EFFECTS OF A NOVEL MICROACOUSTIC TRANSMITTER ON SURVIVAL, SWIM PERFORMANCE, AND MOVEMENT ECOLOGY OF OUT-MIGRATING JUVENILE SEA LAMPREY IN LABORATORY AND FIELD SETTINGS

By

Taylor F. Haas

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ABSTRACT

EFFECTS OF A NOVEL MICROACOUSTIC TRANSMITTER ON SURVIVAL, SWIM PERFORMANCE, AND MOVEMENT ECOLOGY OF OUT-MIGRATING JUVENILE SEA LAMPREY IN LABORATORY AND FIELD SETTINGS.

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Migration, defined as “a relocation of the animal that is on a much greater scale and involves movement of much longer duration, than those arising in its normal daily activities” is a time of great uncertainty in animals’ life. As an evolved behavior, migration dictates that fitness benefits on the species level outweigh the cost of translocation, however risks on the individual level remain. Benefits include but are not limited to, access to breeding grounds and food availability; and risks include mortality or depleted energetic reserves.

In the Upper Great Lakes an invasive migratory fish, the Sea Lamprey, has inhabited the region since its initial establishment in the region around 1930. High efficacy treatment measures target Sea Lamprey in their larval stage and have curbed populations by 90%, yet information of subsequent phases is lacking and warranted. Specifically, information on the feeding migration (River to Lake) is necessary for refining population models and possible management, as this is the last time Sea Lamprey are in a confined space.

A novel microacoustic transmitter can inform researchers on this phase, and these two experiments tested this technology’s ability in Sea Lamprey. The first experiment details a proof-of-concept study examining the physiological effects of tag implantation within a laboratory setting and the second explores the tag’s ability in a field setting. The laboratory experiment investigates swimming ability, tag retention and survival for 61-days post-implantation relative to a control group; the field experiment focuses on habitat related mortality, the movement ecology of these organisms, and the telemetry equipment’s ability to inform on these topics.

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CHAPTER 1: An Examination of the Physiological Effects from Surgically Implanting a New Acoustic Microtransmitter in Juvenile Sea Lamprey

ABSTRACT:

Little is known about the “transformer” stage of the sea lamprey (*Petromyzon marinus*) life cycle, a brief but critical period that includes out-migration from rivers to lakes or oceans to begin parasitic feeding. The extensive Sea Lamprey control program implemented by the Great Lakes Fisheries Commission primarily focuses on the lamprey’s larval stage, but there is interest in learning more about the outmigration to identify additional control opportunities. Additionally, information about this life-stage could have conservation implications for Sea Lamprey in their native European range where they are considered imperiled. A newly fabricated acoustic microtransmitter proven effective in American eel (*Anguilla rostrata*) and Pacific lamprey (*Entosphenus tridentatus*) has the potential to reveal behavior of sea lamprey out-migrating from their natal habitat. We investigated the physiological effects of tag implantation on transformer-stage sea lamprey in a controlled, laboratory environment. Through a 61-day holding period, a group of juvenile sea lamprey implanted with deactivated transmitters, and an untagged control group, were subjected to a series of experiments to determine the effects of tag implantation on swim performance and survival. Tagged animals on average swam 7.6 cm/s slower (22.5%) than control animals in burst-swim speed tests ($p < .01$) but were not significantly different in endurance tests (p =.32, .18). Amongst tagged animals, a composite wound healing score was a significant predictor of maximum burst swim speed. A 10% improvement in the wound condition was associated with a gain of 1.8 cm/s (p < .01). Over the course of the experiment, 29% of tagged animals died vs. 15% of the control group ($p = .01$). The difference was due largely to early mortalities in the tagged group. Five of 17 (29%) tagged group mortalities occurred within 4 days of implantation vs. 0 of 8 control group deaths. Size (TL, mass, condition factor) was not a predictor of mortality for tagged animals, but each gram of mass was associated with -1.2 composite wound score units ($p = .02$). We offer recommendations for field use of this technology in juvenile lampreys to ensure assumptions of movement studies are met.

INTRODUCTION:

Migration is a time of both heightened threat and heightened uncertainty regarding the risk of predation and the localization of critical resources (Sabal et al. 2021). This is particularly so when migration occurs early in life, when variation in daily growth and survival may be substantial and determinative of recruitment to the adult phase (Houde 1989). Population declines in desired fishes that exhibit juvenile out-migration from rivers into lakes or oceans including salmon (*Oncorhynchus* spp.) and lake sturgeon (*Acipenser fulvescens*), as well as a desire to manage invasive migratory species (e.g. sea lamprey *Petromyzon marinus* in the Laurentian Great Lakes) has prompted considerable interest in ascertaining the behavior, timing, and survival of juvenile fishes as the move downstream (Jones 2007, Rechisky et al. 2013).

The migratory lampreys include species that range from imperiled and highly desired (e.g. Pacific lamprey *Entosphenus tridentatus*, European river lamprey, *Lampetra fluviatilis*), to pestilential and targeted for reduction (sea lamprey in the Great Lakes). These lampreys are spawned in rivers, after which newly hatched larvae (ammocoetes) bury in stream sediments for up to seven years, harmlessly feeding on organic detritus and algae (Dawson et al. 2015). At the end of the larval stage, lampreys transform into their juvenile stage while still in the substrate of their natal stream (Beamish 2011, Mcgree et al. 2008, Goodman et al. 2015, Potter 1980). Eventually, juveniles (sometimes termed transformers when actively migrating but not yet feeding) leave the substrate, likely responding to environmental drivers (e.g. seasonal changes in discharge and water temperature), migrating downstream into estuaries or large lakes where they commence parasitic feeding on fishes (Dawson et al. 2015; Baer et al. 2018; Evans et al. 2021). This period of physical and geographical transition is of short duration compared to the larval and parasitic feeding stages, yet is considered critical to the development of effective conservation and management practices. For example, out-migrating Pacific lamprey typically must transit through a gauntlet of dams and their affiliated water intake structures, resulting in physical injury, increased predation, and direct or delayed mortality (Moser et al. 2015). Providing for safe passage through these structures is necessary for the protection of the species (Goodman et al. 2017).

In the Laurentian Great Lakes, where a single parasitic juvenile may consume upwards of 21 kg of fish biomass, the sea lamprey has proven a devastating invader, initially driving down the populations of several fishery species to below the limit of commercial sustainability (Irwin et al. 2012, Smith & Tibbles, 1980). Since the middle twentieth century, the governments of Canada and the United States have been in protracted and expensive battle to stem population growth through control and research (Knight & Bocking, 2016; Brant 2019). Control is achieved by the placement and maintenance of low-head dams to block access to spawning habitat in rivers, and by the application of two selective pesticides (lampricides) to kill larvae in streams prior to transformation (Marsden and Siefkes 2019; Burkett et al. 2021). Rivers are selected for lampricide treatment based on their larval population size (i.e. prior to transformation), informed by population models and expert opinion (Jones et al. 2009). Gleaning mortality estimates from studies of outmigration behavior could prove useful to informing lampricide application strategies, especially if survival is regulated by ecological or geomorphologic attributes of rivers that vary across systems (e.g. the presence of drowned river mouth lakes rich in piscivorous predators). Specifically, the ability to estimate the fate of out-migrating sea lampreys at the population scale would allow treatment decisions to be made based on probable parasite production vs. larval population size, incorporating system-specific differences in rates of survival through migration. Stage specific spatial population models for sea lamprey currently assume equal transition probabilities from transformer to parasite for all infested rivers, failing to account for either habitat variation or intraphase time specific mortality (Howe et al. 2012, Robinson et al. 2013).

The most frequently used tool to monitor the movements of fishes and other aquatic organisms over large spatial extents is telemetry, involving the implantation of a transmitter that is detected by a receiver when the fish moves into the range of detection (Hussey et al. 2015). A primary assumption of telemetry analysis is the fish's nominal movement behavior (e.g. swim speed, timing) is not substantially altered by bearing the tag, or because of the implantation process. It has generally been assumed that a transmitter with a weight < 2% that of a fishes body (dry weight) meets this criteria (Bridger & Booth 2003; Hondorp 2015; Winter, 1983). Yet, several detrimental effects of telemetry tags in fishes have been noted, including decreased growth, increased mortality and decreased swim performance (Frost 2010, Watson et al. 2019). The latter, as well as increased blood plasma production have been documented in lamprey species (Close et al. 2003, Mueller et al. 2006)

Until recently, small (≤ 12mm) passive integrated transmitters (PIT) tags were the only transmitters available for the study of outmigrating lamprey. PIT tags lack an internal power source and instead pass coded “disruptions” of a radio frequency produced by a powered antenna when passing over the antenna. Fishes must swim within approximately 140 cm of the antenna, depending on the orientation of the tag, to be detected (Baker et al. 2017, Nightengale et al. 2018). The proportion of PIT-tagged larval and outmigrating lamprey detected by PIT antennas is relatively low, with detection rates ranging from 5-14% (Dawson et al. 2015; Miehls et al. 2019). Further, PIT antennas are generally restricted to relatively narrow and shallow rivers, precluding use in the lower reaches of large rivers. Internally powered telemetry tags (acoustic and radio) offer an alternative that substantially increases the detection range (tens to hundreds of meters) and detection probability (80-100%) at a single receiver (McMichael et al. 2010). Acoustic transmitters have several desirable properties for use in small fishes; in particular, they do not require an external trailing antenna that (as radio telemetry does), resulting in reduced impacts to swim performance, lower likelihood of predator attack, and higher survival in tagged individuals (reviewed by Crossin et al. 2017 and references therein).

Historically, acoustic transmitters have proven too large to implant into small fishes with narrow body cavities, due to the direct relationship between battery life and tag size. Transmitters with sufficient battery life to support demographic studies of fishes require physically large batteries that impeded movement and survival in the subject of study (Leidke 2019). However, the fabrication of a novel microbattery by United States Army Corps of Engineers (USACE) and Pacific Northwest National

Laboratory (PNNL), originally designed for use in salmon smolts, has been repackaged into a microacoustic transmitter suitable for use in juvenile sea lamprey – the Eel-Lamprey Acoustic Tag or ELAT (Deng et al. 2015, Deng 2018, Leidtke 2019). This could be a breakthrough in juvenile lamprey movement studies. At approximately the same size as the PIT tags used in previous transformer lamprey studies (12mm x 2mm, .08g), this is the first acoustic telemetry tag that does not violate the 2% body mass standard for surgical implantation (Mesa et al. 2012, Mueller 2006, Simard et al. 2017). This tag uses JSATS (Juvenile Salmon Acoustic Telemetry System) technology also developed by USACE with a detection range of 80-140m; a distance 100x greater than the approximate range of a 12mm PIT tag. (Deng et al. 2018). Pilot field studies using the ELAT tag have demonstrated the suspected high detection rates (>95%) in both Pacific lamprey (*Entosphenus tridentatus*) in the United States' Pacific Northwest and American eel (*Anguilla rostrata*) on North Carolina's Atlantic Coast (Deng 2019, Deng et al. 2018, Leidtke et al. 2019). If proven similarly effective in the transformer phase of sea lamprey, it is conceivable that this technology could extend its viability into other anguilliform species of similar size and research interest such as the regionally endangered American brook lamprey (*Lethenteron appendix*) of the United States Eastern Seaboard, the previously petitioned for Endangered Species Act protection American eel, and the critically endangered European eel (*Anguilla Anguilla*) (Department, N.H. Fish and Game, IUCN Red List of Threatened Species, Shepard 2015).

We assessed tag retention, survival, wound healing, and swim performance effects of implantation of an ELAT transmitter in newly transformed sea lamprey, a species of substantial management interest. Our broader goal was to perform a comprehensive evaluation of the impacts of ELAT transmitter implantation to support the establishment of criteria for use in field studies designed to enumerate critical demographic parameters (e.g. stage-specific mortality rates) and the movement ecology of actively migrating transformers. We were particularly interested in survival and impacts to swim performance, as the tag is designed for use in movement studies. Survival rates have varied extensively in previous studies with PIT tags performed on larval and transformer lamprey species (25% - 100%;

Dawson et al. 2015, Moser et al. 2017, Mueller et al. 2019, Simard et al. 2017). Additionally, we focused on the animal's burst swim abilities, a facultative behavior suggestive of ability to escape potential threat, and swim-to-exhaustion capabilities, a characteristic of long stretches of active swimming during a migration (Dominici 2010). Wound health was chosen as a predictor covariate of the tagged animals because of its tangibility and the immediacy of which it can be judged post-operation.

METHODS:

The objective of this study was to examine the effects of the ELAT tag on sea lamprey survival, condition, and swim performance. To achieve this objective, we surgically implanted ELAT tags into 59 newly transformed juvenile parasitic sea lamprey and examined tag retention, survival, wound healing, and swim performance over a 61-day period. Wound healing assessment involved two scoring metrics, wound closure and wound irritation, and a composite score that combined the two measures into an overall measure of wound condition. Swim performance was analyzed by comparing two performance metrics, burst swim speed and (day 20 post-surgery) and time-to-exhaustion (day 30 post-surgery). The swim measures were separated by ten days to ensure the stress of the burst swim test did not influence the results of the time-to-exhaustion test. The measures of swim performance were statistically compared to a group of 54 control animals that did not experience the anesthesia, surgery, or tag implantation. Mortalities for both tagged and control groups were enumerated daily. Due to the difficulty in acquiring this life history stage in sea lamprey, subjects were collected from both Great Lakes and Atlantic basin drainages. Where possible, source was included as a covariate in the statistical models.

Collection and housing of subjects:

Sea lamprey used in this study came from two sources, tributaries in the Great Lakes Basin (N = 64), and the Sawmill River, MA; a tributary to the Connecticut River that flows into the Atlantic Ocean (N = 49). We selected 113 sea lamprey transformers ranging 140mm-160mm total length based on recommendations from previous studies using similarly sized PIT tags in juvenile sea lamprey (Simard et al. 2017) and Pacific lamprey (Mesa et al. 2012). We chose to include animals across a range of sizes near the median of the size distributions in the Great Lakes and the Atlantic basin (Figure 1.1) to examine the relationship of body size to wound healing and swim performance.

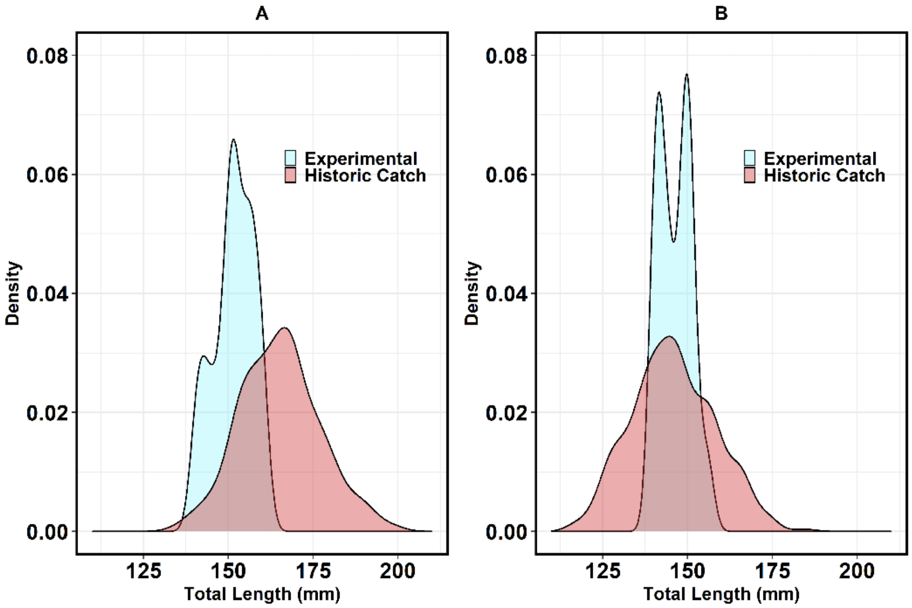

Figure 1.1. (a) Density plots of total length (mm) for historic catches of out-migrating juvenile sea lamprey (red, N=267) and subjects used in this experiment (blue, N= 59) for animals captured from Great Lakes streams. (b) Density plots of total length for historic catches of out-migrating juvenile sea lamprey (red, N=653) and subjects used in this experiment (blue, N=54) for animals captured from Atlantic drainages in the northern United States. Data for historical catches was provided by J. Hume, Michigan State University.

Subjects were housed at the U.S. Geological Survey Hammond Bay Biological Station (HBBS) from February 11, 2020, to April 13, 2020. Lampreys were kept in eight separate 23L 40cm x 22cm x 26cm tanks that were supplied with constant flow-through water from Lake Huron and continuous aeration. As our findings are intended to inform use of the ELAT tag in natural rivers, the holding tanks were constructed to include certain natural features the animal would experience during outmigration. First, previous tagging effects studies observed fungal growth and infection on experimental subjects held in the laboratory (Christiansen 2013, Moser 2017, Mueller 2006). To ensure the microbiome the sea lamprey were exposed to was akin to the natural flora, we lined the tanks with a 4 cm layer of mixed substrate (cobble, sand, fine-grained sediment) collected from nearby Schmidt’s Creek. In addition, unfiltered inflowing water from Lake Huron was heated to a temperature typical of central Lake Michigan tributaries during the fall migration times (Nov.1-Nov.30, ~4.5° C, USGS).

Surgical implantation of the transmitter:

An ELAT transmitter contains a 147 dB microbattery with an estimated life of ~30-40 days in a plastic encasing with dimensions 12mmx2mm, .08g dry-weight, and transmits at a frequency of 416.7 kHz (± .5%). Currently, the standard PRI (Pulse Rate Interval) of five seconds allots approximately 32 days of use (Deng, Pers. Comm. 2020, Deng et al. 2021). This experiment used a modified ELAT where the microbattery was replaced with a PIT transmitter to allow for individual identification of the subjects via a hand scanner. On February 12, 2020, 59 fully transformed sea lamprey were surgically implanted with modified ELAT transmitters (30 Great Lakes and 29 Atlantic drainage), and 54 entered the experiment as control animals (34 Great Lakes and 20 Atlantic drainage). Animals in the tagged group measured (mean ± 1 SD) 150.16 ± 5.69 (total length, mm) and weighed 4.37 ± 0.64 g. Animals in the control group measured (mean ± 1 SD) 148.30 ± 6.08 (total length, mm) and weighed 4.18 ± 0.50 g.

The implantation surgery followed protocols established by Moser et al. (2017) and Christiansen (2013). An anesthetic bath of AQUIS-20E (10% eugenol) was prepared to sedate the animals undergoing the tagging procedure. Anesthesia concentrations from prior studies (.02-.06 ml l^{-1}, USFWS INAD, Simard 2017) proved ineffective at inducing stage-IV anesthesia in pre-surgery screening (per criteria in Summerfelt & Smith 1990). Similar occurrences have been noted for other anesthetic agents applied to juvenile lamprey when using doses recommended for teleost fishes. Stage IV anesthesia was induced in (mean ± 1 SD) 17.0 ± 4.5 min via immersion in a solution of 0.7 ml l^{-1} AQUIS-20E (eugenol concentration = 70 ppm). When each animal reached stage-IV anesthesia, it was placed on a damp surgery board and the surgeon (T.F. Haas) made a lateral 3mm incision into the body cavity using a Premier Edge Restricted Depth 3mm microscalpel (OASIS® Medical). A disinfected (immersion in 70% ethanol for ≥ 2 min) transmitter was inserted posteriorly into the opening until it was completely enveloped in the animal's body cavity. After the transmitter was fully inserted, each animal was placed into an oxygenated recovery tank until active swimming or suction attachment to the side of the tank was observed, indicating recovery (mean ± 1 SD time to recovery = 102.08 ± 67.13 min, range = 18-414 min). After full recovery, the subjects were returned to their holding tanks and monitored daily for shedding of the transmitter and mortality by visually searching the substrate for transmitters and immobile animals. Immobile animals were tapped with a net to determine if the subject was non-responsive. Dead animals and shed tags were removed from tanks and recorded daily until the end of the study.

Wound healing and condition:

Wounds were visually evaluated at days 4, 20, 29, 44, and 61 for all animals alive and retaining a transmitter at the time of observation. Assessment criteria were modified from that of Wagner et al (2000) and Moser et al. (2017), where wound closure and wound inflammation were scored separately on a scale of 1-4 (Table 1.1). An additional metric, a composite wound condition score, was produced from the wound closure and wound inflammation scores. This was formulated by plotting the wound closure and wound inflammation scores on an X-Y plane (axes range from 0-4) and measuring the Euclidean distance from the origin to the observed scores (Equation 1). To ease interpretation, that distance was then rescaled to a range of 0-10, based on the minimum (0) and maximum (4.24) possible distances:

(1)
$$\left(\frac{Euclidean\ Distance - \sqrt{2}}{(\sqrt{32} - \sqrt{2})/10} \right)$$

Relationships between each of three size measurements (TL in mm, Mass in g, and Fulton’s Condition factor (Equation 2, Ricker 1975) and each wound score were explored through simple linear regression (R package “stats” v4.04).

(2)
$$\frac{mass(g)}{TL(mm)^3 * 10^6}$$

Table 1.1. Criteria for assessing wound closure and wound inflammation, modified from Moser (2017) and Wagner (2000).

Score	Wound Closure	Wound Inflammation
1	Severed tissue is rejoined and completely healed.	No inflammation or discoloring internal or external to the wound.
2	Tissue is apposed and remains severed.	Slight grey or pink tissue internal or external to the wound is present. Organs completely internal.
3	Portions of the wound are apposed. This may include apposition around a protruding tag.	Some tissue internal and external to incision is inflamed or discolored (grey or red). May also be characterized by intestines distended through incision site.
4	No severed tissue is apposed.	All tissue internal and external to wound is inflamed or discolored (grey or red). May also be characterized by intestines completely protruding and external from body cavity through incision site.

Swim performance:

Twenty days after implantation, we measured maximum burst swim velocity in all implanted and control animals remaining in the study. Animals were placed in a 155x13x10cm plastic trough (Bayhead) filled with 8cm of water at ± 1°C of the holding tank temperature. A plastic mesh grid marked in 5 cm intervals was positioned in the bottom of the trough to measure distance moved, and all interior surfaces were covered with plastic mesh to prevent animals from attaching to the trough surface. Each animal was placed in the lower end of the trough and allowed a five-minute acclimation period prior to testing. After the acclimation period, animals were induced to burst swim by squirting approximately 3 ml of water from a 5ml pipette (Dauble et al. 2006, Mueller et al. 2006). Each animal underwent three burst trials with a 3-minute recovery period in between trials. A Go-Pro camera (60 fps) was mounted above the trough to record trials, and video footage was processed and analyzed using Kinovea® motion analysis software. Burst speed was measured as the distance the animal traveled in the initial 30 frames (0.5 sec) immediately following the first frame showing ripples produced by the pipette ejection. The maximum observed speed (cm s^{-1}) of the three trials was used in analyses below.

On days 30-32 post-surgery, all implanted animals remaining in the study (n = 30) and 32 control animals chosen at random from approximate same source proportions were subjected to an endurance swimming test (time-to-exhaustion) in a swim tunnel. Animals were individually placed in a 48.2 L mesh-lined chamber of a 121-L Blazka-type swim respirator, with a Leeson Washguard Adjustable Speed AC Motor and Controller. The impeller was powered to 4.5 Hz (water velocity approximately 4 cm s^{-1}). The inner-mesh lining of the swim tunnel was necessary to prevent subjects from attaching to the side of the tube, but rendered the manufacturer's regression equation linking power units of the swim-tunnel impeller to water velocity imprecise.

After a 3-minute acclimation period, animals were induced by water flow to freely swim against a current. As the test progressed, animals would become impinged on the mesh barrier at the downstream end of the tunnel. If the impinged animal maintained active swimming motions while resisting the current, elapsed time continued to be recorded. In the first instance an animal became impinged with a continued absence (10 seconds) of anguilliform movement resisting the water current, a Smith-Root backpack electro-shocking unit sent a brief 12V, 1 hz, 5% duty cycle electrical current into the rear of the swim tunnel. This mild voltage was intended to irritate rather than stun the animal so swimming could recommence with full musculature control. Trials continued for animals induced to resume swimming within ten seconds of continuous electrical current. We defined exhaustion as, and the trial complete when, either of these events occurred: (1) an absence of anguilliform swimming for ten seconds after the second impingement, or (2) no resumption of active swimming within ten seconds of electrical current after the initial impingement. If the animal continued to swim for 60 min without exhaustion, the trial was ended.

Data analysis (tag retention and survival):

Daily mortality data recorded from a 61-day holding period were used to generate Kaplan-Meier survival curves and estimates for control and tagged animals and a log-rank test (Mantel-Cox) was used to assess the difference in survival among the two groups. The *p*-value resulting from a Log-Rank test determines the level of significant difference in survival between tagged and control groups for the entirety of the experiment. This potentially creates "blind spots" in the analysis, such as intra-experiment temporal components existing in distinct windows of time (e.g. delayed post-surgical mortality). These have high informative value for future studies, especially for field studies seeking to use this technology (e.g., setting the post-surgical holding period if surgery related mortality is delayed by a few days). We explored the data with further analyses to determine if present when these effects manifest. To do this, we subset the survival data to where a new dataset was produced for each day (day$_{i}$) including data from day$_{i}$ until the end of the experiment. This nullified deaths prior to day$_{i}$ thereby establishing day$_{i}$ as day 0 in the analysis for each dataset. A Log-Rank test of each dataset produced *p*-values for the period following day$_{i}$ that were evaluated by generating Kaplan-Meier survival curves. This progressive *p*-value gives insight into the presence of blind spots by illustrating the pattern of the significance level in the difference between the tagged and control groups survival through time.

Upon reviewing the survival curves of the tagged and control groups, it was apparent there was a time-dependent component in the survival curves. Mortalities appeared to occur in punctuated events within a group (i.e., were not homogenous throughout the 61-day holding period). Kaplan-Meier based survival analyses, restricted to only one covariate, are unable to capture this effect. Therefore, additional analyses were performed using Cox-Proportional Hazard regression (R package "survival" version 2.44-1.1) with a time-dependent covariate (TDC) to determine if tag implantation was associated with an increased risk of mortality, and to what extent the interaction with time played. The time-dependent covariate was a binomial categorization that was set to one for tagged and zero for control animals surviving to day 32, which gave the model an explicit value to measure the significance and magnitude of a tag effect from days 32-61. This model was compared using Akaike Information Criterion (AIC) to a null model of one covariate (Group) to assess the role of the TDC in the model's fit. We used a counting process form data frame to build the TDC into the dataset, constructed using methodology similar to that of Zhang et al. (2018) and Therneau et. al (2020). An individual animal is represented by one row if mortality was experienced prior to Day 32 and two rows if mortality was experienced after Day 32 or the animal survived the experiment in entirety (covariate set to 1 if tagged, 0 if control). Day 32 was chosen as the break point as it coincided with the first mortality event recorded in the control group. Schoenfeld residuals were examined to determine if the assumptions of a proportional hazard model were met. In both the Kaplan-Meier and Cox-Proportional Hazard analyses, tagged animals that shed their tag were not right-censored at the time of the shed event to preserve statistical power through sample size.

Animals experiencing early mortalities (<5 days) were compared to animals surviving >5 days through separate two-way unbalanced ANOVA's with the three size metrics as predictors. Source (Great Lakes vs. Anadromous) was the additional covariate.

Data analysis (wound healing and condition):

The three wound healing scores were assessed through time by ANOVA comparison with assessment number as the independent variable and wound as the predictor. Post-hoc Tukey-HSD tests explored the significance of relationships between wound scores and assessment number (time) (R-packages “stats” v. 4.0.4, “rstatix” v. 0.7.0).

Data analysis (swim performance):

A two-way unbalanced ANOVA (R-package “cars”) was performed to determine the relationship between maximum observed burst speed and treatment group (Control vs. Tagged) with source (Great Lakes vs. Anadromous) as a covariate. Separate simple linear regression models determined the relationship of size and composite wound score to maximum burst speed for the tagged animals. A time-to-event analysis was used to compare the tagged and control group's time-to-exhaustion probabilities by evaluating their respective Kaplan-Meier survival curves via log-rank test (R package “survival” version

2.44-1.1; survival = continuing to swim). Plotted through time (log-seconds) on the x-axis, survival probabilities dropped on the y-axis as members of the respective groups reached their time of exhaustion. The log-rank test assessed the statistical difference between the cumulative exhaustion probabilities of each group. To assess significance, the log-rank test statistic, where the expected value is the product of the risk of event (number of exhaustion events/number unexhausted) and the number of unexhausted animals at the given time, is compared to the critical value (chi-square) for one degree of freedom (Goel et al. 2010). Additionally, an unbalanced two-way ANOVA tested the null hypothesis that there was no significant difference between swim to exhaustion time and covariates group, and source.

RESULTS

Four days into the experiment one holding tank of anadromous sea lamprey (N=14 tagged, 1 control) experienced 24 h without inflowing water or aeration. These animals were censored from any analysis after that date (per Mantel, 1966).

Tag retention and survival:

Eleven animals shed their tags throughout the experiment. Two events occurred when handling animals during swim performance tests. The majority (5/9) of the remaining events occurred within the first four days post-implantation, and all animals that shed their tags had wounds that were completely open with no apposition in the initial wound assessment on day 4 (wound closure score = 4). The four additional shedding events were recorded on days 19, 20, 29 (x2).

Twenty-five sea lamprey died during the experiment (8 in the control group, 17 implanted with ELAT transmitters). The tagged group experienced increased mortality at the commencement of the experiment, with five animals dying within four days post-surgery. Unbalanced ANOVA test found no size metric or source a significant predictor (Total length: $p = 0.1, F = 2.7,$ Source: $p = .46$, $F = .52$; Mass: $p = .49$, $F = .48$, Source: $p = .98$, $F = .0005$; Condition Factor: $p = .64$, $F = .20$, Source: $p = .59$, $F = .29$). The cumulative survival probabilities (mean ± 95% CI) were 0.849 ± 0.092 and 0.647 ± 0.124 for the control and tagged groups, respectively. The observed difference in survival was significant (Mantel-

Cox log-rank test, p=0.011). Examination of the Kaplan-Meier survival curves and the progressive P-value (Figure 1.2) suggest distinct periods of elevated mortality in both groups. The principal differences in survival between tagged and control groups appear in the four-day period immediately post-surgery, and Days 18-30, roughly corresponding to the period following the burst swim tests (Day 20). Prior to date of the swim-to-exhaustion test (Day 30), no mortalities were recorded in the control group. Following this test, both groups exhibited similar reductions in survival.

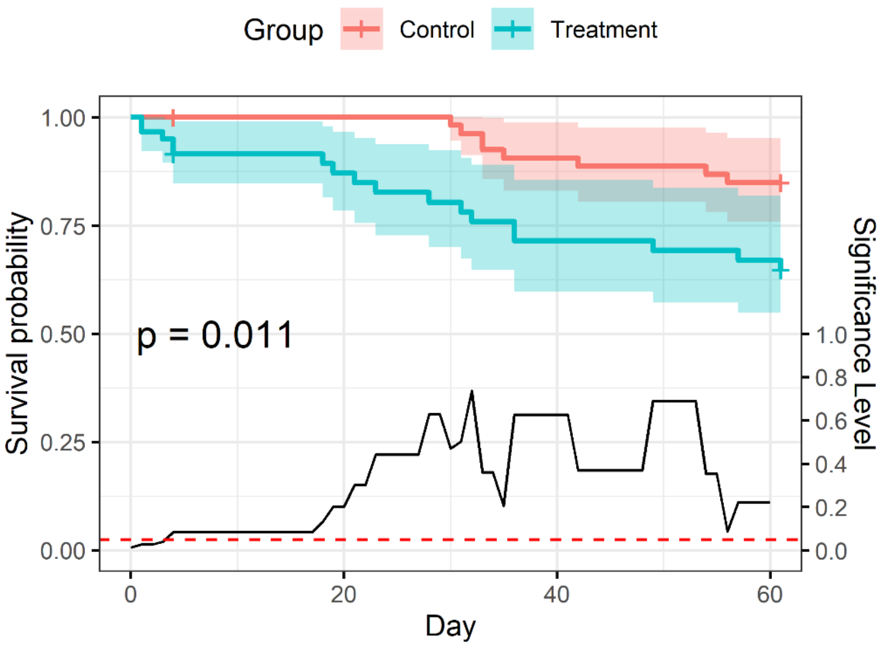

Figure 1.2. Kaplan-Meier survival curves with 95% confidence intervals for control (red) and tagged (green) groups with the overall significance (Mantel-Cox log-rank test). A (+) symbol denotes a right-censorship event in the respective group. The progressive P-value is (black line, right Y-axis) portrays the significance level associated with Log-Rank tests throughout each day of the experimental period. Each point on the line corresponds to the p-value for a Log-Rank test, adjusting the experimental period to begin on that day. The red dashed line represents a significance level of 0.05.

The Cox-Proportional hazard model suggested tagged animals were 7.4 times more likely to experience mortality in the first 32 days of the experiment vs. control animals (coefficient = 2.00, HR = $e^{coefficient}$, 7.4, p = 0.008). The time dependent covariate coefficient was -1.80 (p = .065, 95% CI: -3.7 - .11, se = .97) which implies that after 32 days, the increased risk of mortality in the tagged group was reduced to a factor of 1.22 ($e^{2.00-1.80}$). The ΔAIC (1.86) relative to the null model supports the assertion that the difference of associated risk through time between the two groups is not homogenous. Moreover, the global Schoenfeld residuals of the time-dependent covariate model (p = .63) present less heteroscedasticity than those of the null model (p = .10)

Wound healing and condition:

No animals received a composite score of 0 indicating a completely healed wound by the end of the study period. One animal had a completely closed wound (wound closure = 1) on the final wound assessment, but mild irritation was present (wound inflammation = 2). The initial composite wound score (Day 4) was unrelated to total length (p = .07, Adjusted R^2 = .04, SE = .06) or condition factor (p = .27, Adjusted R^2 = .005, SE = 2.5) but negatively associated with mass (p = .02, Adjusted R^2 = .08, SE = .5). Each addition gram of mass was associated with an improvement of 1.2 composite score units (i.e. a 12% improvement in wound condition). Both wound closure and wound inflammation scores improved through the experimental period, with the greatest improvement occurring between the first and second observation dates (Days 4 and 20, post-surgery). ANOVA revealed time was a significant predictor for all wound scoring metrics. Post-hoc Tukey tests revealed a significant improvement in wound scores performed after day 20 (Table 1.2).

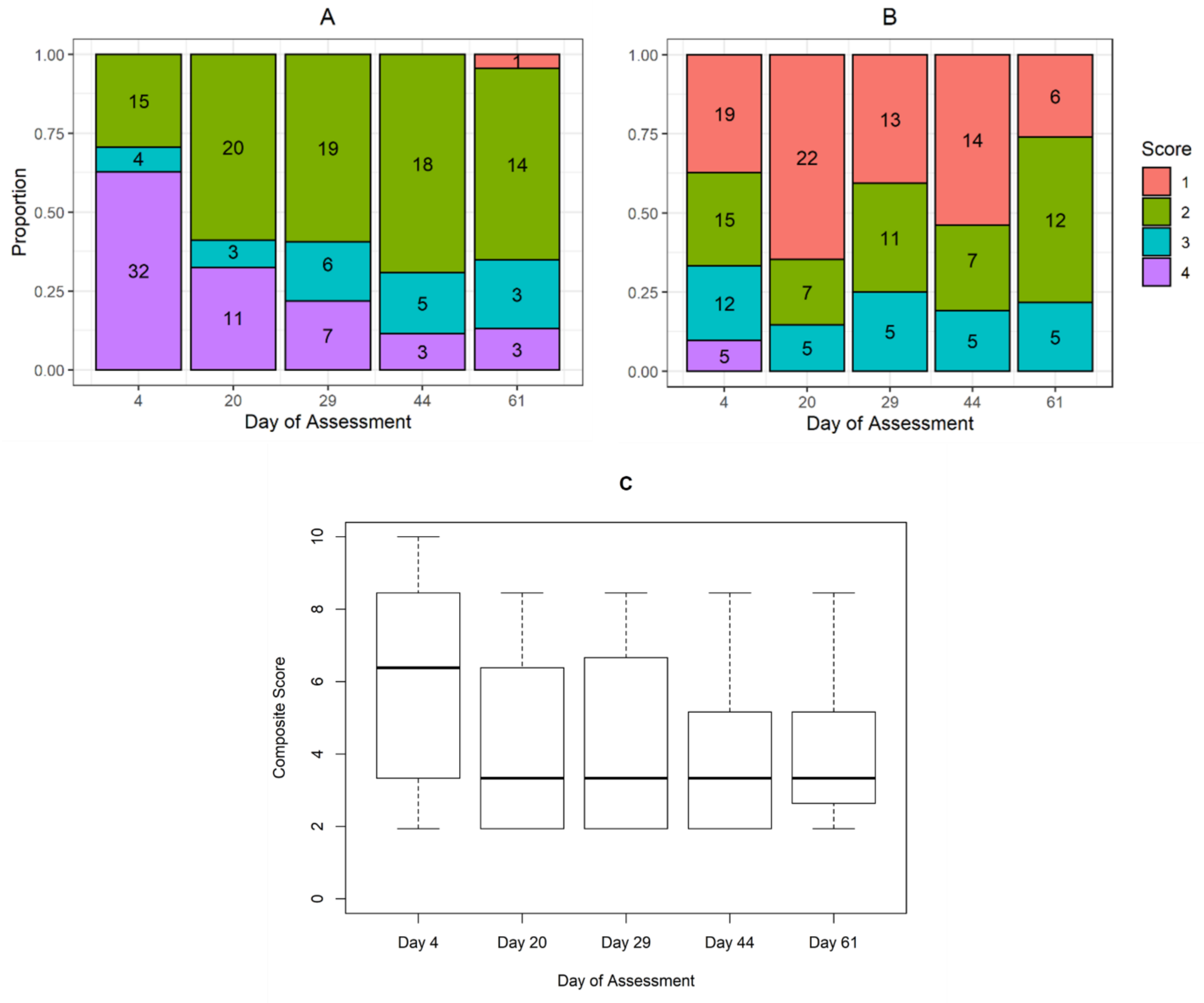

Figure 1.3. Wound assessment scores. (A) Distribution of wound closure scores for animals remaining in the study at the time of assessment. (B) Distribution of wound inflammation scores for animals remaining in the study at the time of assessment. (C) Boxplots of composite wound scores for animals remaining in the study at the time of assessment, showing median (black line), and maximum and minimum values (lines)

Table 1.2. Cumulative wound scores (closure, inflammation, composite) ANOVA comparison through time. Total *p* values and Tukey-HSD results between successive assessments are presented.

Assessment Type	**Total *p***	***p*: Assessment 1-2**	***p*: Assessment 2-3**	***p*: Assessment 3-4**	***p*: Assessment 4-5**
Wound Closure	>.001*	.01*	.98	.89	1.0
Wound Inflammation	.03*	.02*	.47	.91	.72
Composite Score	>.001*	.003*	.99	.85	.96

Swim performance:

Maximum burst swim speed significantly differed between control and tagged groups (ANOVA: p = 0.003, F = 9.51), but was not related to origin of the animals (Great Lakes vs Atlantic drainages; p = 0.33, F = 0.9). Mean maximum burst speeds in cm/s (± 1 se) for tagged and control groups were 26.22 ± 1.81 and 33.83 ± 1.42, respectively (Figure 1.4). The highest burst speed recorded in each group was 57.02 cm/s for tagged animals and 56.68 cm/s for control animals.

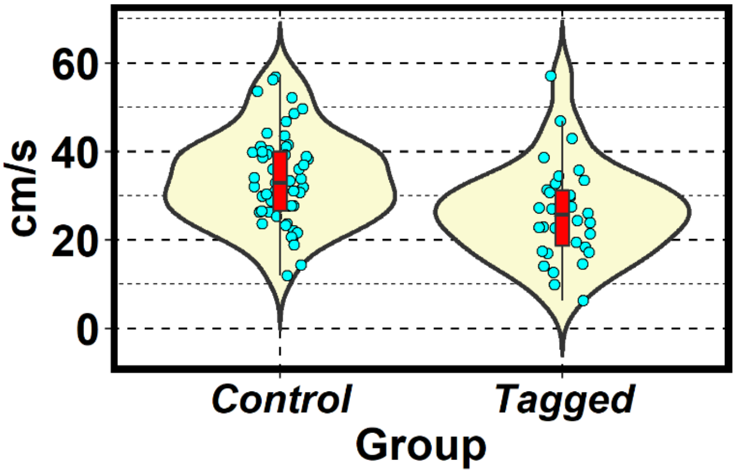

Figure 1.4. Violin plots of recorded maximum burst speeds for control and tagged sea lamprey, overlaid with box plots exhibiting median (black bar), 25% and 75% quartiles (boxes) and non-outlying maximum and minimum speeds (lines). Data are jittered on the X-axis to ease interpretation.

In the tagged group measures of body size were unrelated to maximum burst swim speed (linear regression: condition factor, p = 0.36; total length, p = 0.36; mass, p = 0.97). There was a significant negative correlation between observed maximum burst speed and each of the wound scores recorded on Day 4 post-surgery (linear regression: wound closure, p = 0.031, adjusted R^2 = 0.12; wound inflammation, p = 0.022, adjusted R^2 = 0.12; composite wound score, p = 0.007, adjusted R^2= 0.18, Figure 1.5). However, the composite wound score recorded on the day of the burst swim test (Day 20) was not a significant predictor of maximum burst swim speed (linear regression: p = 0.22, adjusted R^2 = 0.02).

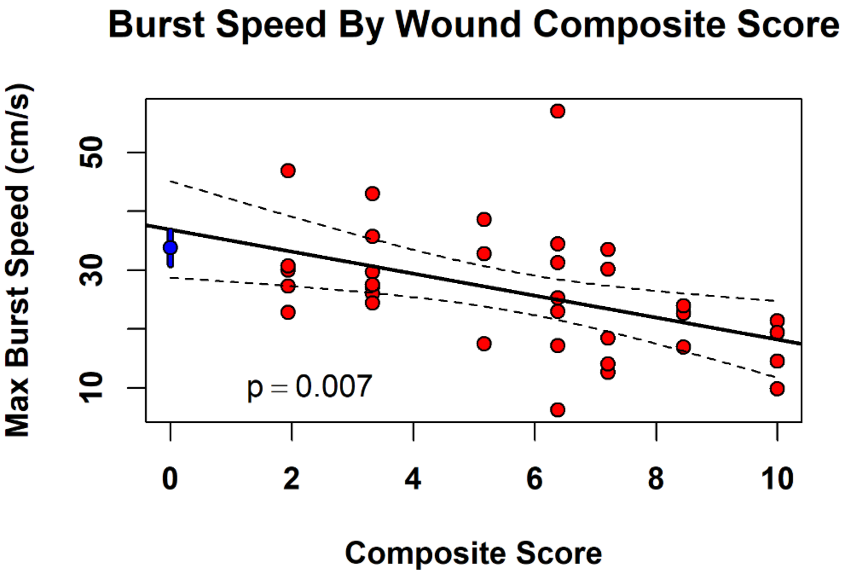

Figure 1.5. Scatterplot and regression of the maximum burst swim speed vs. composite wound score. For reference, the mean (± 95% CI) maximum burst speed for the control group is plotted at a value of 0 on the x axis (blue).

Three animals in each of the tagged and control groups could not be induced to swim in the swim tunnel and were not evaluated for swim-to-exhaustion. Two additional animals in each group exhibited lethargy upon retrieval from their holding tank and were censored from the analysis. One animal from the control group completed the full trial without exhausting, whereas all animals from the tagged group exhausted prior to 60 min. Time-to-exhaustion did not significantly differ between control and tagged groups (ANOVA: p = .32, F = 1.02), and was not related to origin of the animals (Great Lakes vs Atlantic drainages; p = .17, F = 1.96). Mean time-to exhaustion in min (± 1 se) for tagged and control groups were 3.07 ± 1.14 and 7.04 ± 2.38, respectively (Figure 6A). Similarly, no difference in the Kaplan-Meier survival curves was detected (log-rank test, *p* = 0.18; Figure 1.6B).

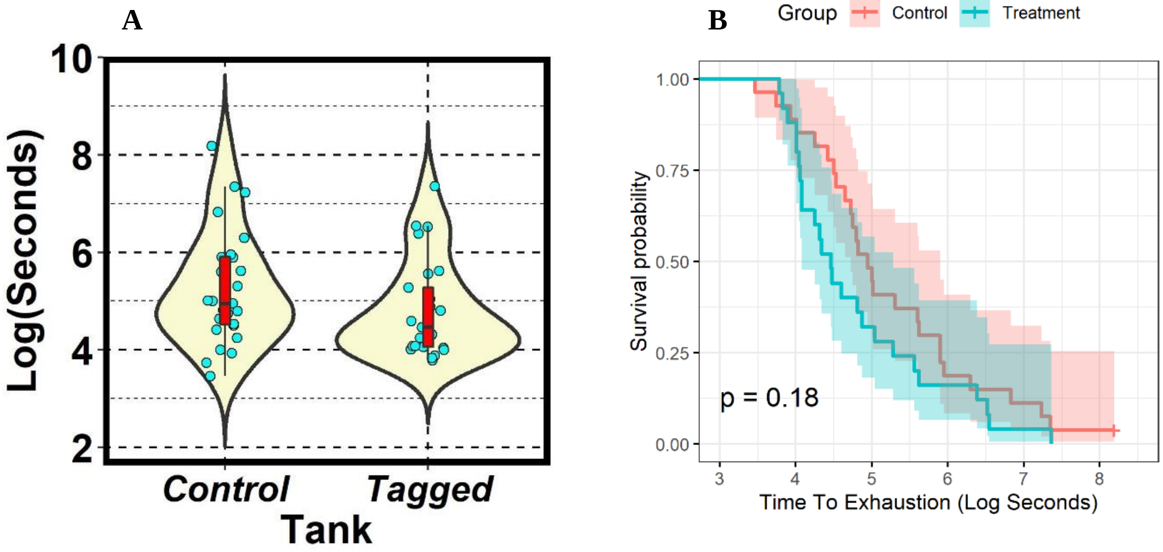

Figure 1.6. (A) Violin plots of recorded time to exhaustion for control and tagged sea lamprey, overlaid with box plots exhibiting median (black bar), 25% and 25% quartiles (boxes) and maximum and minimum values for non-outlying results (lines). Data are jittered on the X-axis to ease interpretation. (B) Survival (exhaustion) curves for control (red) and tagged (blue) animals in Swim-to-Exhaustion tests (p-value refers to the result of the log-rank test comparing curves).

DISCUSSION:

The results of this study suggest the ELAT transmitter can be used to tag newly transformed sea lamprey with survival and tag retention akin to that for similar sized PIT tags. The 61-day survival of our implanted animals was 65%, well within the range reported in previous studies with larval and juvenile lampreys (Dawson et al. 2015, Moser 2017, Mueller 2006, Mueller 2019)). Importantly, survival until the expected lifespan of the ELAT battery (32 days) improved to 76%, despite holding animals without access to food for several months prior to the start of the experiment. The mortalities and tag losses we observed generally coincided with the immediate post-surgical period (4 days), or immediately following handling associated with the swim performance tests. The lack of a clear size relationship in the early mortalities suggests a surgeon effect rather than tag internalization, possible by nicking the gastrointestinal tract or other internal organs (Cooke et al. 2003; Dawson et al. 2015; Moser et al. 2017). This is supported by both the lack of a subsequent mortality for two weeks and the stabilization of improved composite wound score means after the initial four days. Dawson et al. (2015) reported nicking of intestines as leading to early onset mortality in juvenile sea lamprey (10% of study animals), as well as animals exhibiting protruding intestines post-operation, which we also observed.

That the survival analysis demonstrated a significant difference in the timing and magnitude of mortality during the study (vs the control group) should not dissuade researchers from the use of this technology. The progressive *p*-value evaluation suggests the significant difference between the two groups is heavily weighted toward the first four days of the experiment. In other words, was a consequence of the stress associated with handling, anesthesia, and surgery. This assertion is supported by the time-dependent covariate coefficient in the Cox proportional-model and the comparable swim-to-exhaustion results in tagged and untagged animals. The low coefficient value for the time-dependent covariate in the Cox-Proportional Hazard model relative to the first time-period coefficient suggests that the treatment effect became non-significant after 32 days. Unfortunately, we could not test the effect of the time dependent covariate for the first 32 days, as the complete lack of mortality in the control group prevented the model from converging. We are hesitant to say with certainty the increased mortality in tagged animals is completely absent after 32 days due to the high standard error, but if present, the effect is extremely diminished. We are also wary of both sample size limitations and the punctuated mortality events when considering these results. Specifically, in the control group, in which the group’s initial mortalities occurred immediately following swim to exhaustion tests. Unlike those that underwent surgery, the swim-to-exhaustion test was these animals first exposure to a prolonged physical stress event; and like the tagged group post-operation, a punctuated mortality event occurred directly afterwards (5 deaths within < 5 days).   These data suggest that the swim-to-exhaustion test was a stressor leading to increased mortality in both groups group. Further, as all animals in this study were not fed after capture, it is likely diminished energy reserves in animals that had completed metamorphosis but not yet begun parasitic feeding was an additive factor. The mirrored mortality in the tagged group during this time-period and the Schoenfeld residual values support that this was not a violation of the hazard proportionality assumption (George et al. 2014, Zang 2018).

Wound healing rates in our study lagged from the most similar study assessing wound scores in implanted in Pacific lamprey. Though on a different scale, our results on day 20 appear similar Pacific lamprey larvae held in the field after 14 days (Moser et al. 2017). Furthermore, six laboratory specimens in their study showed complete healing after 14 days whereas only one in ours had a completely closed incision through 61 days. This could be a result of a 3.5x lower water temperature in our tanks and/or that our animals were not fed.

We allowed a 4-day holding period prior to the first wound assessment to prevent shed events from handling but there is a high likelihood that this knowledge can be attained sooner and preserve microtransmitter life, as 80% of the animals that had the worst possible composite score were noted as having significant trauma immediately post-surgery. To maximize this technology's ability to inform in field studies, a brief holding period after recovery from anesthesia and before release to assess wound condition after recovery is recommended. If the wound does not appear to have inflammation over a moderate level and/or a complete lack of apposed tissue around the incision, it is likely that the animal will have limited, if any, physical incapacitation compared to an untagged conspecific.

A core assumption in field studies using implanted telemetry tags is that tagged individuals are characteristic of the natural population in terms of movement behavior and fate. Consequently, it is important to consider the effect of the size of the study animals relative to the historic catch data (Hondorp 2015). Our experimental animals were somewhat smaller than the historic mean size observed in the Great Lakes and did not encompass the full range of size. It is common for tag effect studies to recommend minimum size limits for use of animals in telemetry work, based on the desire to satisfy the criteria of minimal tag effect on the animal's performance. Here too, the surgeon reported difficulties inserting tags into sea lampreys with small body cavities. However, this practice conflicts with the need to use representative animals, as demographic measures such as mortality are highly size-dependent in fishes, specifically those in larval or juvenile states (Bailey & Houde, 1989; Sogard, 1997). In other words, preferential use of subjects that are drawn from the right-side of the size distribution may bias estimates of vital rates made using those animals in field studies. Whether this is compensated for by the impairments imposed by the tag is worthy of further study. Similar studies to ours in larval and juvenile Pacific and Sea Lamprey have reported minimum size recommendations based on the relationship of mortality and total length (Mesa et. al 2012, Mueller et. al 2006, Simard et al. 2017, Schreck et al 1999), yet these recommendations are quite variable (120-150 mm). Our results suggest total length may not be the ideal measurement to base these thresholds. While there was no significant correlation of any size measurement and mortality in our tagged animals, larger mass was associated with an improved composite wound score. Total length does not characterize the three-dimensional space the tag is inserted into. The intestines of a sea lamprey range laterally throughout the body of the animal, so it may be the ratio of the tag to intestinal length is less important than the ratio of tag to available space between the intestines and body wall (Manzon 2015). We posit that girth rotundity or a metric that includes mass in concert with total length such as condition factor, or Δobserved vs. expected W in the classic power function relating fish length and weight, $W=\alpha L^n$ could be more suitable metrics to set the minimum threshold for implantation. To support this notion of a 3-dimensional metric as a new implantation threshold, several lamprey exhibited discoloration posterior to the implanted tag proximate to surgery completion. This is a symptom of blood impediment through the dorsal aorta caused by pressure from the tag, documented by Dawson et. al (2015). This symptom was obvious from a cursory visual inspection and appeared prior to recovery from anesthesia, however, was not an indictment of impending mortality. Two animals displaying this symptom proximate to post-operation no longer exhibited discoloration by the first wound assessment on day 4 and survived the length of the study, perhaps by the mechanism of a posed by Moser et al. (2017) of a posterior shift in tag position.

We observed a 22% reduction in maximum burst swim in tagged animals relative to the control group, suggesting a significant negative impact to high-speed acceleration as a consequence of tag implantation. Though their mean percent difference (7%) was smaller than ours, a statistical difference was also seen by Mueller et al. (2006) in juvenile Pacific Lamprey. This difference was unrelated to the source of the animal, suggesting populations in the Great Lakes and the Atlantic basin exhibit similar capacities at this life history stage. In addition to the burden of the tag, our results suggest this attribute of swim performance was also related to condition of the wound four days post-surgery. Although our relatively small sample size restricts a powerful statistical analysis, the mean burst speed of animals with composite wound scores < 6 ($n = 15$) were within 9% of the mean speed observed in the control group. This is further supported by the observation that the mean maximum burst swim speed observed in the control fish was similar to that predicted for a tagged animal with a composite wound score of zero (fully healed). Conversely, there was no significant difference in the time to exhaustion when placed in the swim tunnel 10-12 days later. The lack of a significant difference between tagged and control groups in swim-to-exhaustion testing indicates either the effect of implantation is minimized by day 30, that animals healthy enough to survive to day 30 are in similar physiological shape as untagged controls, or that impairment of high acceleration burst swimming is mechanistically different than impairment of sustained swimming. As fish accelerate through the water column, speed is modulated by the amplitude of the body region responsible for generating motion (i.e. head, body, caudal) (Alexander 2003, Biewener 2003). In another anguilliform swimmer, the Atlantic Needlefish (*Strongylura marina*), it has been noted that body amplitude increases with water speed which could explain our results (Liao, 2002). It is plausible there is an amplitude threshold where tag retention begins to restrict swimming ability in fishes. This is magnified in anguilliform swimmers, where full body oscillations deem requisite that the tag is in the kinematic curve creating thrust and that this threshold is between the amplitude sizes produced in steady and burst swimming. This is important to note for field studies because reduced burst swim ability could affect predator avoidance in natural environs leading to overestimates of natural mortality during outmigration.

The ELAT transmitter has the potential to open the door to a greater understanding of the outmigration phase of the sea lamprey's life cycle. The ability to gain insight into the fate of migrants as a function of the features of the rivers that regulate mortality (e.g. predator density, habitat type, etc.) is likely to lead to the development of new control methods target sea lamprey in their last phase before the initiation of parasitism (Johnson & Meihls 2014). In addition, it allows for the investigation of the effects of habit degradation and barriers to downstream migration (dams and weirs, water intake structures), and overharvesting; the principal threats to several migratory lampreys in their native range (Hansen et al. 2016, Jones 2007; Maitland 2003, Mateus et al. 2012, Moser 2015). The fact this technology has now proven feasible in laboratory settings across multiple anguilliform species, is promising to other Anguilliformes with relevant behavioral unknowns, such as the regionally endangered American Brook Lamprey (*Lethenteron appendix*) of the United States Eastern Seaboard and the critically endangered European Eel (*Anguilla Anguilla*) (Department, N.H. Fish and Game , IUCN Red List of Threatened Species).

CHAPTER 2: Modeling Juvenile Sea Lamprey Survival and Migratory Behavior with New JSATS Technology.

ABSTRACT:

Migration is an evolved action unrestricted by taxa, where species trade the energetic cost and risk of mortality in exchange for fitness benefits a new habitat provides. Often, migration is tied to a movement to and from breeding grounds or the search for food. Such is the case for the invasive Sea Lamprey in the Great Lakes, where newly transformed juveniles disperse downstream from natal habitat to begin their piscivorous life-stage, before migrating once more back upstream to spawn. Little is known about the Sea Lamprey between the time they transform and the time they commence their breeding migration. The time during the outmigration is the last feasible opportunity to implement management measures within the Great Lakes ecosystem, thus there is considerable interest in learning the species' nuances during this time. We performed an experiment with novel acoustic telemetry technology to shed light on the behavior and cumulative survival of outmigrating Sea Lamprey by tagging 56 animals and releasing them in a river/lake system with eight receivers interspersed throughout. Our objectives were to assess the utility of ELAT tags and JSATS technology for the first time in the Great Lakes region, determine reach specific survival estimates for outmigrating sea lamprey, and to use collected data to pinpoint any behavioral patterns. We found nautical twilight the time centered around the initiation of dispersal (±16.21 minutes), and for it ($p = .001$) as well as water discharge ($p = .009$) to be a significant predictor of punctuated movement within the outmigration. Detection results were not sufficient to produce definitive reach specific survival estimates from Cormack-Jolly-Seber Mark Recapture analysis, but simulations performed give guidance for future research. As animals moved downstream through the study area detections decreased, however a simulated model using a staggered release provide methodology for maximizing detection output. Through the analysis of these results, we provide valuable information for managers targeting this phase in the efforts to control and research Great Lakes Sea Lamprey and offer recommendations for future studies of similar nature.

INTRODUCTION:

Migration is defined by Dingle & Drake (2007) as “a relocation of the animal that is on a much greater scale and involves movement of much longer duration, than those arising in its normal daily activities”. Migration is an adaptive strategy evolved over countless generations where the costs of long-distance movement through unfamiliar territory (e.g., energetic, mortality) is surpassed by the fitness benefits garnered by occupying habitats rich in resources for growth or reproduction (Brönmark et al. 2014). As humans continue to modify and fragment nature, migratory species are especially at risk due to their dependence on multiple habitats for proliferation (Lennox et al. 2019). In fish, fragmentation of migratory pathways typically occurs as structural impediments blocking streams (i.e. dams, roadways) that prevent them reaching habitat critical to their lifecycle, and has led to a mean global decline in abundance of 76% in freshwater fish (Dienert et al. 2020). Questions regarding the impact barriers have on fish migration patterns and survival are important to distinguish for efficient management strategies for these species (Lennox et al. 2019). Conversely, many diadromous and oceanodromous fishes are commercially harvested. Thus, understanding these movements are important for both marine conservation and food supply management (Lowerre-Barbieri et al. 2019). To try and answer these questions, electronic tracking (“telemetry”) is the foremost used technology because it allows for passive data collection of animal movements through space and is unrestricted by the need for physical recapture of specimen. Acoustic telemetry, a type of electronic tracking, is widely used in fishes due to its ability to detect movements in both freshwater and marine environments, large detection range (>100m, tag dependent), and long tag life (10+ years, tag dependent) (Hussey et al. 2015).

Small fishes, including early life stages and small-bodied adults that fuel production in larger fishes (so-called ‘forage’ fishes), are of special note as they typically experience higher mortality risk. Further, lifetime mortality is highest at larval and juvenile life-history stages – the time when recruitment to the adult population, and thereby population size, is determined (Anderson 1988, Bailey & Houde, 1989, Grausgruber & Weber, 2020, Sogard, 1997). Compounding these risks with migration, are species like Salmon and Lamprey which migrate from natal habitat as small subadults. Therefore, bettering our collective understanding of these factors would accentuate management efforts in species with especially vulnerable early stages or small fishes of conservation interest.

Generally, the rule of thumb in aquatic telemetry is the implanted transmitter should <2% of the fishes dry weight (Winter 1983). Though that rule has been challenged empirically many times over, it remains a general guideline with a conservative extendibility of tag burden to 6-10% (Brown et al. 1999; Jepsen et al. 2004; Smircich and Kelly 2014). With this extendibility considered, small-bodied fish remain at a disadvantage in telemetry research due to technological limitations affecting transmitter size (Deng et al. 2021). Recently, the PNNL fabricated the smallest cylindrical battery in existence with a capacity of >1 mAh and encased it in a novel microtransmitter that could break through the aforementioned size restrictions. This new microtransmitter is approximately the size of a PIT (Passive Integrated Transponder) tag (12.xmm, .08g), but with an estimated detection range of 80-140m (Deng et al. 2021). These dimensions make it possible to study the movement and behavior patterns of fish smaller than ever before, thereby allowing the possibility to answer these important questions previously unviable.

Pilot studies assessing the feasibility of this tag have been successful in Pacific Lamprey (*Entosphenus tridentatus*) and American Eel (*Anguilla rostrata*). Each study had detection rates > 95% and the translatability of the collected data to management decision making was witnessed when the results of the American Eel movement analysis illuminated the imperiled species' preferred migration corridor which led to the construction of an eelway around an intermediary dam (Deng et al. 2018, Deng 2019, Deng 2021, Leidtke et al. 2019). In our experiment from Chapter 1, we examined the effects of this tag when implanted in juvenile Sea Lamprey (*Petromyzon marinus*) in a laboratory setting. We established that swim-performance and survival rates were similar to findings from previous PIT tag assessments, and that the tag merits further examination in field studies to determine its utility to answering movement behavior questions in small anguilliform species weighing >4.5g.

In the Great Lakes basin, there has been an ongoing battle of nearly seventy-five years to curb the population of this dynamically invasive species (Knight & Bocking 2016). Sea Lamprey populations are currently held in check by an extensive pesticide application regime that targets larvae aggregated in stream beds prior to metamorphosis into the harmful parasitic phase. Sea Lamprey undertake two migratory events during their life cycle; first, when they emerge from substrate as larvae and disperse from their natal habitat to commence parasitic feeding in the lakes, and the second, their migration back into rivers to spawn after they have completed their parasitic phase. Current population models, a valuable tool in control decision making, are focused on larval population numbers, the primary target of pesticide control. However, as the goal of sea lamprey control is to limit damage done at the parasitic phase, the ability to estimate survival during outmigration would improve the models' ability to predict damage to lake fishes by accounting for variation in outmigration survival across rivers that vary in habitat size and type (Howe et al. 2012, Robinson et al. 2013). When Sea Lamprey larvae emerge from the substrate to outmigrate from their natal habitat, they enter a new three-dimensional setting with new risks; predator and environmental induced mortality (Lucas et al. 2001). In the well-studied Pacific salmon, research has shown that smolt migrants experience mortality at a rate >70%, and that mortality is a function of both distance traveled and predator density (Anderson et al., 2005, Clark et al., 2017; Goetz et al. 2015, Michel et al., 2015; Welch et al., 2009). If similar pressures influence outmigratory Sea Lamprey mortality, then current population models both overestimate outmigrant survival to the parasitic phase and fail to account for distance or habitat related predator density (Bhagat & Ruetz, 2011). For example, tributaries along the western shore of Lake Michigan frequently include a Drowned River Mouth lake. Geomorphologically akin to drowned river mouth estuaries in marine systems, these areas are locales of high production (Elliot & Whitfield 2011, Jude & Pappas 1992). With increased production, including predators, it is likely outmigrant survival varies across river systems in the Great Lakes Ecosystem in response to the presence and size of lakes in the river continuum. As little is known about this phase of Sea Lamprey life, any insight into the behavior of the organism could aide mitigation (Evans et al. 2021). Currently, there are no active control measures targeting outmigrating Sea Lamprey, but non-physical cues such as light, sound, electric current and alarm cue have shown promise in preliminary trials (Johnson et al. 2014, Johnson et al. 2020, Mickle et al. 2018).   Outmigrant capture is conducted via the deployment of nets across river channels but catch-per-unit effort (CPUE) is quite low (Grunder et al. 2021, Steeves and Barber. 2020, Barber and Steeves, 2021). Knowing when a Sea Lamprey is likely to be actively navigating a river during outmigration could compliment future control implementation and maximize CPUE for specimen collection.

Mark-Recapture studies are a popular technique for analyzing animal populations that involves marking a fraction of a population and later recapturing the marked individuals to estimate growth, survival, recruitment, abundance, or movement (Royle et al. 2013). Current available estimates of mortality in sea lamprey during the juvenile phase derive from relatively low efficiency (7.8%-12%) active-recapture methods requiring physical recapture when the animal migrates into rivers to spawn (e.g. coded wire tags, colored dye injection; Hanson & Swink 1989, Swink & Johnson 2014). Until the development of the PNNL tag, small (8-12mm), Passive Integrated Transponder (PIT) tags were the only passive-recapture technology suitable for implantation on larval or recently metamorphosed Sea Lamprey. However, their very small detection range (~1m) also lead to poor recapture rates (5-14%), and are only used in relatively narrow and shallow rivers (Dawson et al. 2015, Miehls et al. 2019). The new PNNL tag, with the same roughly the same dimensions as a 12mm PIT tag, has the capacity to vastly improve passive recapture of outmigrating sea lamprey. Using JSATS acoustic receivers, these tags can be heard at distances of 80m-140 m in river environments (Deng et al. 2021), greatly improving the likelihood of passive recapture in rivers large and small. This technology also opens the door on studying the movements of a broad array of important small fishes. For example, understanding the timing and magnitude of dispersal movements in Round Goby (*Neogobius melanostomus*), an invasive small-bodied fish that is an important egg predator of nesting game fishes, is needed to accurately assess and predict fishery impacts (Kornis et al. 2012). More broadly, the United States Fish and Wildlife Service (USFWS) Endangered Species list identifies 86/140 (61%) of fish listed as endangered as varying types of small-bodied fish (FWS, search terms: “chub”, “dace”, “darter”, “gambusia”, “madtom”, “minnow”, “pupfish”, “shiner”, “stickleback”). The Sea Lamprey itself is extirpated in portions of its native European range and was considered vulnerable by Maitland 2000. The Pacific Lamprey is considered a species of concern by the USFWS, primarily because of abundance and distribution reductions partially stemming from migratory barriers (Lamprey Technical Work Group 2020, OFWO 2021). If viable, this technology could have overarching implications for control and conservation management across a wide array of fishes.

In the winter of 2020/21, we performed a field experiment to test the efficacy of this new technology at providing more robust detection results for Mark-Recapture and behavioral analyses such as movement timing, ground speed, and the relationships between these and environmental covariates. Our objectives were to provide the first robust insight into the survival rates of recently transformed juvenile sea lamprey (“transformer”) outmigrating from their natal habitat downstream, and to determine if varying habitat types (lacustrine vs. riverine) were affiliated with changes in movement timing and/or survival rate. Additionally, we sought to evaluate performance of the technology in a typical Great Lakes stream to refine future research efforts using it. Entities such as receiver spacing are important aspects to Mark-Recapture experimental design, as more space between receivers leads to fewer recaptures, which leads to model bias and imprecision (Efford 2012, Royle 2013). Therefore, we assessed our recapture results to determine where experimental design improvements could occur.

METHODS:

Eight telemetry receivers (ATS SR3001 *Trident*) with onboard dataloggers were deployed throughout the complex in a variety of habitat types in the White River/Lake complex (Oceana and Muskegon counties, MI), a tributary to Lake Michigan. Throughout a 34-day data collection period we accumulated detection data from 56 transformer Sea Lamprey and analyzed a variety of aspects regarding Sea Lamprey behavioral, movement, and survival patterns. To advance knowledge on transformer behavior we used the collected data to establish ground speed metrics, fit a mixed effect logistic regression predicting downstream movement with external environmental covariates that can be gathered in real time, calculated, and analyzed diel timing of downstream movement, and calculated the speed of downstream movement. In addition, we tested the technology itself for detection range.

We also fit a spatial Mark-Recapture model with output parameters: survival rates (Φ), and detection probability (p). A separate goal with potentially broader implications, was to test the efficacy of the technology in general. Our sample size in this experiment was relatively small primarily due to the innate challenges of trapping downstream migrants, but that would likely be the case for imperiled animals as well (Katapodis et al. 1994). To assist future research and management, we simulated models with varying sample sizes and replicated detection histories from poor and robust Φ and p point-estimates to parse out minimum input needs for stable parameter estimates. The size of this tag dictates a relatively short battery life, an important realization in our study because dead tags could lead overestimates in mortality, especially in unidirectional (migratory) studies. To account for this, we also evaluated the effect of a simulated two-site staggered-release model on parameter variation of downstream sites.

Equipment & Equipment Testing:

Lamprey movements were detected by eight individual acoustic receivers (Advanced Telemetry Systems SR3001 Trident) with built in dataloggers recording to internal 32GB SD memory cards. Supplemental 12 cell battery packs ensured the prolongation of receiver life (an additional ~55 days, total of ~ 100 days) throughout the entirety of the experiment. Prototype Eel Lamprey Acoustic Transmitter (ELAT) microacoustic transmitters built by Pacific Northwest National Laboratory (PNNL) and Army Corps of Engineers (ACOE) were implanted into newly transformed juvenile sea lamprey. This tag emits a frequency of 416.7 kHz at a fixed source level of 148dB powered by lithium/carbon fluoride microbattery with an estimated life of ~30 days at a 5 second ping rate interval (PRI) (Deng et al. 2021).

Range testing was performed at three receiver locations before and during the experiment with a tag configured for a high ping rate (PRI = 1 second). The range test tag was taped to a lightly anchored rope, submerged, and towed behind a kayak (~1.5m behind GPS unit) in the river's thalweg starting approximately 300m upstream to 300m downstream of each receiver. GPS coordinates were recorded every second using a Garmin (GPSMAP® 64x) handheld GPS unit (GCS WGS 1984), time-synched with the receivers. Receiver data was filtered (JSATS Autonomous Receiver Data Filtering Software v. 1.04, Deng et al. 2017) for recorded detections of the test tag and the time of detection was matched with the recorded GPS location at that time. The haversine distance (R package *geosphere* v. 1.5-10) of receiver location and the first (upstream) and last (downstream) detection of each drift was recorded. This gave two replicates per drift; two drifts were done at three different receiver sites for a total of 12 replicates.

Additional range estimation was performed using empirical data of implanted tags gathered from receivers collected during the experiment. Estimated travel speeds (m/s, one outlier removed via Grubbs Test, $p < .001$, see : *Estimating Ground Speed and Movement Timing*) of animals collected from receivers 1-3 were multiplied by the number of seconds between the first and last detection for each receiver and the product divided by two to estimate the detection radius for each travel event between the three receivers ($n = 104$, Receiver 1 = 39, 2 = 37, 3 = 28). This is not an explicit measure of range testing as there is an assumed constant speed and thalweg positioning of the animal within the registered detection data, therefore we term this ‘realized ground speed’. In this calculation, ground speed metrics from movement events between receivers I and II were used in estimated range for receiver II. Additionally, one-way ANOVA and corresponding Tukey HSD tests checked for significant differences between receiver detection ranges (R-package “stats”, version 4.0.4).

Site Selection, Design, and Deployments:

The White River complex (Oceana, Muskegon Counties, MI) was selected for the variability of the habitat and regime types within the system. The system is contained in a relatively shallow river channel (primarily ~ 1.5m) that flows into a wetland area near Hilts Landing (Whitehall, MI) before entering the drowned river mouth (DRM) of White Lake that discharges to Lake Michigan through a hardened shipping channel.

Eight receivers were deployed starting approximately 33.25 km upstream (ArcMAP 10.7.1) from the confluence channel of White Lake into Lake Michigan at locations selected by accessibility and habitat characteristics. Three receivers were place in the riverine portion of the system approximately equidistant from each other (mean = 4.8km, ArcMAP linear referencing tool), one was placed in the wetland habitat at Hilts Landing, a "gate" of two receivers with overlapping detection radii was placed at the head of the DRM (White Lake), and two were placed at the terminus of White Lake with non-overlapping detection ranges (Figure 2.1).

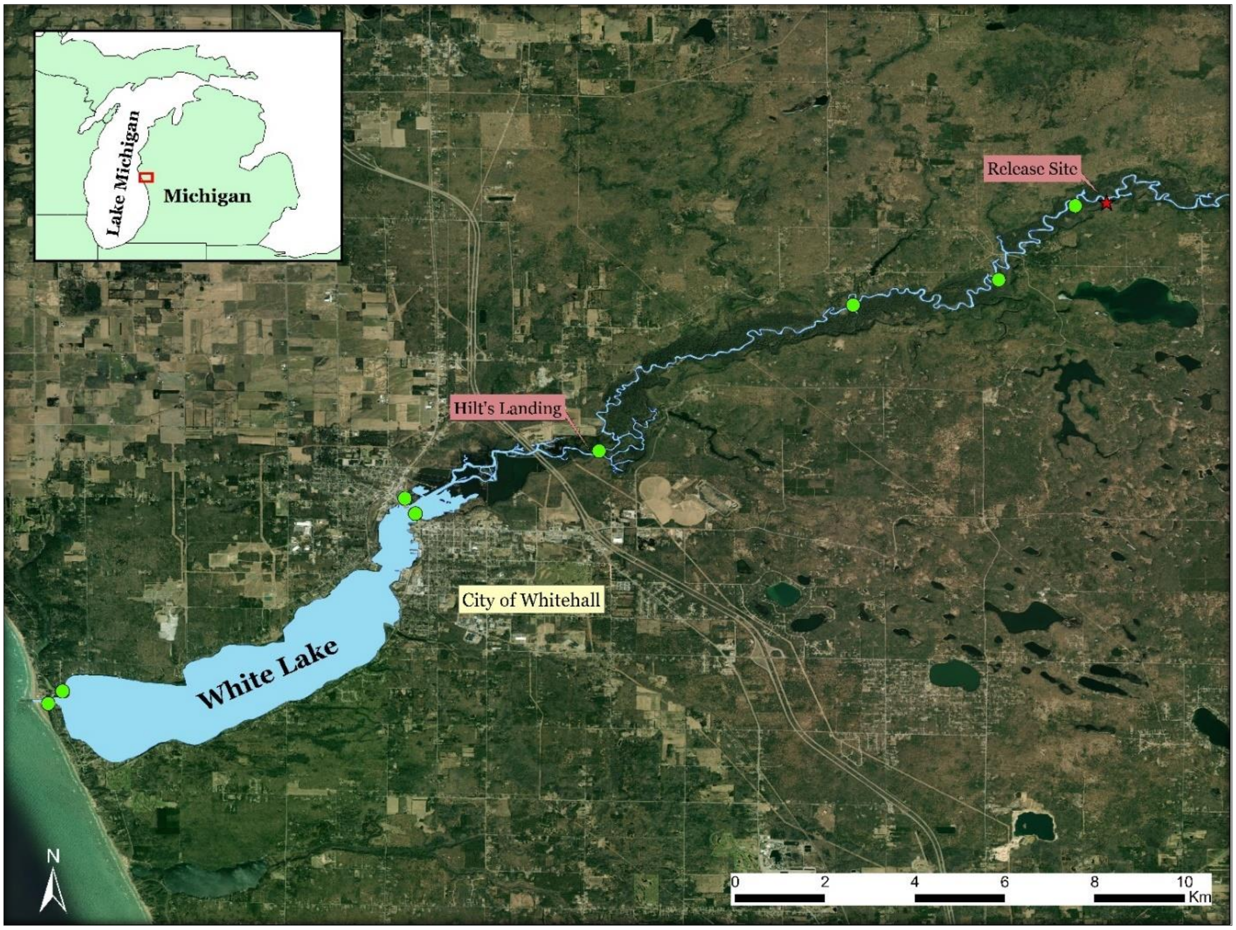

Figure 2.1. Map of the study area through the White River/White Lake complex. Green dots represent receiver locations. The study area consisted of a riverine portion beginning at the release site (red star) and bearing the first three receivers. Receiver IV (Hilts Landing) was placed in the wetland portion of the system, and the two proximate receivers downstream were a gate with overlapping detection ranges at the onset of White Lake. The two terminal receivers were the downstream extent of the study area with non-overlapping detection ranges at the confluence to Lake Michigan.

Covid-19 restrictions prevented complete range testing prior to the start of the experiment, therefore, to determine specific locations at each site for deployments (i.e. line of site, radius of independent/dependent receivers) we used the low end of the estimated detection range (80 m) supplied from the manufacturer of the tags (PNNL). Receivers were fixed to anchors by a short section of chain and a quick-link connector. A galvanized steel cable or rope connected the anchor to a fixation point on all receivers except the final downstream receiver which was sunk in the channel connecting White Lake to Lake Michigan. Riverine receivers were fixed to trees on the banks of deep (>2 m) sections with line-of-sight distances of >75m extending in straight lines both downstream and upstream. Two HOBO Pendant® MX Temperature/Light Data Loggers were fixed to the equipment anchoring the upstream most receiver to gather temperature (°C, ±0.5) and light (Lux, ± 10%) data throughout the experiment. Status of receivers were checked, and data retrieved approximately every two weeks during the experiment. The receivers were removed 40 days (10 days beyond expected tag life) after the final release to conclude the experiment.

Surgery, Handling, and Releases:

Fifty-six transformer sea lamprey were collected via drift net while outmigrating in Furlong Creek (Mackinac Co. MI), a tributary to Lake Michigan, were surgically implanted with tags and held for three days post-operation to monitor for mortalities or injury from implantation (27 Nov -12 Dec 2021, Hammond Bay Biological Station). Surgical protocol followed that established in Chapter 1, with an increase in anesthetic agent to decrease time to stage-IV anesthesia (AQUIS-20E,10% eugenol), 0.8 ml/L, 80 ppm active ingredient. To maximize the likelihood of animals encountering a freshet event to spur downstream movement, surgeries and releases were done in three batches three days apart (01 Dec 2021: n =16; 04 Dec 2021: n = 20; 07 Dec 2021: n = 20). After the holding period, animals were transported in an aerated cooler filled with Lake Huron water to the release site. Water temperature in the transportation cooler was checked every hour during transport (~4 hours) to ensure water temperature remained within 5°C of that in holding tank. Prior to release, river water was poured into the cooler to slowly lower temperature to within 2 °C of that in the river. To give animals adequate time to acclimate to the environment prior to the suspected nocturnal movement, animals were released in the early evening (>1hr before Nautical Twilight) at Diamond Point Campground (Oceana County, MI).

Estimating Ground Speed and Movement Timing:

We collated receiver data from the first six receivers between the release site and the entrance to White Lake and filtered to capture detections made by two consecutive receivers within the same 24 h. period (i.e. a single movement night). The last detection time from the upstream, and first detection time of the downstream receiver were used to estimate the time (hours) spent traveling between receivers. Linear referencing software (ArcMap v. 10.7.1) determined the river distance (Km) between all receivers, which was then divided by time between detections on consecutive receivers to produce an estimate of ground speed in Km/h. The ground speed estimates generated from receivers I and II, detection times recorded on receiver I, and the river distance between release point to receiver I allowed us to back-calculate the approximate time of movement commencement for animals that were detected on receivers I and I on their day of release (N=38). To evaluate diel movement patterns, we compared these dispersal time estimates to sunset and three twilight phases (±1 minute) (Civil, Nautical, and Astronomical), and measured light levels (Lux) in the water from the first release day. In addition, the first detection time for an animal on a given day was converted to a 360° circular scale with the end of nautical twilight on detection day set as the median (180°) point. There was correlated movement between animals on the first night (53/54 animals dispersed), wherein thereafter movement was largely punctuated. Analysis here was structured to determine if time of day was a driver for resumption of movement, and replicates from the first night had a different treatment from subsequent replicates (releasing animals in a new environment). To prevent bias from immediate movement stemming from release, lamprey movements in the first 10 hours after release were censored. We performed a Rayleigh Test of Uniformity (R package "circular" v. 0.4-93) to determine if there was a significant clustering of detection times centered at nautical twilight.

We used a mixed-effect logistic regression fit to detection data to analyze the relationship between river discharge (USGS gage #04122200 near Whitehall, MI) and the timing of movements (date). The first detection for each tag from receiver 1 started the observation period and the final detection independent of receiver was the endpoint of observation. Using the results from the diel movement analyses (above), we defined a 'lamprey day' as the 24 h period commencing at 18:00 EST and extending overnight until 18:00 EST the following day. This allowed us to define a single nocturnal movement period as a 'day', despite spanning two consecutive calendar days. Each lamprey day during each animal's observation period was treated as a separate observation, with a binary dependent variable denoting detection (1) or absence of detection (0) for each lamprey day. Mean daily discharge recorded every 15 minutes (z-transformed) and the 24-hr change in discharge prior to a given lamprey day were interactive covariates, with the mixed effect of individual (transmitter number) being additive. Detections between release and 18:00 EST the following day were also censored here to remove bias, however detections during that period could denote an initiation of the dispersal period albeit not accounted for in the modelling. This model was compared via ΔAIC to two null models; a fixed effect logistic regression with the same covariates and a model constructed similarly but with all covariates set as random effects.

Spatial Mark-Recapture Modeling:

To model survival and transition probabilities throughout the study area we performed a Cormack-Jolly-Seber (CJS) Mark-Recapture analyses using Bayesian frameworks. The model used detection histories of all animals to estimate survival probability (Φ) and detection probability (p) at each receiver. We applied the Bayesian discrete state-space implementation of the CJS model presented by Kéry and Schaub 2012, using JAGS interface for Rstudio ("JagsUI v 1.5.2.). The observation matrix with dimensions n = number of individuals and I = number of spatial occasions, was filled with 1's or 0's to denote a presence or absence of an animal at a given receiver. We allowed the model to have varying estimates through spatial states to capture reach specific survival Φ_i with the assumption that both survival and detection probability p_i vary independently throughout space as fixed effects. However, all individuals were assumed to have equal detection probabilities at any specific site. Conceptually, there were three aspects that were unique to our model due to experimental design. The two receivers with overlapping detection radii prior to the entrance of White Lake represented one amalgamated location, there was no receiver at the release point, therefore no p parameter was estimated for that location. Φ_7, the survival probability from the seventh and eighth receiver, approximately 30m apart was presumed to be 1; this allowed the estimation of p_7 separately from Φ_7 (Figure 2.2).

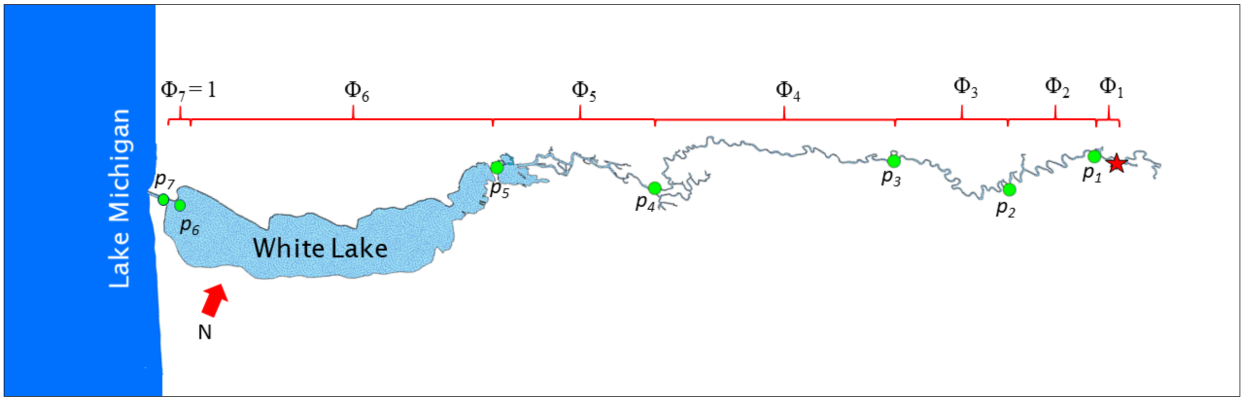

Figure 2.2. A conceptual illustration of the Cormack-Jolly-Seber model. The red star denotes release point, and each downstream green dot represents a sampling "occasion". Phi values represent reach specific survival, p values indicate detection probability.

Priors for both space-specific survival and space-specific detection probabilities were modeled as draws from the uniform distribution between 0 and 1. Latent state variables (z) were modeled as draws from the Bernoulli distribution conditional on the animal being alive at time t. That is, z_{t+1} could not be 1 if $z_t = 0$. The Markov Chain Monte-Carlo (MCMC) consisted of 3 chains with 20,000 iterations each, a burn-in at 5,000 and was thinned at a 1/10 rate. To assess the goodness-of-fit of the discrete space model, we subjected it to a series of simulations designed to determine (a) the sample size needed to reach stabilized parameter estimates and (b) how varying simulated observation results effected mean Φ and p results.

Sample Size Simulations:

A high-performance computer at the Institute for Cyber-Enabled Research at Michigan State University ran 1,000 iterations of our model using our point-estimate results at hypothetical sample sizes of 25,100,200,300,400,500 and 1,000 tagged individuals. Each iteration simulated a new observation matrix by Bernoulli trial using our point estimates to determine if an animal survives and if so, is detected at a receiver location (Kéry and Schaub 2012). Each iteration provided a new set of point estimates; the variances for Φ parameters were then compared to assess sample size effect on uncertainty in survival estimates, and at what sample size does survival uncertainty stabilize. MCMC specifications for these simulations were: 3 chains at 1,000 iterations each, a 1,000-iteration burn-in period and 1/10 thinning rate.

In spatial experiments like this one, unless survival is 100% and all animals complete their outmigration within the tag's batter life, detection sample sizes decrease through space. This is practically a biological impossibility so there was ample opportunity for high variance levels to arise across our point estimates, especially those furthest downstream. In an exploratory attempt in dampening this variance, we also ran simulations of the same sample sizes in a staggered release formula, where half of the animals were released at the experimental release point and half released at a point in the river upstream of receiver 5 (the entrance to White Lake).

Varying parameter effects simulations:

The second goodness-of-fit assessment involved simulating observation matrices of our sample size (56) with low, high, and our point-estimates of parameters. This allowed us to evaluate how well-fit models from relatively low sample sizes are at different Φ and *p* values. These simulations used the same framework and MCMC specifications as the sample-size simulations, but with varying point-estimates creating the simulated observation matrices in each simulation instead of varying sample-size. Low parameter values were assumed to random draws from the uniform distribution between 0.1 and 0.3 and high, between 0.7 and 0.9. Goodness-of-fit was determined as the percentage of each parameter across the 1,000 iterations within the High-Posterior Density Interval for each iteration (R package “Coda”), and the mean absolute value difference of Φ point-estimates from the true value constructing the simulated observation matrix (Kellner 2021).

RESULTS:

Equipment Testing:

In situ tag drags had a mean detection radius of 31.97m ± 1 se (range = 5.3m-78.39m, 6.04m), whereas the mean range observed from dispersing lamprey was 47.98m ± 1 se (range = 5.5m – 121.43m, 2.69m). Receiver range did not vary significantly (ANOVA, $p = 0.21$, F = 1.87) amongst the receivers in tag drags with receiver means of 33.22m, 16.7m, and 41.46m for receivers 1,2,3 respectively. A Tukey-HSD post-hoc test found no significant difference between the receiver ranges (*p*’s: I-II:0.32, II-III: 0.22, I-III: .96). Incidentally, receiver 2 had the largest detection range in data collected from the experimental period, however the type of test (drag vs. in-experiment) was not a significant predictor (ANOVA, $p = .051$, F = 3.87). For in-experiment range results, receiver means were of 40.9m, 58.8m, and 43.2 for receivers I,II,III, and held statistical significance in predicting detection range ($p = .009$, F = 4.93). A post-hoc Tukey-HSD test found a statistical difference between receivers I and II ($p = .01$), but not between II and III ($p = .051$) or I and III ($p = .93$) (Figure 2.3).

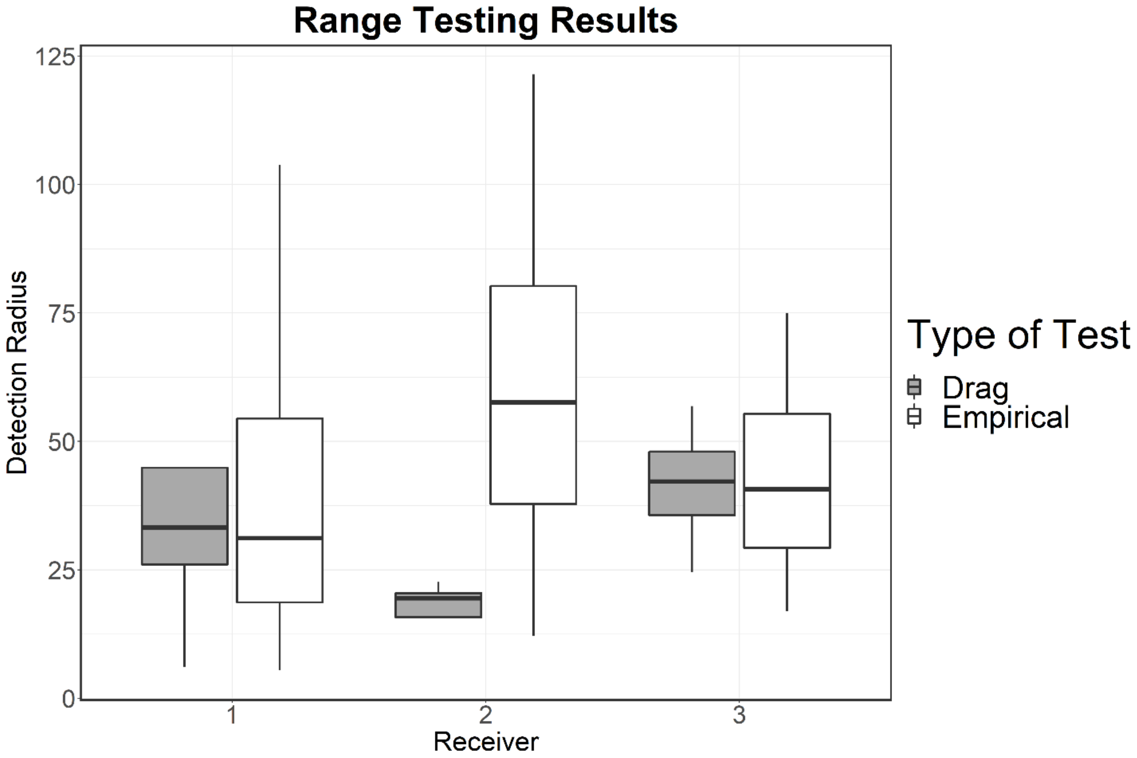

Figure 2.3. Box plot of detection radii for three receivers in the study area. Dark grey boxes show tag drag results; white boxes show results configured using calculated movement speeds of animals during the experiment

General Results:

Mean total length (±1 se) of all animals undergoing surgery was 173.84cm ±1.4 (Range = 160mm – 205mm), and mean mass (± 1 se) 7.65g ± 0.18 (Range = 5.1g-12.5g). Mean time (± 1 se) to stage-IV anesthesia was 11.32 minutes ±.39 (Range = 5 min. – 21 min.), and animals recovered from anesthesia at a mean (± 1 se) of 22.61 minutes ± 1.31 (Range = 6 min. – 53 min.). Mean time (± 1 se) for surgery completion was 1.42 minutes ± .09 (Range = 1 min. – 4 min.).

There were no mortalities nor apparent injuries during the 3-day post-surgery holding period. Additionally, no animal died or exhibited behavior indicating stress during transport from the holding facility to the White River. Upon release into White River animals moved quickly to the bottom and sought cover among rocks or leaf litter or burrowed into the sediment. Fifty-four of 56 animals (96%) were contacted on at least one receiver, all but one of which was first detected within the first 8 hours post release (mean = 5.64 hours, ± 1 se = 2.38, range = 1.36 – 131.66). The number of unique sea lamprey detected declined moving downstream through the extent of the study area, with only one individual detected on the terminal receiver in the channel of White Lake/Lake Michigan (Table 2.1) There was a total of three "misses" on receivers, defined as a transmitter not detected on a receiver, but subsequently detected on the next downstream receiver.

Table 2.1. Unique detections on all receivers with receiver "misses" illustrated in the right column.

Rec. #	Unique Hits	"Misses"
1	53	1
2	49	0
3	36	2
4	28	0
5	12	0
6	12	0
7	2	0
8	1	0

The latest detection of an animal at large in the study system was 28 days post-release, with a mean days at large, defined as the date of last detection, of 6.78 ± 1.06 days. Nineteen animals were last detected within one day of release; however, 14 of the 19 traveled downstream to the second receiver, with one navigating to the fourth receiver within 15 hours of release (Figure 2.4).

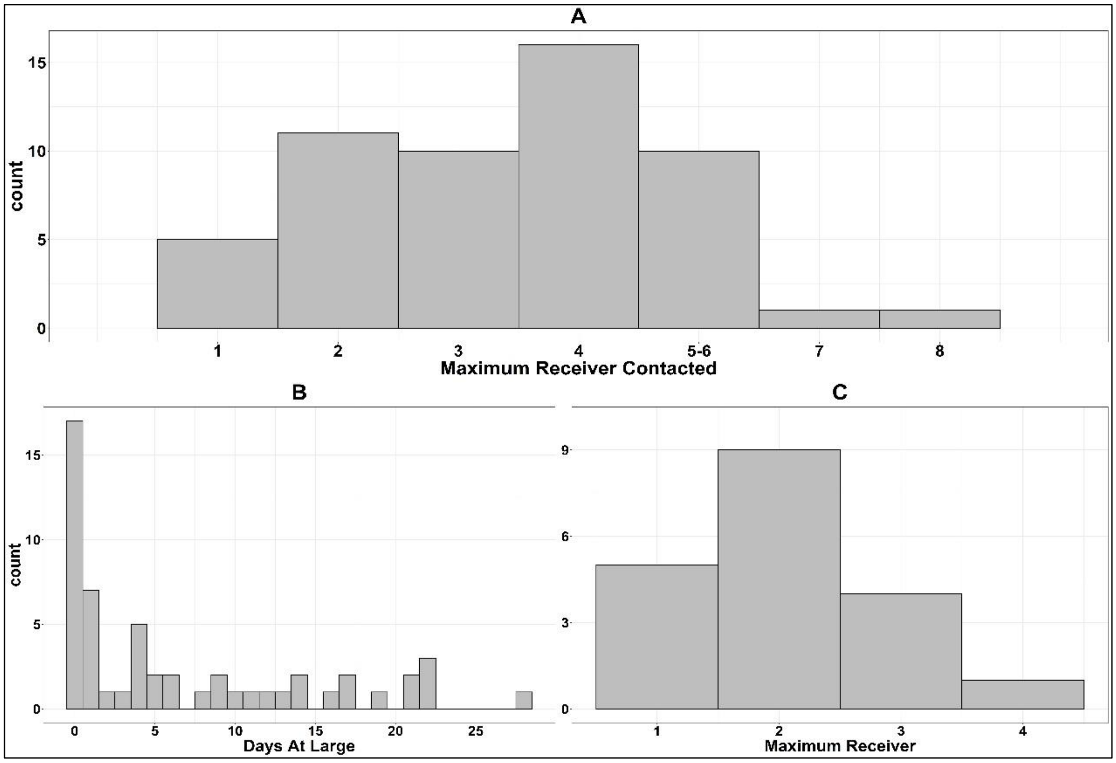

Figure 2.4. (A) Histogram of Maximum Receiver Contacted for All Contacted Fish. (B) Days At Large For all Contacted Fish. (C) Maximum Receiver Reached for Fish < 1 Days at Large

Travel Speed and Movement Timing:

Travel speeds (Figure 2.3) were fastest (*p* = <.001, F = 58.34) through the grouping of receivers II and III and slowest through the wetland area of Hilt's Landing between receivers IV and V. A post-hoc Tukey-HSD test showed significant differences between all receiver groupings except III-IV and IV-V (Table 2.2)

Table 2.2.Tukey-HSD significance results from ANOVA comparing ground speeds between receiver sets.

Receiver Grouping	***p***
I-II – II-III	<.001
I-II – III-IV	<.001
I-II – IV-V	<.001
II-III – III-IV	<.001
II-III – IV-V	<.001
III-IV – IV-V	.052

Mean travel speed for all receivers was 1.88 Km/h, se = .08. The fastest dispersal was 3.08 Km/h, measured from an animal travelling between receivers II and III.

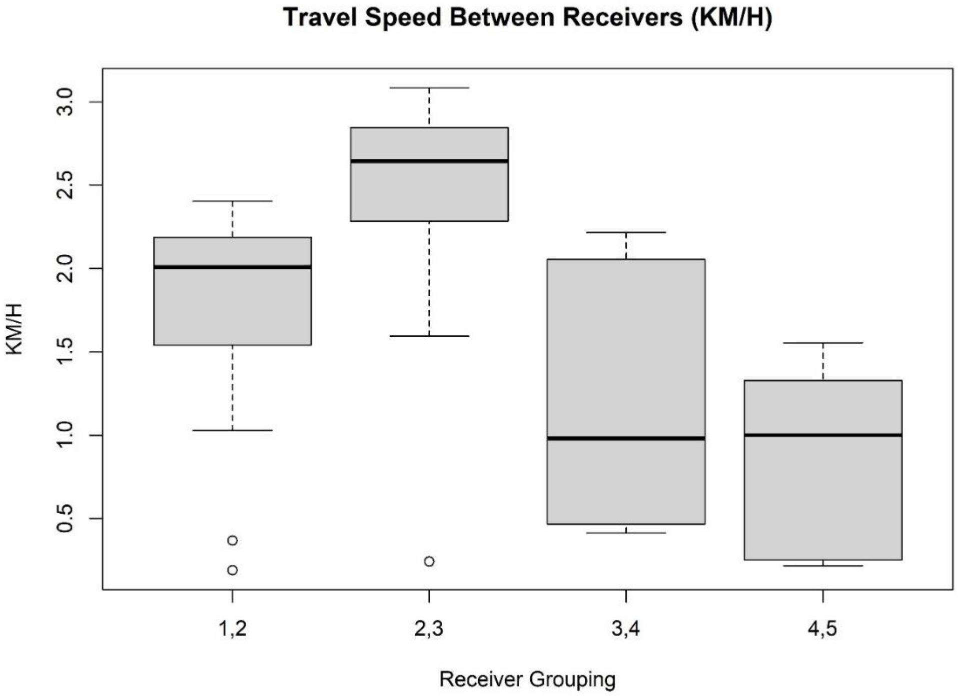

Figure 2.5. Boxplots of travel speeds calculated from the last detection of the upstream receiver and first detection of downstream receiver. Vertical lines represent the range of non-outlying results, horizontal black lines represent median speeds and circles represent outlyers. Only animals with subsequent receiver detections in a 24-hr. period are presented.

Time of Dispersal and Punctuated Movement Commencement:

Sixty-eight percent (38 of 56) animals were detected on both receivers one and two on their first night of movement. Back calculating their travel speeds between receivers one and two showed estimated dispersal commencement times within ±16.21 (±1minute) of nautical twilight (se = 3.59). Mean time between a recorded reading of 0 lux and estimated dispersal commencement time was 58.46 minutes (se = 4.08).

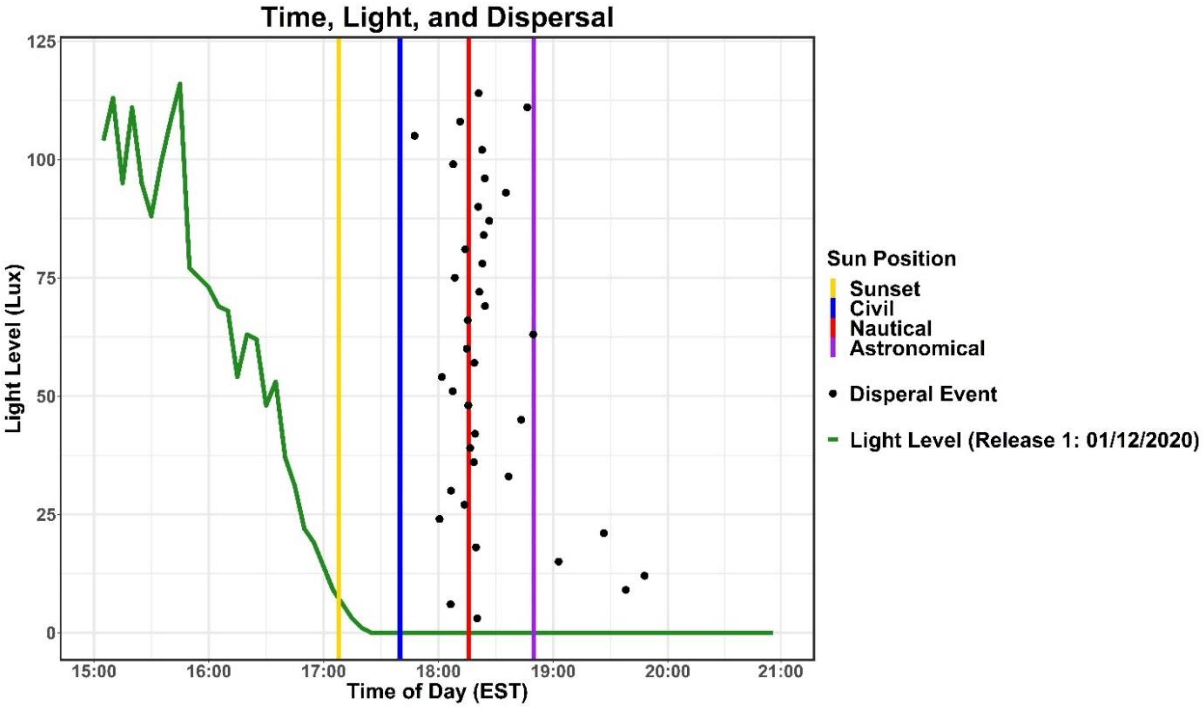

Figure 2.6. Dispersal Commencement times for animals detected at receivers one and two on night of release, overlayed with sunset and three twilight phases (±1 minute). The green line represents light readings at the bottom of the water column recorded by a Hobo logger fixed to receiver one.

A Rayleigh test determined there was a statistical unimodal distribution of dispersal times around nautical twilight (*p < .001*)

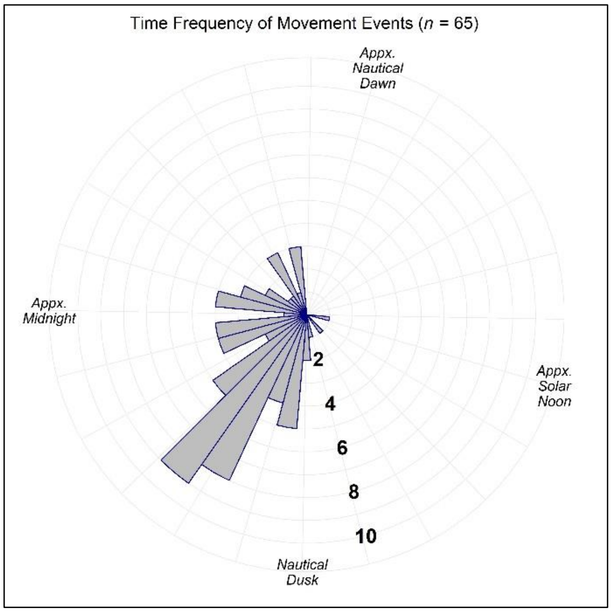

Figure 2.7. Circular distribution of first detection time/day for individual lamprey. Movements in the first ten hours after release are removed to prevent bias from a change of environment.

Modeling Dispersal Events:

Our mixed effect logistic regression (Figure 2.8) showed movement decisions were significantly related to higher daily mean discharge, 24-hour discharge difference and the interaction of the two variables were not significant (Table 2.3). Each unit of scaled mean daily discharge corresponded with an increase of 66% probability of movement initiation. The theoretical pseudo-R^2 showed a well-fit model at .33, with a standard deviation of 1.13 for the random effect of individual (Table 4). ΔAIC of null models were 14.7 for the all random-effect model and 26.3 for the fixed effect logistic regression.

Table 2.3. Variable results from Mixed Effect Logistic Regression Predicting Movement**.**

Variable	se	*Z*	*p*
Mean Daily Discharge (scaled)	.28	-3.21	.001
24-hr. Discharge Difference	.20	3.31	.193
Mean Daily Discharge (scaled) * 24-hr. Discharge Difference	.006	-1.637	.102

Table 2.4. Fixed effect Parameter results from our mixed-effect logistic regression. Individual animal was a random effect

Fixed Effect	Estimate (Logit Scale)	Std. Error	95% CI	*p*
Scaled Mean Daily Discharge	.66	.28	0.27 - 1.08	.0009
24-hr. Discharge Difference	.01	.01	-0.01 - 0.03	.19
Scaled Mean Daily Discharge*24-hr. Discharge Difference	-.01	.006	-0.02 - 0.00	.10

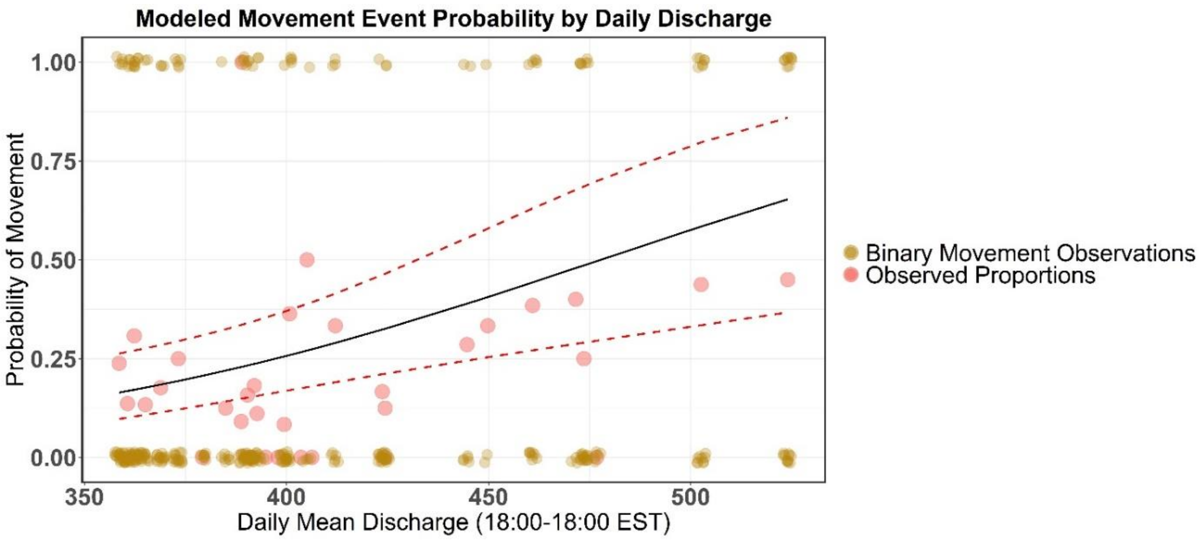

Figure 2.8. Plotted Mixed Effect Logistic Regression, with Daily Mean Discharge (15-min. intervals) on the x-axis, and Probability of Movement on the y-axis.

Spatial Mark-Recapture:

Our model successfully converged as determined by all model parameters having $\hat{r}$ values < 1.01, all parameter mean estimates resided within their 95% highest posterior density intervals (HPDI). Mean Φ_i estimates remained >.7 throughout the riverine portion of the study area where they then dropped as the study area entered the wetland and lake habitats. Mean p_i estimates remained > .7 throughout the entire study area except the terminal receiver. Cumulative survival ($\Pi\Phi_i$) throughout the study area was 0.05.

Table 2.5. Parameter Point-Estimates (Mean), Standard Deviation, and 95% Highest Posterior Density Interval Results of our Discrete-Space Cormack-Jolly-Seber Mark-Recapture Model

Parameter	Mean	Sd	95% HPDI
Φ_1	.952	.029	0.897 - 0.999
Φ_2	.895	.044	0.808 - 0.971
Φ_3	.785	.064	0.654 - 0.898
Φ_4	.736	.085	0.563 - 0.892
Φ_5	.529	.148	0.252 - 0.821
Φ_6	.178	.097	0.023 - 0.369
p_1	.960	.026	0.910 - 0.998
p_2	.974	.025	0.924 - 0.999
p_3	.897	.054	0.796 - 0.985
p_4	.926	.067	0.789 - 0.999
p_5	.771	.163	0.471 - 0.999
p_6	.756	.196	0.361 - 0.999
p_7	.498	.224	0.066 - 0.879

Simulations:

Sample Size Simulation:

Our sample size simulations suggest a substantial reduction in variance at 250 individuals released, wherein further increases in sample size show minimal improvement. Aside from $\Phi_{5,}$ all Φ parameters reached a variance of < .0025 upon a simulated sample size of 100. Φ_5 did not reach this threshold with simulated sample sizes up to 1,000, where it reached a trough of .00275. Staggered release simulations had slightly higher variances at upstream receivers but decreased variance in downstream Φ values at our smallest simulated sample size (*n* = 25) by 17% for Φ_5 and 35% for Φ_6 (figure 7). At an *n* of 1,000, these improvements increased to 43% and 39%

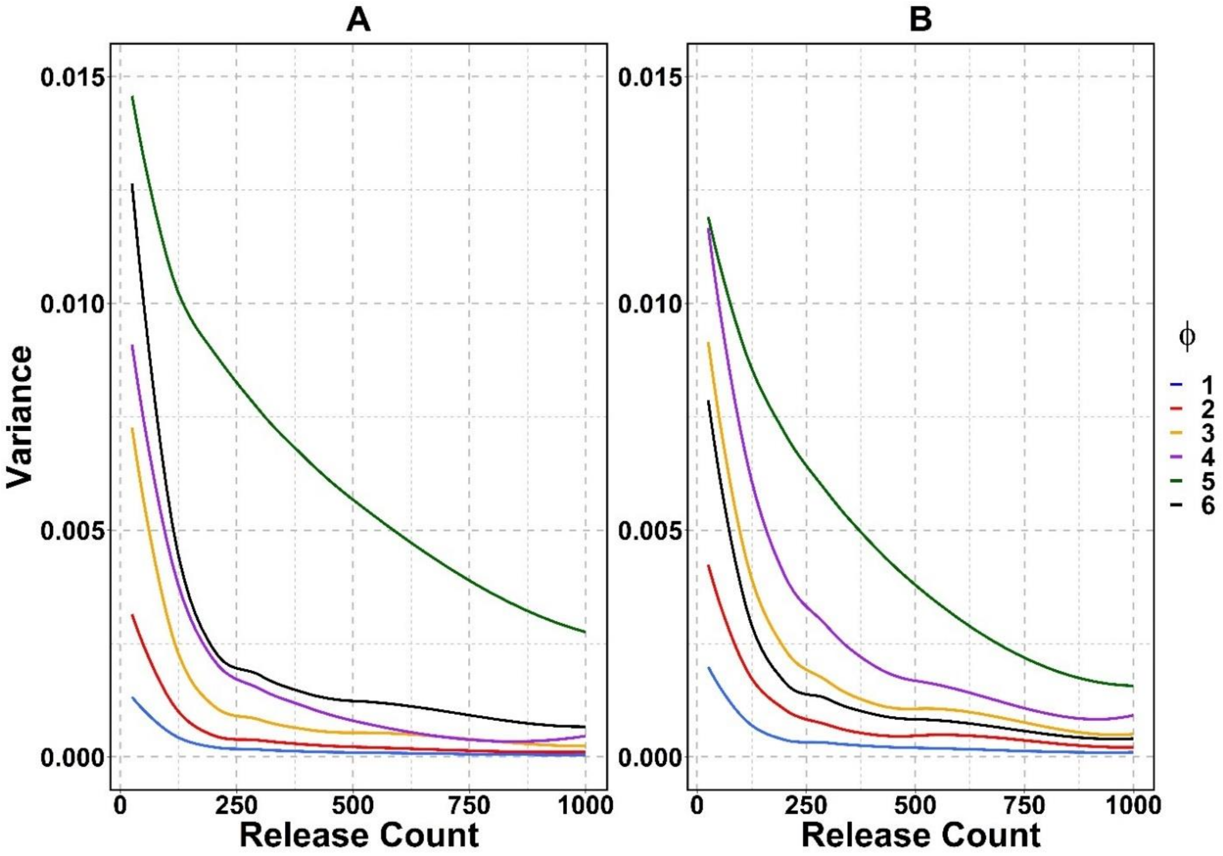

Figure 2.9. Parametrically Smoothed Variance Measured for Each Φ Parameter Estimate Across a Range of Sample Sizes 25-1000. (A)Single Release Model, (B)Staggered Release Model.

Table 2.6. Cumulative Φ Parameter Variances across 1,000 Simulated Iterations of our Model at Varying Sample Sizes

<table>
<tr><th colspan="7">Standard Release</th></tr>
<tr><th><i>n</i></th><th>Φ_1 σ2</th><th>Φ_2 σ2</th><th>Φ_3 σ2</th><th>Φ_4 σ2</th><th>Φ_5 σ2</th><th>Φ_6 σ2</th></tr>
<tr><td>25</td><td>0.00137</td><td>0.00325</td><td>0.00753</td><td>0.00929</td><td>0.01484</td><td>0.01304</td></tr>
<tr><td>100</td><td>0.00045</td><td>0.00109</td><td>0.00237</td><td>0.00422</td><td>0.01027</td><td>0.00478</td></tr>
<tr><td>200</td><td>0.00025</td><td>0.00055</td><td>0.00133</td><td>0.00229</td><td>0.00913</td><td>0.00267</td></tr>
<tr><td>300</td><td>0.00016</td><td>0.00037</td><td>0.00082</td><td>0.00150</td><td>0.00763</td><td>0.00180</td></tr>
<tr><td>400</td><td>0.00013</td><td>0.00029</td><td>0.00064</td><td>0.00117</td><td>0.00663</td><td>0.00146</td></tr>
<tr><td>500</td><td>0.00010</td><td>0.00022</td><td>0.00053</td><td>0.00078</td><td>0.00565</td><td>0.00122</td></tr>
<tr><td>1000</td><td>0.00005</td><td>0.00011</td><td>0.00024</td><td>0.00046</td><td>0.00275</td><td>0.00067</td></tr>
<tr><th colspan="7">Staggered Release</th></tr>
<tr><th><i>n</i></th><th>Φ_1 σ2</th><th>Φ_2 σ2</th><th>Φ_3 σ2</th><th>Φ_4 σ2</th><th>Φ_5 σ2</th><th>Φ_6 σ2</th></tr>
<tr><td>25</td><td>0.00214</td><td>0.00457</td><td>0.00986</td><td>0.01191</td><td>0.01232</td><td>0.00844</td></tr>
<tr><td>100</td><td>0.00081</td><td>0.00194</td><td>0.00464</td><td>0.00677</td><td>0.00918</td><td>0.00325</td></tr>
<tr><td>200</td><td>0.00043</td><td>0.00116</td><td>0.00251</td><td>0.00418</td><td>0.00718</td><td>0.00189</td></tr>
<tr><td>300</td><td>0.00033</td><td>0.00069</td><td>0.00173</td><td>0.00290</td><td>0.00580</td><td>0.00127</td></tr>
<tr><td>400</td><td>0.00025</td><td>0.00054</td><td>0.00124</td><td>0.00211</td><td>0.00477</td><td>0.00104</td></tr>
<tr><td>500</td><td>0.00020</td><td>0.00045</td><td>0.00104</td><td>0.00166</td><td>0.00377</td><td>0.00080</td></tr>
<tr><td>1000</td><td>0.00010</td><td>0.00022</td><td>0.00050</td><td>0.00092</td><td>0.00157</td><td>0.00041</td></tr>
</table>

Varying Parameter Simulations:

Varying parameter simulations showed that low parameter results can skew Φ estimates largely, up to 174% on downstream Φ estimates. Despite this variation, all parameters in all iterations were within the 95% High Posterior Density Intervals. Largely, high Φ and *p* estimates create high integrity Φ results that vary from true estimates between 6%-12%. Our point-estimates created results that generally cohered to the true values (<10% on riverine Φ's), however integrity faltered in downstream Φ's (Figure 8). In both the high parameter simulation and our point-estimate simulation all parameters were within the 95% High Posterior Density Intervals.

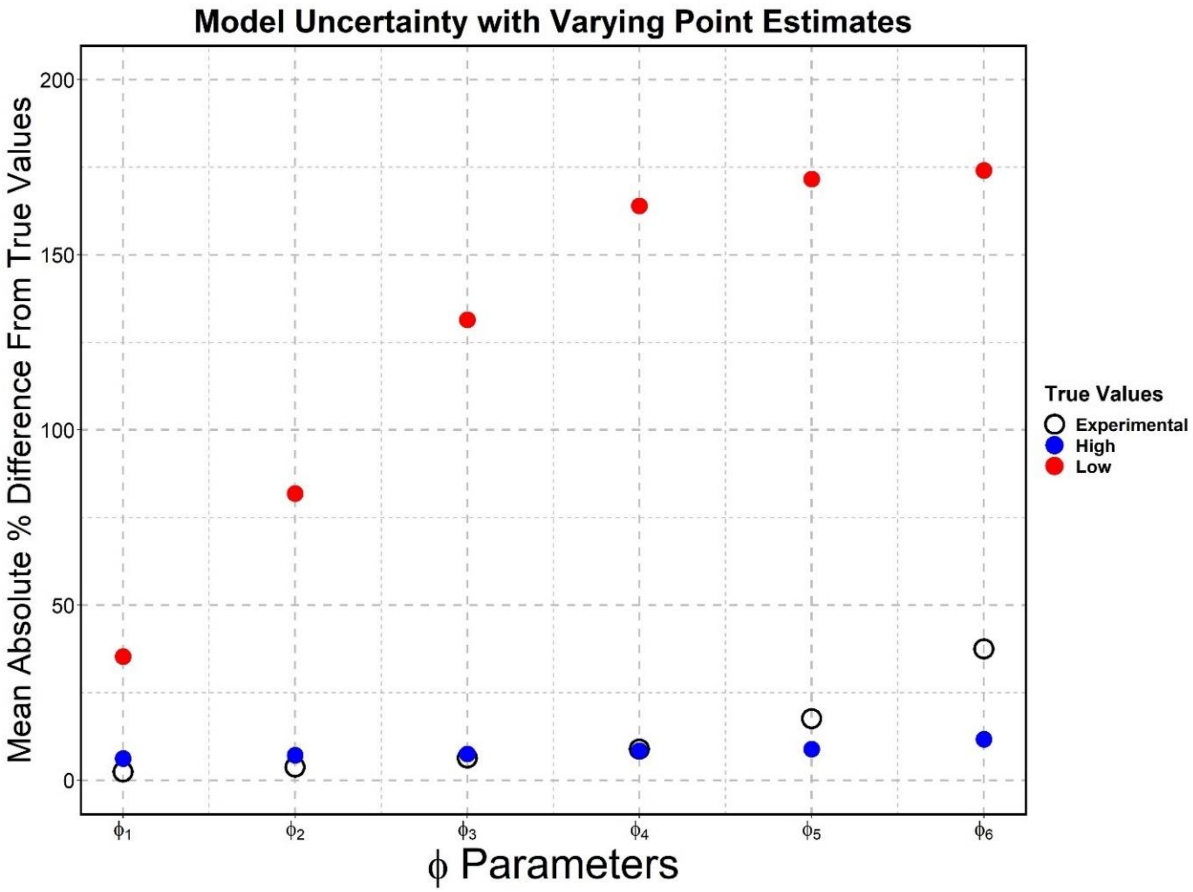

Figure 2.10. Mean Absolute Percent Difference in Modeled Φ Point-Estimate Results and True Values for High, Low, and Experimental Result Input Φ and p Parameters.

DISCUSSION:

This study demonstrates the new ELAT transmitter targeted for anguilliform fishes performs well in a medium-sized Great Lakes watershed, as it did in the Pacific Northwest and Atlantic Coast (Deng et al. 2018, Deng 2019, Deng 2021, Leidtke et al. 2019). Our recorded detection range tests on average proved smaller than other estimates, but range detection in acoustic telemetry receivers is known to vary in response to environmental factors (e.g., salinity, water current, substrate type, precipitation, wind), and specifically shallow water with limited line of sight, where our tests took place (Chittenden et al. 2008, Deng 2021, Finstad et al. 2005, Gjelland & Hedger 2013, Leidtke 2021). This did not appear to affect our study, as only 1.5% of detection opportunities were 'missed' by receivers. Two limiting technological factors that likely impacted our results were the number of receivers, specifically in the lacustrine zone, and the life of the transmitter battery relative to the temporal length of the outmigration. Our riverine receiver's detection range spanned the width of the channel, so the likelihood of detection within that area was high. However, as animals entered the wetland and lacustrine zones, there was far more receiver space than detection range. Many times, our data shows animals seemingly immobile in our study for several days before resuming downstream movement. In the riverine zone, this punctuated movement-rest behavior was of little issue, as the corridor encompassing detection range detected and logged movement as it resumed. However, in the lacustrine this likely became a factor with ~9km of receiver spacing between the onset, and terminus of the lake. Low detection rates in these zones could stem from numerous factors: The animal could be dead, it could be burrowed in substrate and immobile, or it could have entered the new regime and began feeding, a behavior undocumented in Great Lakes but seen in European populations by Silva et al. (2013). If one of the latter two, the possibility that it remained in that state, or a combination of the two, for the rest of the battery life of the tag is plausible. To determine more exact survival estimates in large regimes like White Lake, it is necessary to maximize receiver count throughout the area to better determine the animals' whereabouts.

Although we did not gather water speed data, our back-calculated travel speeds support the notion offered by Applegate and Brynildson (1952) and enumerated by Miehls et al. (2019) that juvenile Sea Lamprey drift during outmigration. Mean travel speeds between receivers in the river zone were highest before dropping as animals entered the more voluminous, slower moving wetland/lake complex. Onset of movement on a given night was associated with nautical twilight, commencing about 1 h after full darkness, in agreement with observations for in-migrating adult sea lamprey in Lake Huron (Meckley et al. 2014), and outmigrating sea lamprey in Lake Champlain (Miehls et al. 2019). Unlike Miehls et al. (2019) however, was the fact that 98% of detected animals were first contacted within 8-hours proximity of release, likely because animals used in this study were captured actively migrating.

These findings, in concert with the confirmed statistical significance of nautical twilight and water flow as movement triggers could shed light on the environmental drivers of this animals' life history. As Sea Lamprey transform from their larval state, emerge from the substrate, and begin outmigrating, they enter a new world so to speak, full of new biotic and abiotic entities, as well as risks including predation. They enter this new world in a small and vulnerable state with potential predators in all directions. To complete the migration to their feeding grounds they must first navigate through highly productive hydrologic regimes, White Lake in our study, or estuarine interfaces where the behavior evolved (Correll 1978, Uzarski et al. 2005). It is sensible to consider that a small, unscaled, cartilaginous fish is more likely to survive a migratory event by electing to traverse risky habitat during times of low-light, increased turbidity, and when a majority of predatory fish are inactive (Helfmann, 1986). It is also sensible to consider that part of their life-history strategy evolved around remaining vulnerable in a confined river for as little time as possible. If lamprey primarily passively drift downstream during outmigration, then doing so during increased flow gets them downstream at a quicker rate (Applegate & Brynildson 1952, Miehls 2019) Our results support these conjectures by showing lamprey in a paused phase for more than a day during outmigration were significantly more likely to resume movement during increased discharge, and to do so at night. Speculation of evolutionary drivers from these findings need isolated empirical documentation for confirmation, but these findings at minimum elicit valuable information for management of both invasive and imperiled Sea Lamprey populations. By determining occurrences during their outmigration period where lamprey are likely to be moving, prospective management methods such electric current, sound, or alarm cue can have a more direct effect as they are refined. Likewise, in areas where lamprey are imperiled this information can be used to assist safe-passage. Moser et al. (2015) noted the conflicting nature that screens designed to protect fish species from high-head turbines may inflict mortality on lamprey outmigrants and suggested exploring lifting those during times of lamprey passage. This information can further refine that protocol.

Mark-Recapture estimates from our study system showed higher survival rates in the riverine portion than the lake, however wide HPDI’s for lake survival estimates should be considered if using these results. Cumulative survival ($\Pi\Phi_i$) for outmigrants in our model was 4.6%, but the large amount of receiver space downstream provokes a warning to refrain from using this estimate as canon. The lack of detections at the terminus of the migration path dictates this estimate should be used in concert with experimental design rather than a realistic estimate of this animals biology. When an animal is undetected it is impossible to know if the animal is dead or simply outside the detection area, and in our case detections at the terminus of White Lake were 17% of those at the onset (Kéry and Schaub 2012). This study shows this technology works well systems such as White River/Lake. The next step toward garnering realistic survival estimates is to decrease receiver space in the study system to maximize the documentation of lamprey throughout time and space.

The small sample size and lack of detections collected from DRM receivers inhibited the ability to produce a reliable estimate of reach specific survival; consequently, our estimates of survival should be viewed through the lens of diagnosing system performance issues, and transitions in detection and survival probabilities that accompanied movement between major habitat types. However, the modeled simulations portray a robust model framework computing low variance estimates at relatively low sample sizes; a key when working with hard to obtain or protected animals. The GLFC treatment program is extensive and effective (> 90% decrease in population from pre-treatment estimates), constraining the ability to easily collect transformers. Yet, there is substantial interest and a recognized research need to better understand Sea Lamprey mortality estimates across lake and river source tributaries (GLFC "What is at Risk", 2021; Jones, 2007). Our sample size simulations show the propensity to do that with relatively low sample sizes, depending on preferred variance threshold. At a sample size 100, our variance estimates for all but one Φ_i estimate was > .0025; at 250 animals, variance estimates had reached a stable trough and decreased minimally therein after. Strictly speaking, at a sample-size doubled from ours, a high-quality estimate can be reached with matched parameter point-estimates. Contrasting our raw detection results (98% fish detected somewhere within the study area), with a similar designed experiment with PIT tags (14%) shows the enormity of the advantage this tag holds (Miehls et al. 2019). Speaking linearly within raw results, to obtain a detection *n* of unique animals equal to 100, this tag requires only 102 animals whereas PIT tags require approximately 715. With an equal sample size the statistical power difference between these two methods is portrayed by our varying parameter simulation results. With detection rates between 0.1 and 0.3, point estimates from similar sample sizes are expected to vary from true values by up to ~150%.

Simultaneously releasing animals at multiple locations, especially near transitions in habitat type, would improve the certainty of mortality estimates in the wetland complex and DRM habitats without sacrificing the accuracy of the upstream river estimates. The consequence of this release strategy is a more accurate and reliable estimate of total natural mortality during outmigration throughout the watershed. Heterogeneity in migratory behavior is not an uncommon result in unidirectional Mark-Recapture models, but it produces subsequent heterogeneity within detections and/or survival (Buchanon & Skalski, 2010, Breteler et al. 2007). This by definition is a violation to the assumption in CJS models that every animal in a population during a detection period (receiver, in ours) has an equal probability of recapture (Amstrup et al. 2005). The consequences of this violation are well studied, but of importance to our study and to future lamprey studies is the behavioral and/or survival heterogeneity producing low detection rates at downstream receivers (Begon 1983, summarized in Amstrup et al. 2005). This is demonstrated in our study by the range in time it took animals to reach downstream receivers (White Lake entrance = 1-16 days, White Lake exit = 6-21 days), and the range of time it took the two animals contacted at the terminal receivers to traverse White Lake (1 and 10 days).

To circumvent this, our model simulation results from a staggered release show a viable method. By releasing half of your animals downstream, you are ultimately sacrificing certainty in upstream estimates in exchange for certainty in downstream estimates. In detection results similar to ours, that was not an issue as our upstream estimates were quite high. Simulated staggered release results reached a trough at a similar sample size than the single release-point simulations, albeit with higher upstream uncertainty, but the minimized variance in downstream estimates gives an option to managers willing to part with precision in areas of already high certainty.

Cormack-Jolly-Seber models have been utilized countless times since its inception and is widely accepted as a keystone in varying survival modeling, so the functionality of the model was not a question for us (Lebreton et al. 1992, McRea & Morgan 2014). However, it was important to note how the model behaved in a low sample-size study such as ours and potential future studies. Our detection data and consequent survival estimate data results were robust enough to provide stable estimates, but that cannot be expected to always be the case. Therefore, it was important to note how the model behaved at low detection results, and how they varied compared to high detection results. Our varying parameter simulations show, as expected, that low detection results skew output parameters with a similar trend as our sample size simulation, a general increase in magnitude as distance increases; however, even at low detection data (0.1 - 0.3) all 1,000 iterations had point estimates within their HPI's across all parameters. This tag has proven to boost detection results from previous estimates using PIT tags, but the trade-off is in cost in technology; however, this difference in technological costs would be mitigated substantially when considering the additional personnel, animal handling, and time costs included by scaling sample size up to achieve adequate detection results (Dawson et al. 2015, Miehls et al. 2019). Depending on the precision warranted, these simulations show that Mark-Recapture models remain a viable tool as long as the study design can produce detection rates at the 0.1 - 0.3 threshold.

Although our survival estimate failed to confirm with enough certainty to dictate management decisions for this invasive species, our general results suggest that these animals did spend more time in the drowned river mouth of White Lake than in White River. By doing so, this exposes them to a suite of predators prior to entering Lake Michigan which, theoretically, could mean predation is higher in these areas. Within our data we have evidence to supports this hypothesis. Our results show survival rates at the receiver in the wetland habitat at Hilts Landing were 28% less than that at the most proximate upstream reach, but speed metrics within these two reaches showed no statistical difference. With speed controlled for, the survival rate differential could be evidence of reach specific survival being dictated by predator density. A study with a higher sample size must confirm, but if true, this could direct a more efficient allocation of treatment spending. Larval populations in strictly riverine tributaries would have a higher likelihood of entering the parasitic feeding phase of the lamprey life cycle, thereby being at a higher need of larval treatment. This would also infer that barriers preventing upstream spawning migrations in strictly riverine tributaries prevent more larvae from reaching the parasitic phase, thereby holding more importance.

We offer the following recommendations for future studies using these tools based on our results. First, the need for more receivers is necessary for more realistic estimates of this animals biology; specifically, if a goal is to determine reach specific survival. The short tag life compounded with our sample's heterogenous migratory behavior produced gaps in our results, specifically downstream. Our riverine detection results portray a technology well-suited for covering bank-to-bank and producing high detection rates, but animals began to disappear in our detection data. As there is no way to know the ultimate fate of those animals, it is imperative to close those gaps by decreasing receiver spacing and producing stricter estimates, thereby painting a more realistic picture of what happened. Second, if receiver count is inhibitive, we suggest a minimum sample size of ~200 animals as that is where variance estimates reached a stable trough in our simulations. Additionally, if future studies take place in a similar river-to-lake regime or other area where receiver spacing may be maximized, we recommend a staggered release to ensure more robust estimates in these areas. As estimates closer to release sites are already quite good, the ensuing loss in certainty in those from a staggered release is more than made up for in the returns from downstream estimates.

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