 4.2C). There were no differences in ground speed between treatment in the Upper array (EMM ± se: control = 0.99 ± 0.03 BL s^{-1}, alarm cue = 0.90 ± 0.03 BL s^{-1}, $p > 0.05$, Table 4.3, Fig. 4.2C). The model accounted for 22% of the variance, but individual differences contributed significantly to the overall explanatory power of the model (conditional $R^2 = 0.676$).

LMM for tortuosity revealed no overall effect of treatment on tortuosity ($p = 0.915$), but a significant main effect of zone was detected with increased tortuosity observed in Zone 2 ($\beta = 0.13$, $p < 0.05$), Zone 3 ($\beta = 0.12$, $p < 0.05$) and the Upper array ($\beta = 0.20$, $p < 0.001$) compared to Zone 1 in the control group (Table 4.1). A significant interaction between treatment and Zone 2 ($\beta = 0.35$, $p < 0.001$) indicated that fish in the alarm cue treatment group exhibited markedly greater tortuosity in Zone 2 relative to sea lamprey in the control group (Table 4.1, Fig. 4.3B). No significant treatment effect was observed in Zones 1, 3 or Upper array (Table 4.3). Tortuosity values from estimated marginal means were similar between treatments in Zones 1, 3 and Upper array (EMM differences < 0.04 ± 0.06, all $p > 0.05$, Table 4.2, 4.3, Fig. 4.3B), sea lamprey in the alarm cue treatment displayed significantly more tortuous paths in Zone 2 (EMM ± se: control = 1.18 ± 0.04, alarm cue = = 1.54 ± 0.04, $p < 0.001$, Table 4.3, Fig. 4.3B). No other pairwise contrasts reached significance after adjustment for multiple comparisons (Table 4.4). Marginal and conditional R^2 (0.228 and 0.247, respectively) revealed nearly all the explained variance was due to treatment and zone.

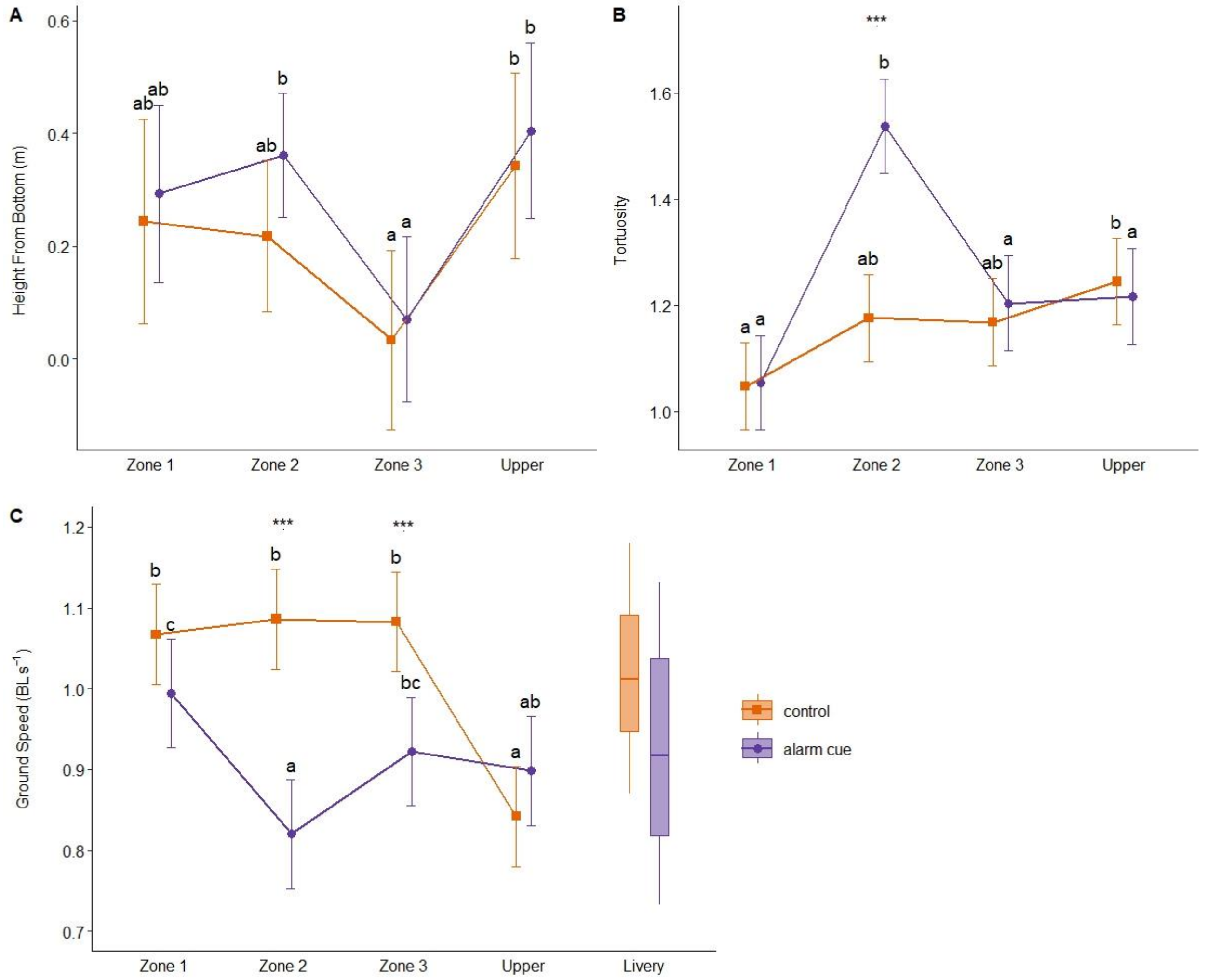

Figure 4.3. Behavioral responses of fish to alarm cue exposure across four longitudinal zones of the river. (A) Mean height from the bottom (m), (B) tortuosity, and (C) ground speed (body lengths per second, BL s^{-1}) are shown for fish in control (orange, square) and alarm cue (purple, circles) treatments. Data are presented as estimated marginal means ± 95% confidence intervals. Letters above error bars indicate significant between zones within each treatment differences across zones (Tukey-adjusted $p < 0.05$). Asterisks and brackets denote significant between-treatment differences within zones (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Boxplots in panel C represents the median (solid line), interquartile range (boxes) and range (whiskers) of ground speeds (BL s^{-1}) from the upper array to canoe liver 15.1 rkm upstream for each treatment.

RQ2: when sea lamprey encounter predation risk, do they select paths that prioritize safety or danger cues?

Sea lamprey in the control group were non-uniformly distributed across the river channel at all 117 transects (X^2 range = 25.87 – 138.18, all $p < 0.01$, Fig. 4.4C). Similarly, sea lamprey in the alarm cue treatment showed non-uniform distribution at 115 of the 117 transects (X^2 range = 18.21 – 80.03, all $p < 0.05$, Fig. 4.4F); alarm cue distribution at transects 59 and 64 failed to reject the null hypothesis of uniform distribution (X^2 = 10.33 and 14.25, $p > 0.1$, Fig. 4.4F).

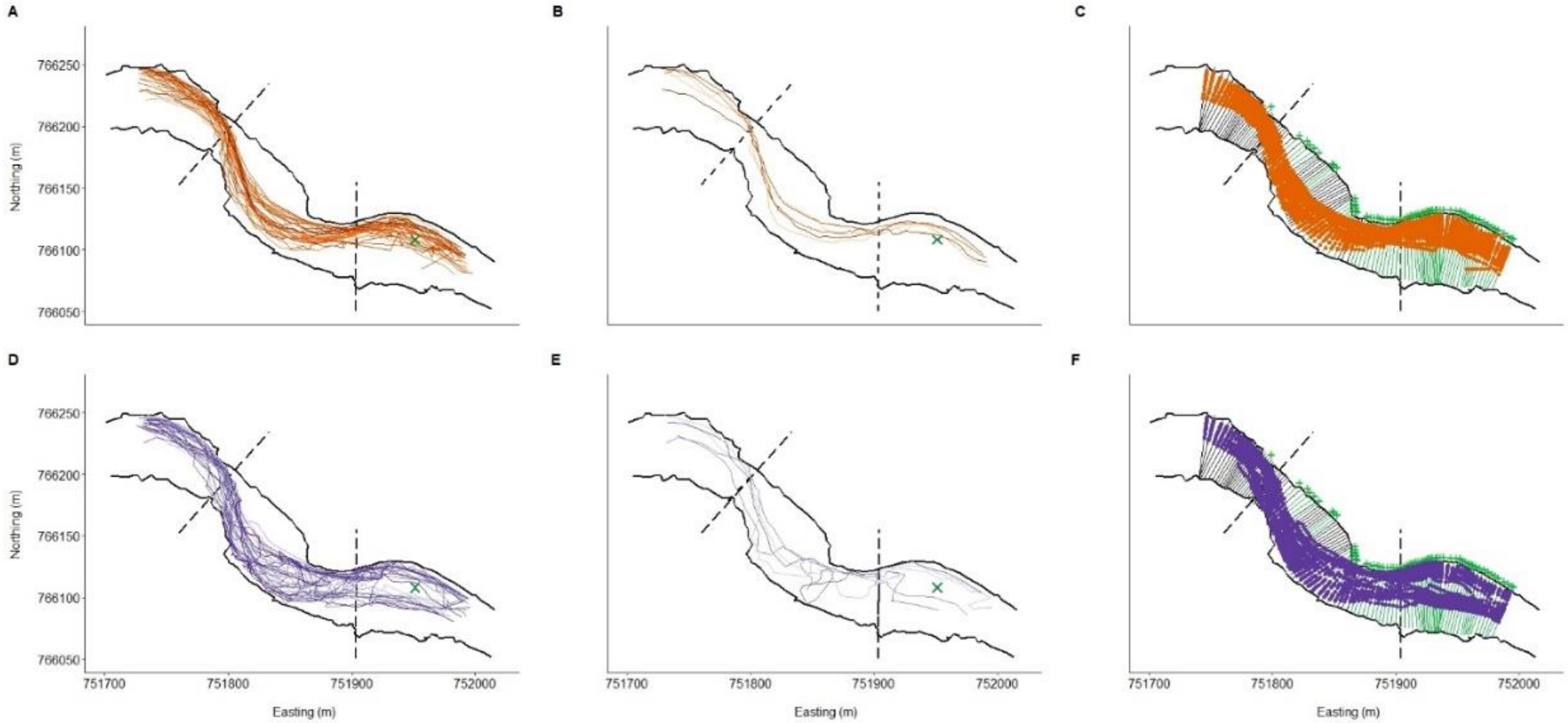

Figure 4.4. Sea lamprey tracks in the main array under two treatment conditions: (A) control and (D) alarm cue. Green x indicates the location of odorant application. Exemplar tracks from five individuals from (B) control and (E) alarm cue. Lateral distribution of sea lamprey positions across river transects under (C) control and (F) alarm cue treatments. Each dot represents an individual position at a transect. Transects highlighted in green and indicted with a cross (+) represent significant differences in lateral distribution between treatments based on Fisher's exact test ($p < 0.05$).

Fisher's Exact test showed lateral distribution between treatments is similar for transects in Zone 1 (transects 1 – 25, *p* > 0.05, Fig 4.4C, D). Lateral distribution between treatments begins to diverge in Zone 2 (transects 26 – 31, 33 – 36, 38, 44 – 46, 58 – 64, 68 – 80, *p* < 0.05, Fig 4.4C, D). All transects in Zone 3 revealed a significant difference in lateral distribution between alarm cue and control treatments (all *p* < 0.05, Fig 4.4C, D). The binomial regression the Fisher's Exact test probability of significance revealed transect 51 as the point where lamprey lateral space use between treatments changes (Fig. 4.5).

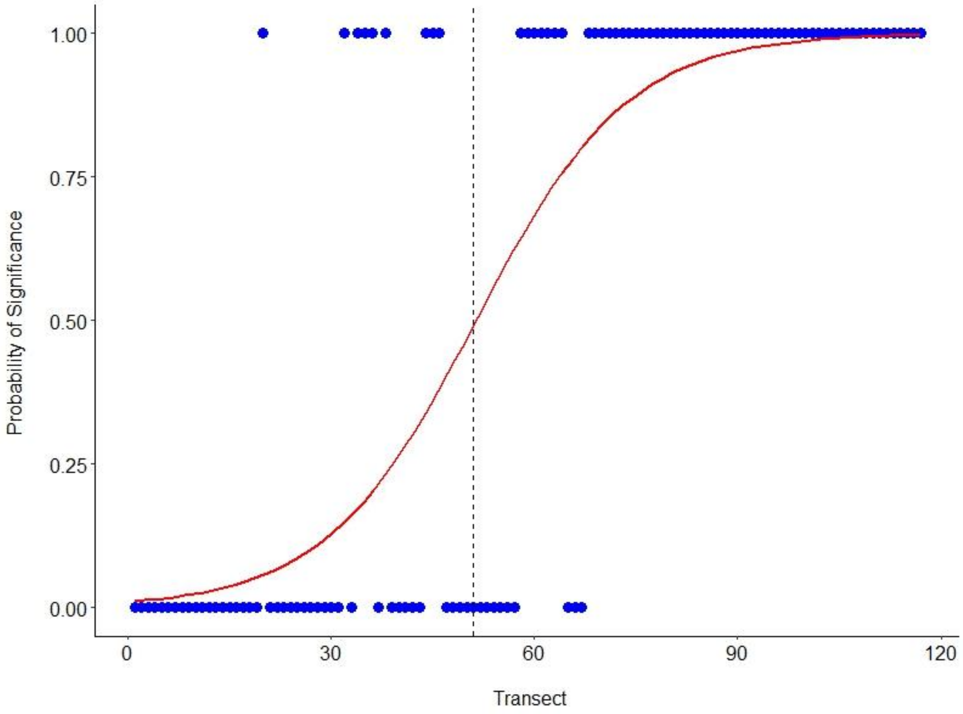

Figure 4.5. Probability of significant differences in sea lamprey lateral distribution between control and alarm cue treatments across river transects. Blue points represent individual Fisher's exact test outcomes, and the red line shows the fitted logistic regression. The dashed line at transect 51 indicates the inflection point (Probability = 0.5), beyond which significant treatment effects become more likely.

We performed Hartigan's Dip Test on 67 transects identified from the binomial regression (transects 51 – 117). All 67 transects under the control treatment exhibited unimodal lateral distribution (range D = 0.03 – 0.08, all *p* > 0.05), indicating a single choice path around the control odorant (Fig. 4.6). Lateral distribution for alarm cue treatment showed multimodality at transects 61, 62, 69 – 76, 86 – 116 (range D = 0.09 – 0.13, all *p* < 0.05), suggesting a split in path choice around the alarm cue odorant. The binomial test on control animal tracks revealed a non-equal split around the odorant application point, with 74% control fish choosing paths aligning with the deeper portion (*p* < 0.01, 95% CI: 0.60, 1.00).

Paths during alarm cue treatment suggested no bias towards either bank, rather paths split to both sides (57% choosing deeper paths) around the odorant application point ($p > 0.1$, 95% CI: 0.42, 1.00).

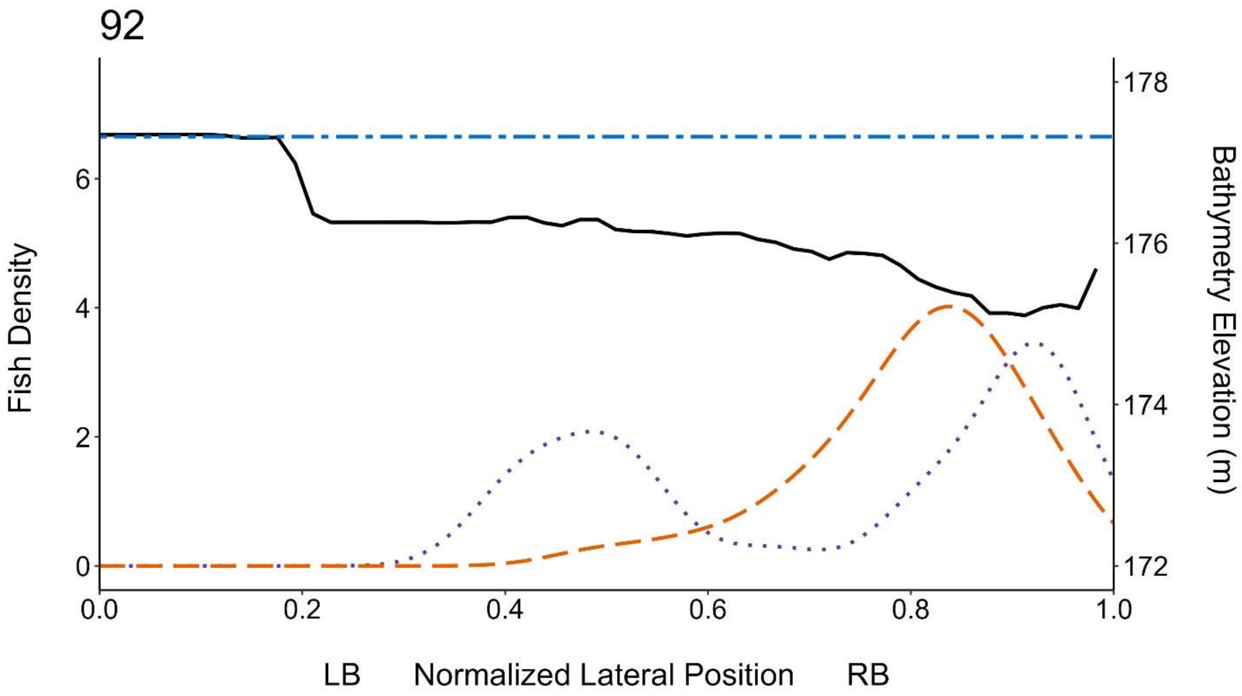

Figure 4.6. Sea lamprey normalized lateral distribution and water depth at transect 92. The bathymetry profile (solid black line) relative to the nominal water surface elevation (blue horizontal line) and the kernel density estimate for fish in alarm cue (purple dotted line) and control (orange dashed line). Hartigan's dip test indicated unimodality for control distribution ($p > 0.05$) and multimodality for alarm cue distribution ($p < 0.05$).

Table. 4.1. Model estimates for linear mixed effects models for height from bottom (m), ground speed (BL s^{-1}) and tortuosity as a function of treatment and zone. All models included individual fish as a random effect. Parameter estimates for fixed effects are presented with standard error in parentheses. Significant differences are bolded and indicated with asterisk. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

	Height from Bottom (m)	Ground Speed (BL s^{-1})	Tortuosity
Intercept	**0.24** (0.09)**	**1.07*** (0.03)**	**1.05* (0.04)**
Treatment (AC)	0.05 (0.12)	-0.07 (0.05)	0.01 (0.06)
Zone 2	-0.03 (0.09)	0.02 (0.03)	**0.13* (0.06)**
Zone 3	**-0.21* (0.10)**	0.02 (0.03)	**0.12* (0.06)**
Upper	0.10 (0.10)	**-0.22*** (0.03)**	**0.2*** (0.06)**
Treatment (AC) x Zone 2	0.10 (0.11)	**-0.19*** (0.04)**	**0.35*** (0.08)**
Treatment (AC) x Zone 3	-0.01 (0.13)	**-0.09* (0.04)**	0.03 (0.08)
Treatment (AC) x Upper	0.01 (0.14)	**0.13** (0.04)**	-0.03 (0.08)
Observations	1024	287	287
Marginal R^2	0.057	0.220	0.228
Conditional R^2	0.137	0.676	0.247

Table 4.2. **Estimated marginal means for height from bottom (m), ground speed (BL s^{-1}), and tortuosity across zones and treatments**. Standard errors are presented in parentheses. Values reflect model-adjusted means accounting for random effects and temporal autocorrelation.

		Height from Bottom (m)	Ground Speed (BL s^{-1})	Tortuosity
Control	Zone 1	0.24 (0.09)	1.07 (0.03)	1.05 (0.04)
	Zone 2	0.22 (0.06)	1.09 (0.03)	1.18 (0.04)
	Zone 3	0.03 (0.08)	1.08 (0.03)	1.17 (0.04)
	Upper	0.34 (0.08)	0.84 (0.03)	1.24 (0.04)
Alarm Cue	Zone 1	0.29 (0.08)	0.99 (0.03)	1.05 (0.04)
	Zone 2	0.36 (0.05)	0.82 (0.03)	1.54 (0.04)
	Zone 3	0.07 (0.07)	0.92 (0.03)	1.20 (0.04)
	Upper	0.40 (0.08)	0.90 (0.03)	1.22 (0.05)

Table 4.3. Pairwise differences (control – alarm cue) in estimated marginal means (standard errors in parentheses) within each zone for height from bottom (m), ground speed (BL s^{-1}) and tortuosity. P-values were adjusted using Tukey's method for multiple comparisons. Significant differences are bolded and indicated with asterisk. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Height from Bottom (m)	Ground Speed (BL s^{-1})	Tortuosity
Zone 1	-0.05 (0.12)	0.07 (0.05)	-0.01 (0.06)
Zone 2	-0.14 (0.08)	**0.27*** (0.05)**	**-0.36*** (0.06)**
Zone 3	-0.04 (0.10)	**0.16*** (0.05)**	-0.04 (0.06)
Upper	-0.06 (0.11)	-0.06 (0.05)	0.03 (0.06)

Table 4.4. Pairwise differences in estimated marginal means (standard errors in parentheses) between each zone within treatments for height from bottom (m), ground speed (BL s^{-1}) and tortuosity. P-values were adjusted using Tukey's method for multiple comparisons. Significant differences are bolded and indicated with asterisk. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

			Height from Bottom (m)	Ground Speed (BL s^{-1})	Tortuosity
Control	Zone 1	Zone 2	0.03 (0.09)	-0.02 (0.03)	-0.13 (0.06)
	Zone 1	Zone 3	0.21 (0.10)	-0.02 (0.03)	-0.12 (0.06)
	Zone 1	Upper	-0.10 (0.10)	**0.22*** (0.03)**	**-0.20** (0.06)**
	Zone 2	Zone 3	0.18 (0.08)	0.003 (0.03)	0.01 (0.06)
	Zone 2	Upper	-0.13 (0.08)	**0.24*** (0.03)**	-0.07 (0.06)
	Zone 3	Upper	**-0.31** (0.09)**	**0.24*** (0.03)**	-0.08 (0.06)
Alarm Cue	Zone 1	Zone 2	-0.07 (0.07)	**0.17*** (0.03)**	**-0.48*** (0.06)**
	Zone 1	Zone 3	0.22 (0.09)	0.07 (0.03)	-0.15 (0.06)
	Zone 1	Upper	-0.11 (0.09)	**0.10** (0.03)**	-0.16 (0.06)
	Zone 2	Zone 3	**0.29*** (0.07)**	**-0.10** (0.03)**	**0.33*** (0.06)**
	Zone 2	Upper	-0.04 (0.07)	-0.08 (0.03)	**0.32*** (0.06)**
	Zone 3	Upper	**-0.33*** (0.08)**	0.02 (0.03)	-0.01 (0.06)

DISCUSSION

Exposure to conspecific alarm cue produced structured and predictable changes in sea lamprey movement behavior consistent with the use of odor-guided rheotaxis to navigate around areas of perceived predation risk. These movement changes were spatially localized, with nominal migratory behavior interrupted by intensive search in the odor plume then resuming nominal behavior shortly after passing the odor source. When choosing between paths around the alarm cue source, sea lampreys exhibited no preference for deeper, safer routes. Rather, they split around the odor source in a manner consistent with executing a contra-lateral turn to avoid the area of high odor concentration near the center of the plume (i.e., those on the left side of the plume tended to turn leftward, and vice versa). Collectively, these findings demonstrate that sea lampreys detect and respond to alarm cue plumes with navigational strategies that utilize information contained in the plume geometry to quickly and effectively avoid the riskiest area without experiencing migratory delay.

RQ1: How do sea lampreys navigate around an area of high predation risk when migrating in rivers?

When exposed to alarm cue, sea lampreys altered their movement paths in ways consistent with the use of odor-guided rheotaxis to localize and avoid the source of the odor. Up to approximately 200 m downstream of the odor source (Zone 1), movement paths were very similar between control and alarm cue treatment groups. In Zone 1, ground speed and tortuosity of alarm cue paths were no different from the control group (P1). All paths exhibited low tortuosity and were well aligned with the river thalweg, consistent with patterns described in a previous tracking study in the same area (Griffin et al., 2025). In Zone 2, sea lampreys exposed to alarm cue exhibited both a 28% reduction in ground speed (P2) and 27% increase in tortuosity (P3) compared to control paths, indicating a transition to intensive search behavior near the odor plume (Nakamuta, 1985). Estimated spatial dimensions of the search area spanned approximately 32 m in length and across the entire river channel (~48 m). The large search area likely reflected the scale of the alarm cue plume generated by the four odor application outlets. In Zone 3, animals under alarm cue conditions accelerated back to ground speeds observed in Zone 1. There was some evidence alarm cue sea lamprey were moving slower than control animals in Zone 1. After the animals passed the odor source and moved into the upper array, we observed no differences between treatments in height from bottom, ground speed or tortuosity, suggesting responses to the alarm cue were spatially constrained and a quick return to nominal movement behavior where energy savings and preference for deeper and safer routes are the nominal preference in the absence of direct evidence of immediate danger from predators (Griffin et al., 2025). These behavioral shifts mirror those described for other aquatic species navigating odor plumes (Butler & Tankersley, 2020; Moore et al., 1991) and are consistent with odor-conditioned rheotaxis (Weissburg, 2000).

The transition from extensive movement to intensive search and back to extensive movement matches theoretical models of spatial decision-making under uncertainty and supports the interpretation that lampreys perceive alarm cue as a localized and immediate threat. However, the lower detection threshold for the alarm cue mixture remains unknown due to the chemical composition being undefined (Mensch et al., 2022b, 2022a). By activating 20% of the discharge at a concentration of

0.5 PPM, individuals would have been capable of fully avoiding the odor source after contacting space where 50% of the discharge was activated with the odor (per dose-response relationships reported by Wagner et al., 2023). In the present study, lateral distribution between treatments became significantly different ~135 m downstream of the odor source. This distance is likely larger than would occur naturally, where odor released from a single or few wounded animals would produce a narrower plume (Wisenden et al., 2022). However, the pattern of movement consistent with odor-guided rheotaxis would likely be the same (Butler & Tankersley, 2020; Choi et al., 2013; Moore et al., 1991). If sea lamprey evolved this behavioral response to avoid close contact with a predator (Kats & Dill, 1998), and a single attack likely liberates very little alarm cue into the environment (Wisenden et al., 2022), then detecting any alarm cue could be interpreted as being very near in space and time to the attack location. Therefore, detecting alarm cue would represent substantial risk. Recently, Boulêtreau et al. (2020) reported high predation rates of sea lampreys by the invasive European catfish (*Silurus glanis*). Attacks on sea lamprey likely did not produce alarm cue for subsequent migrants to avoid (Wisenden et al., 2022).

RQ2: When encountering alarm cue, do sea lamprey select paths around the risky area that prioritize attraction toward safety or simple avoidance of danger?

Sea lamprey in the alarm cue treatment did not exhibit a preference for the route through the deeper area, instead showing a lateral split around the odor source. This pattern is consistent with our second hypothesis: when encountering highly reliable immediate danger cue, sea lampreys relied on avoidance behaviors rather than prioritizing safety. Migrants in the alarm cue treatment transitioned from choosing paths that are ‘safer,’ similar to those exhibited in the control treatment where there was no information about danger, to prioritizing danger information. Although, we cannot confirm alarm cue or predator kairomones were not naturally present on any nights. This pattern suggests a form of cue prioritization where safety features such as depth guide route selection under nominal conditions, but in danger information becomes more salient and reliable, it overrides safety-based decision-making (Luttbeg et al., 2020). However, the depths in the intensive search area were generally more uniform, which might have impacted their ability to choose the safest path if the decision was made more than ~70 m downstream of odor source.

Paths chosen by sea lamprey in the control treatment closely aligned to findings of a prior tracking study in the same study area, suggesting a repeatable pattern of habitat preferences when choosing migration paths in relatively shallow rivers (Griffin et al., 2025). Both studies took place during a similar period, late May to mid-June. However, there were differences in discharge experienced by animals. Discharge during the first study ranged from 7.96 to 15.26 m^3s^{-1} and most fish encountered flows between 7.96 and 8.50 m^3s^{-1} (Griffin et al., 2025). In the current study, most fish in the control group experienced slightly higher discharges ranging from 10.76 to 11.33 m^3s^{-1} (overall range: 9.49 – 12.92 m^3s^{-1}). However, the water depth in the current study was about 0.10 m lower. Ground speed in both studies was near 1 BL s^{-1}, but slightly higher (1.01 BL s^{-1}) in the present study at than previously reported 0.92 BL s^{-1} (Chapter 3). Chapter 3 revealed a slightly negative relationship between ground speed and water depth, consistent with findings in the present study where ground speed was slightly faster (1.01 BL s^{-1}) in the present study than previously reported (0.92 BL s^{-1}). Additionally, we found no significant difference between animal height from bottom between the treatment groups. Control animals in the present study moved only slightly higher (median height from bottom = 0.16 m) in the water column than previously in this site (median height from bottom = 0.11 m) and similar values to other river tracking studies (0.16 m) (Holbrook et al., 2015). These similarities suggest sea lamprey exhibit consistent migratory behaviors despite moderate shifts in flow and depth.

Implications for Conservation and Management

Sea lamprey movement patterns and their response to alarm cue have implications for managing the invasive populations and conserving native populations. Invasive to the Laurentian Great Lakes, sea lamprey prey on native fish causing ecological and economic damage (Marsden & Siefkes, 2019; Siefkes et al., 2013). Native to Europe and the North American Atlantic coast, sea lampreys are important culturally and ecologically, but they face many threats such as habitat loss and fragmentation (Braga et al., 2019, 2020; Clemens et al., 2021; Hanel et al., 2022; Mateus et al., 2012). Incorporating knowledge of their movement tactics and response to risk information could aid in reaching conservation and management goals.

If managers aim to use alarm cue to guide migrants toward a trap or fish passage device, then they must consider how sea lamprey avoid the odor source in nature. Although the present study created a relatively large odor plume from four sources along the river width, activation of the entire targeted area of avoidance might be required to fully exclude a section of the river. Had we observed most sea lamprey favor safety (Luttbeg et al., 2020) by moving through the deeper section of the river, that preference could be exploited where shallow areas opposite the deep thalweg would not need to be activated with alarm cue to see avoidance. However, the intensive search period occurred in an area with more uniform depth, where the cue that identified safety, labelled the whole river width (Luttbeg et al., 2020). Future studies could explore how activating upstream of an area with a distinct thalweg throughout the intensive search region influences path choice. In this situation, the safer area overlaps the less-risky area, where running to safety and running away from risk align (Luttbeg et al., 2020; MacKay et al., 2021).

It is important to consider how the animal's internal state may change after exposure to alarm cue when designing practices to manipulate movement behavior (Nathan et al., 2008). Exposure to alarm cue can induce a state of neophobia (G. E. Brown et al., 2013; Crane et al., 2024). Hume et al. (2020) found sea lamprey exposed to alarm cue downstream were less willing to move onto a studded ramp (eel ladder). However, in a separate study, capture rates at a trap integrated into a dam were no different between nights with and without alarm cue activating the opposite riverbank (Hume et al., 2015). However, because these high capture rates were observed at a barrier integrated trap where upstream movement was blocked, and time of entry into the traps was unknown, it is possible the captures took place hours after exposure to the alarm cue (Hume et al., 2015). Thus, entry into the device may be delayed, but not prevented, after encountering an odor indicative of high predation risk. In conservation situations, this delay could have repercussions for migration and reproduction. Navigating through fish passage devices has shown to be energetically taxing and results in delays (Castro-Santos, 2004; Castro-Santos et al., 2017; Davies et al., 2021; Quintella et al., 2004). Additional delays from alarm cue exposure could limit migration and reproductive success (Maitland et al., 2015; Marsden & Siefkes, 2019; Siefkes et al., 2013).

Manipulating movement decisions of migrating sea lamprey could have applications beyond guiding towards a fishing device. Currently, invasive sea lamprey control relies primarily on the application of a selective pesticide that targets larvae in spawning tributaries and barriers that prevent migrants from accessing upstream spawning habitat (Marsden & Siefkes, 2019; Siefkes et al., 2013). Applying alarm cue to supplement lampricide application by deterring sea lamprey from entering streams that are difficult to treat (Miehls et al., 2021). This technique could also be utilized for conservation goals where low quality streams are activated with alarm cue to 'push' migrants towards streams where conditions lead to better offspring survival (Maitland et al., 2015; Mesa & Copeland, 2009; Wang et al., 2021). Integration of attractant cues, such as larval odor, to restored habitat with alarm cue could create a push-pull situation for conservation (Wagner et al., 2006a, 2009).

Conclusions

Sea lampreys use odor-guided rheotaxis to avoid localized areas of high predation risk. This tactic provides a simple yet effective mechanism for migrants to navigate complex and dynamic river environments where visual cues may be limited and predator encounter risk elevated. The avoidance response to alarm cue is short-lived and spatially constrained, enabling lampreys to resume upstream movement quickly after bypassing the perceived threat. Importantly, migrants return to prioritizing safety cues and energy-efficient paths shortly after clearing the risk zone, reflecting a strategic balance between predator avoidance and migration optimization. These findings underscore the importance of environmental context when applying alarm cue-based manipulations for management or conservation. Decisions about whether, where, and how to deploy alarm cue must consider river morphology, flow dynamics, and behavioral sensitivity to ensure interventions are effective without unintended side effects. Used thoughtfully, these insights into lamprey risk navigation could improve invasive control strategies or help safeguard native populations through more nuanced habitat steering and migration support.

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APPENDIX

Array Performance

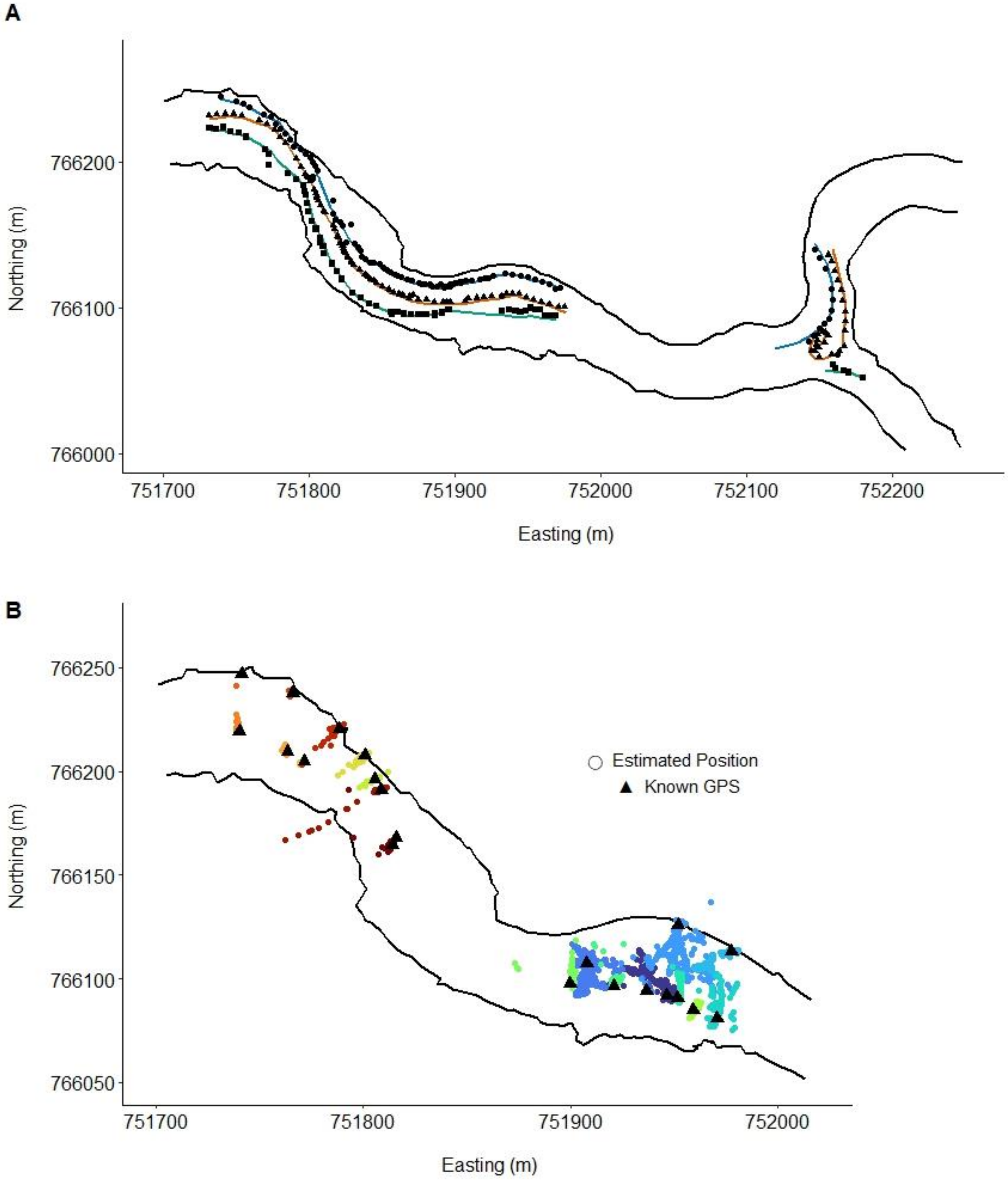

Figure S4.1. Array performance tests. (A) Mobile tests performed by drifting a tag through the acoustic array. Known GPS locations are indicated by solid lines, each test represents a different color. Estimated positions are indicated by solid black shapes, each test is represented by a different shape.

Figure S4.1 (cont'd)

(B) Stationary test locations in the telemetry array. Known GPS location of each test location are indicated by black triangles; filled circles represent estimated positions, each test is indicated by a unique color.

Table S4.1. Accuracy and precision of stationary tests. Accuracy and precision estimates from HR and PPM transmissions (where applicable). Test length and fix rate refer to PPM transmissions only.

Site	n	Accuracy (m)				Precision (m)				Test Length (hr)	Fix Rate
		Mean	SD	SE	Median	Mean	SD	SE	Median		
1	48	1.72	6.12	0.88	0.43	1.47	6.09	0.88	0.15	4.35	92.43
2	4101	3.91	6.96	0.11	1.14	3.76	6.95	0.11	1.07	119.09	85.44
3	1070	1.13	0.27	0.01	1.11	0.17	0.26	0.01	0.12	187.06	88.20
4	11820	2.77	3.38	0.03	1.29	2.60	3.52	0.03	1.12	28.17	85.34
5	1160	16.43	7.61	0.22	17.37	7.80	5.85	0.17	7.43	189.71	86.70
6	167	11.41	5.88	0.46	12.35	5.99	5.51	0.43	5.26	96.33	85.55
7	149	6.97	4.72	0.39	5.48	4.91	4.20	0.34	3.35	23.05	91.22
8	1662	1.95	1.93	0.05	1.07	1.71	2.21	0.05	0.64	22.34	85.47
9	311	3.31	3.08	0.17	3.15	2.11	2.74	0.16	1.41	148.45	90.43
10	823	3.39	2.31	0.08	3.05	1.35	2.13	0.07	0.89	41.45	89.52
11	1455	1.01	0.59	0.02	0.89	0.47	0.47	0.01	0.37	29.85	92.60
12	1215	1.20	0.45	0.01	1.16	0.34	0.55	0.02	0.21	187.09	97.23
13	1970	0.79	0.72	0.02	0.67	0.58	0.81	0.02	0.35	28.18	93.92
14	287	1.20	0.22	0.01	1.21	0.18	0.21	0.01	0.12	189.73	99.10
15	1964	1.50	0.29	0.01	1.52	0.26	0.36	0.01	0.18	96.31	98.35
16	984	2.30	0.94	0.03	1.84	0.91	0.77	0.02	0.62	23.12	60.50
17	251	1.13	0.38	0.02	1.09	0.23	0.45	0.03	0.16	22.04	56.61
18	228	0.52	0.26	0.02	0.47	0.23	0.31	0.02	0.16	148.41	93.79
19	1603	1.23	3.46	0.09	0.64	0.84	3.48	0.09	0.24	39.53	65.89
20	443	1.78	5.51	0.26	1.01	1.63	5.61	0.27	0.74	91.92	74.90
21	330	1.42	2.75	0.15	0.86	1.28	2.71	0.15	1.01	123.34	98.05

Fish position error estimation and data filtering

Fathom position assigned each estimated position an estimate of horizontal position error sensitivity (HPE, unitless). Collocated syn tag positions were also assigned measured horizontal position error (HPEm, m) as the Euclidean distance from the estimated position and known GPS location. To estimate absolute position error (HPE_m*, m), we calculated the relationship between HPE and HPEm values from collocated sync tag positions for each array, first excluding positions with HPE values in the 95th percentile to limit the influence of highly uncertain positions (Smith, 2013). We then calculated the twice distance room mean squared (2DRMS) error, representing twice the square root of the combined variance in the x and y directions for each 1-m bin across all sync tags (Fig. S4.2). Notably, the minimum HPE value assigned to sync tag positions was 2.10. Finally, we regressed 2DRMS against HPE and applied the slope and intercept to HPE values to estimate HPE_m* (Meckley, et al., 2014; Smith, 2013).

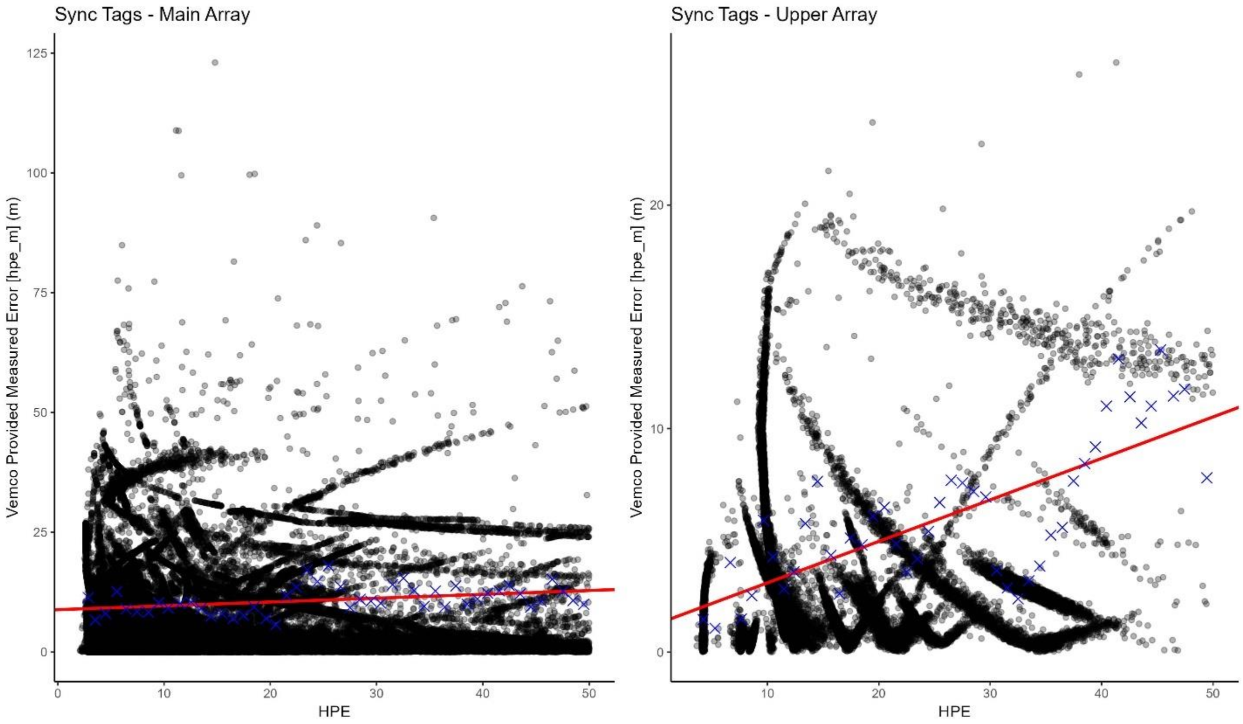

Figure S4.2. Fathom-provided horizontal position error (HPE$_m$) versus horizontal position error sensitivity (HPE) values for each estimated collocated sync tag position in the (A) main array and (B) upper array. The blue x represents twice the distance root mean square error of X and Y components of error within an HPE$_s$ bin of one; 2DRMS is represented by the solid red line running between these points.

To validate this approach, we compared the measured positional error (the Euclidean distance between known GPS location and estimated position) to $HPE_m^*$for stationary (n = 30,438) and mobile (n = 250) test positions. HPE_m^* overestimated positional error for both the main and upper arrays, rather than producing the expected 1:1 relationship (regression equation: HPE_m^* = 9.54 – 0.01 * measured error; R^2 = 0.001). Therefore, HPE_m^* was not a useful metric for filtering erroneous positions.