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American Eel Behavior and Survival in an Impounded River System

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AMERICAN EEL BEHAVIOR AND SURVIVAL IN AN IMPOUNDED RIVER SYSTEM

By

Matthew Mensinger

B.A. Carleton College, 2016

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Wildlife Ecology)

The Graduate School

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December 2020

Advisory Committee:

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AMERICAN EEL BEHAVIOR AND SURVIVAL IN AN IMPOUNDED RIVER SYSTEM

By Matthew A. Mensinger

Thesis Co-Advisors: Dr. Joseph D. Zydlewski and Dr. Erik J. Blomberg

An Abstract of the Thesis Presented
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After beginning life in the Sargasso Sea, American eel enter river systems as juveniles and swim upstream in pursuit of freshwater habitat. Many encounter dams during this migration which act as barriers to upstream movement and limit eel establishment in headwater systems. Some dams have been retrofitted with fishways to improve watershed connectivity, but the individual selection imposed by these structures remains uncharacterized. We considered whether individual differences in behavior (i.e., personality) may be used to predict the propensity of juveniles to use a passage structure, suggesting that eel personality may predict access to habitat upstream of dams. Migrating, juvenile eels (n=63) were captured from a tidal tributary, and we measured the expression of bold and exploratory behaviors in classic animal personality assays (open field and emergence). Then we assessed the propensity for individuals to volitionally climb through a passage structure and assessed passage outcomes. Finally, we compared consistent behavioral tendencies and climbing propensity.

We show evidence for personality in young eels by demonstrating among-individual variation in bold and exploratory behaviors that were consistent across repeated trials in open field and emergence assays. Mean swimming speed in the open field was a predictor of climbing propensity; faster fish were less likely to climb through a passage structure. For successful climbers, climbing time was negatively associated with fish length, offering evidence for potential size-based selection on climbing ability during upstream passage at dams. Our results suggest strong potential for selective pressure on both climbing motivation and ability during fish passage Preventing a subset of individuals from accessing upstream habitat may have unintended consequences for both aquatic ecosystems and American eel populations.

Eels that successfully recruit to habitat upstream of dams may spend decades in freshwater systems before making a single, terminal migration to spawn in the Sargasso Sea. Therefore, individuals that ascended dams as juvenile, must navigate these same dams while moving downstream as mature adults, where passage is commonly associated with mortality and delay. We conducted a four-year acoustic telemetry study that characterized passage risks through two hydropower dams (West Enfield and Milford) in the Penobscot River, Maine, USA. We released tagged fish (n=355) at two sites, estimated survival and delay under variable river conditions, and compared performance among dammed and free-flowing river sections. Survival rates (standardized per river km) were lower at West Enfield ($\Phi_{rkm} = 0.984 \pm 0.006$ SE) and Milford ($\Phi_{rkm} = 0.966 \pm 0.007$ SE), compared to undammed River sections ($\Phi_{rkm} = 0.998 \pm 0.0003$ SE). This accounted for 8.7%, 14.2%, and 8.7% cumulative mortality through sections classified as West Enfield (4.4km), Milford (5.5km), or River (58.1km) respectively. Fish that already passed an upstream dam incurred higher downstream mortality compared to individuals without passage experience. Additionally, fish endured long delays at dams, and >10% of fish were delayed >24h. Low flows exacerbated the risk of mortality and delay. These results offer evidence for direct, latent, and sub-lethal consequences of dam passage for migrating eels..

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TABLE OF CONTENTS

CHAPTER

LIST OF TABLES

LIST OF FIGURES

LIST OF EQUATIONS

CHAPTER 1

PERSONALITY INFLUENCES CLIMBING PROPENSITY IN JUVENILE AMERICAN EELS

Abstract

After beginning life in the Sargasso Sea, American eel enter river systems as juveniles and swim upstream in pursuit of freshwater habitat. Many encounter dams during this migration which act as barriers to upstream movement and limit eel establishment in headwater systems. Some dams have been retrofitted with fishways to improve watershed connectivity, but the individual selection imposed by these structures remains uncharacterized. We considered whether individual differences in behavior (i.e., personality) may be used to predict the propensity of juveniles to use a passage device, suggesting that eel personality may predict access to habitat upstream of dams. Migrating, juvenile eels (n=63) were captured from a tidal tributary, and we measured the expression of bold and exploratory behaviors in classic animal personality assays (open field and emergence). Then we assessed the propensity for individuals to volitionally climb through a passage structure and assessed passage outcomes. Finally, we compared consistent behavioral tendencies and climbing propensity.

We show evidence for personality in young eels by demonstrating among-individual variation in bold and exploratory behaviors that were consistent across repeated trials in open field and emergence assays. Mean swimming speed in the open field was a predictor of climbing propensity; faster fish were less likely to climb through a passage structure. For successful climbers, climbing time was negatively associated with fish length, offering evidence for potential size-based selection on climbing ability during upstream passage at dams. Our results suggest strong potential for selective pressure on both climbing motivation and ability during

fish passage. Preventing a subset of individuals from accessing upstream habitat may have unintended consequences for both aquatic ecosystems and American eel populations.

Introduction

Juvenile dispersal is a fundamental life history process for many taxa and the import of non-natal individuals is necessary for maintaining populations (Trenham et al. 2000; Harrison et al. 2012). In natural systems, dispersal distance and recruitment may be constrained by abiotic (e.g., geography, weather, marine currents) or biotic (e.g., morphology, physiology, species interactions) factors (Gaines and Bertness 1992; Sutherland et al. 2000; Delgado et al. 2010; Vercken et al. 2012; Radinger and Wolter 2014; Hardouin et al. 2014). Anthropogenic influence on natural systems have amplified these constraints by imposing barriers to dispersal through habitat degradation and human development, which have the potential to block, impede, and prolong this life stage (Bulleri and Chapman 2010). Disruptions to the dispersal process can have severe consequences for populations by altering gene flow (Dixon et al. 2007; Marianna 2009), but also for ecosystems that depend on the annual nutrient subsidies transported by immigrating individuals. Through the impoundment of watersheds, dams are one of many human-made structures that have modified the natural processes within ecosystems, populations, and individuals.

There are over 58,000 large dams distributed across the global aquatic landscape. Dam purposes vary by region but are generally designed to support human populations through hydropower production, flood control, or irrigation (International Commission on Large Dams 2020). In contrast to these societal benefits, dams modify the surrounding environment by altering flow regimes, disrupting natural connectivity, and changing ecological communities living within and along impounded watersheds (Graf 2006; Poff et al. 2007; Perkin et al. 2015).

Dam structures also impede inter-habitat movement necessary for many migratory fish to complete their life cycles, and loss of spawning habitat is considered one of the leading causes of diadromous fish declines (Nehlsen et al. 1991; Limburg and Waldman 2009). In response to declining fish populations, dam operators have employed a variety of strategies (elevators, fishways, trap and transport) to facilitate safe and efficient passage through dam structures. While considerable research has been dedicated to assess the population-level performance of fish passage systems (Keefer et al. 2010; Bunt et al. 2012; Cooke and Hinch 2013) very little is known about their selectivity on individuals within these populations. The average efficiency at upstream fish passages is low (< 50%; Noonan et al. 2012), therefore imposing selection at the individual level based on motivation and ability to navigate these passage systems. For many migrating fish, there is potential for selection to occur during adult migration, when some individuals are unable to access spawning habitat (Haugen et al. 2008; Maynard et al. 2017). Alternatively, many catadromous species encounter during upstream movement as juveniles, when dams act as barriers to rearing habitat and may influence early life history processes.

The American eel (*Anguilla rostrata*) is one of many diadromous fish species threatened by dams (Castonguay et al. 1994). After beginning life in the Sargasso Sea, currents deposit young eels throughout coastal waters of eastern North America where they then begin directed movement towards land. During the eel’s initial settlement, there is high variation in movement propensity; some individuals may remain entirely in marine or estuarine systems until maturation, while others swim significant distances upstream to inhabit freshwater environments (Jessop et al. 2008; Clément et al. 2014). In many river systems, individuals that continue moving upstream must navigate dams which are known to delay eel movement and limit establishment in headwater reaches (Wiley et al. 2004; Hitt et al. 2012). Many dam structures are retrofitted with "eel ladders" (irrigated ramps lined with various substrates) that offer opportunities for upstream passage (Schmidt et al. 2009; Welsh and Liller 2013). The effectiveness of these passage systems on individuals and their ability to accommodate among-individual variation in climbing ability and motivation is not well understood.

The ultimate reasons for eels to pursue upstream habitats (and encounter dams) likely rests in tradeoffs between competition, predation, energy expenditure, and resource availability (Gross et al. 1988). Less is known about the proximate controls on eel movement. Edeline et al. (2006) offers evidence that body condition and water temperature may lead to a preference between settlement in salt and freshwater in European eels (*Anguilla anguilla*), and upstream movement may be guided by a magnetic compass (Cresci et al. 2019), but any subsequent variation once in freshwater invokes further exploration. Additional research on this species offers some evidence for differences in size, gene transcription levels, and climbing behavior among fish found upstream or downstream of multiple, lowhead (≤ 2m) dams (Podgorniak et al. 2016, 2017).

In this study, we consider whether personality might influence climbing behavior and provide a potential mechanism for the stratification of eels within river systems. "Personality" refers to behavioral differences among individuals that are consistent through time and across contexts (Wolf et al. 2007; Carere and Maestripieri 2013). Personalities have been observed across taxa and are used to help explain a variety of ecological processes including growth, fitness, movement, and species interactions (Coleman and Wilson 1998; Réale et al. 2000; Réale and Festa-Bianchet 2003; Sneddon 2003; Ward et al. 2004; Brehm et al. 2019). Previous research on fish behavior describes relationships between personality and movement (Fraser et al. 2001; Zavorka et al. 2015; Nakayama et al. 2016; Villegas-Ríos et al. 2018), where bolder and more exploratory individuals had higher movement rates. We considered if behavioral differences in young eels may result in differences in climbing ability and motivation that ultimately promote upstream movement through fish passage structures.

Our primary goals of this research were to 1) use classic personality assays (open field and emergence) to test for among-individual variation in bold and exploratory behaviors, 2) assess climbing propensity in laboratory setting, and 3) test for relationships between repeatable behaviors and climbing outcomes. Given that eel ladders are designed for a single species, we expect any behavior-mediated variation in passage performance to be amplified in other passage systems that must also account for differences in size, experience, and morphology among species. Therefore, American eel are an ideal candidate for investigating the influence of personality on fish passage, where evidence of a relationship would offer a better understanding of watershed connectivity and have major conservation implications for diadromous fishes.

Methods

Fish collection and housing

We dip-netted pigmented (Stage 7 as described in Haro and Krueger 1988) young-of-year American eels from a 1km stretch of the Souadabscook Stream in Hampden, ME, USA (44.76° N, 68.86° W), in late June 2019. This capture location was downstream of all major barriers, so we assumed that all fish had recently entered the river system and lacked any climbing experience. Eels were transferred and housed communally at the Aquaculture Research Center at the University of Maine in a 375L tank maintained at 16C (±1°C) with a 12:12 photoperiod. Eels were fed frozen bloodworms (San Francisco Bay Brand, Newark, California, USA) *ad libitum* daily and acclimated for three weeks prior to marking.

To identify individuals throughout the study, we marked fish with unique color combinations of acrylic paint tags. Animals were anesthetized in MS-222 (100mg/L, buffered with 3.0 mM sodium bicarbonate, pH=7.0) until they failed to maintain vertical orientation. We then measured each fish and injected them with < 50μL of non-toxic acrylic paint subcutaneously in two locations posterior to the anus. After marking, eels were transferred to an aerated cooler for 1h before being returned to housing tanks where they recovered for two weeks prior to behavioral testing

Personality Assays

While bold and exploratory behaviors have been evaluated in a variety of tank designs, we selected the "open field" and "emergence" tests because of their demonstrated ability to reveal repeatable behaviors in other fish species (White et al. 2016; Polverino et al. 2016; Baker et al. 2018; Coates et al. 2019). Tanks (described below) were filled with filtered, oxygenated well water heated to within 1.5°C of housing temperatures. Water was changed after each trial to minimize the effect of olfactory cues from conspecifics on eel behavior. We recorded eel activity with video cameras (ANNKE Y200, Shenzhen City, China) fixed directly above the arena. Tanks were screened with dark fabric to minimize disturbances and were illuminated from below to increase contrast during video processing. After trials ended, we identified individual fish and transferred tested eels into a new housing tank to reduce stress for fish in the testing queue. Fish were left unfed on testing days and all individuals were subjected to the same assay within a single 12h daylight period. Although American eel are largely nocturnal (Hedger et al. 2010; Aldinger and Welsh 2017), previous research on juvenile European eel show high correlation between diurnal and nocturnal behavior (Geffroy et al. 2015), which justifies performing tests during the day. We performed open field and emergence tests weekly for three weeks, and individual eels were allowed at least 36h to recover between assays.

Open Field Test

Open field assays consisted of square (74 x 74cm), natural colored, polyethylene tanks with a convex bottom (Figure 1.1.A). Tanks were filled to a depth of 5.2cm along the perimeter (2.5cm in the center). Fish were individually netted from housing tanks and immediately placed into the open field. Following a 30s acclimation period, we recorded fish behavior for 5min. Videos were analyzed post-hoc using ANY-maze behavioral tracking software (Wood Dale, Illinois, USA), and we measured average speed (*mean speed*) and the proportion of time spent in different sections of the tank (Figure 1.1A). Since many individuals demonstrated climbing behavior in the open field (i.e., breaking the surface of water in an attempt to climb the tank wall), we also counted the number of independent climbing events throughout the trial (*escape attempts*). Some fish were too large for ANY-maze to accurately track movement, so we used ImageJ 1.52a (Schneider et al. 2012) and JWatcher V0.9 (Blumstein et al. 2000) to manually measure *mean speed* and the time spent in different sections, respectively. During a preliminary analysis we observed high agreement comparing ANY-maze to both JWatcher ($R^2 = 0.93$) and ImageJ ($R^2 = 0.99$) outputs.

Emergence Test

Emergence testing started at least 36h following the open field test. The emergence assay was conducted in a rectangular (58 x 74cm), natural colored, polyethylene tank (Figure 1.1B). We used a dark, plastic cylinder (26cm diameter) with a gate valve (5cm diameter) at the base as the “refuge” area, and the tank was filled with enough water to submerge the valve opening. Four

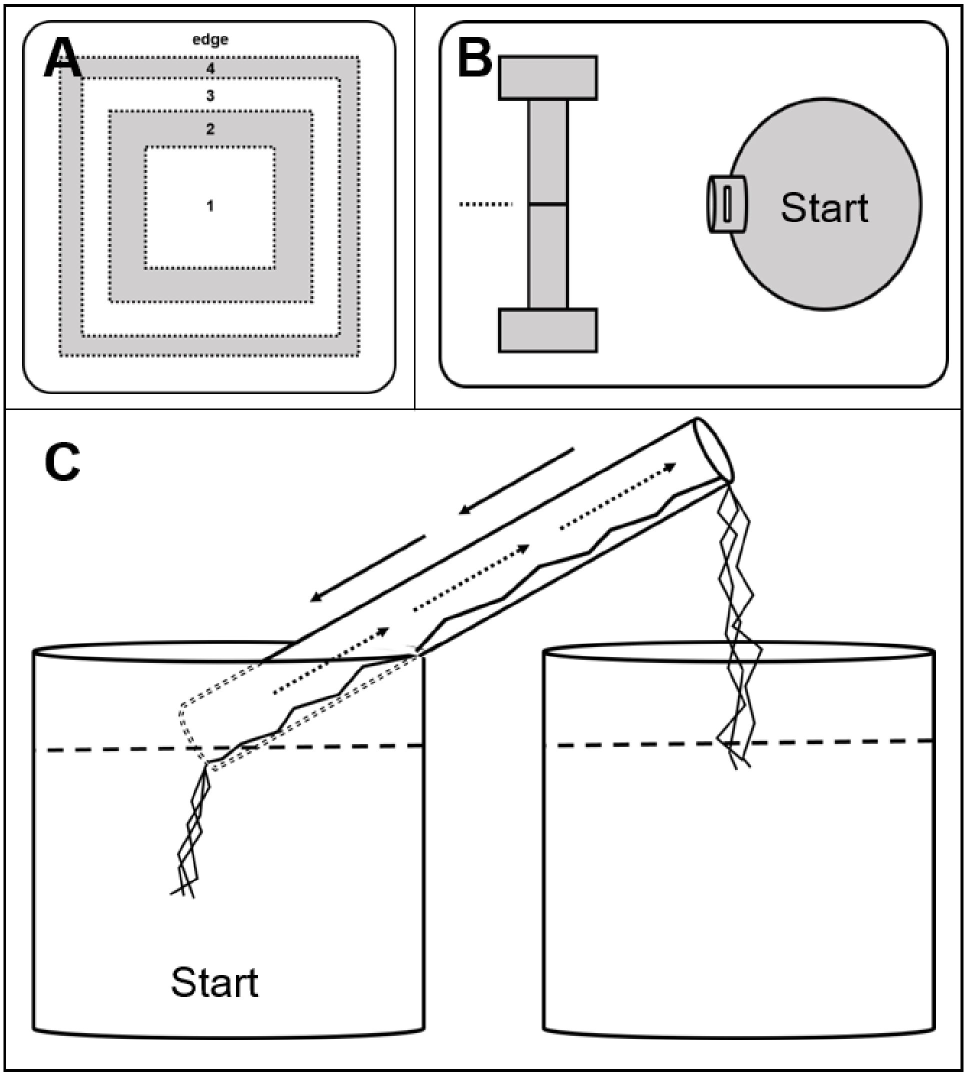

Figure 1.1. Overview of behavior assays. A) Open field. Labels represent different sections of the open field used to estimate the repeatability of proportional behaviors. B) Emergence. Shaded, “Start” region represents covered refuge area with entrance to rest of tank. Shaded rectangles are concrete bricks used as obstacles post-emergence to inhibit eels from immediately crossing dotted line which was used to calculate *exploration time*. C) Climbing test. All eels were placed in start tank and afforded the opportunity volitionally move through irrigated pipe lined with mesh substrate (jagged lines). Dotted arrows = eel movement. Solid arrows = water flow.

concrete blocks were arranged 15.7cm in front of refigure to provide additional obstacles for exploration (see Figure 1.1B). Eels were transferred from housing tanks to the refuge, and the refuge covered to create a stark contrast in light level compared than the rest of the tank. After a 1min acclimation, we lifted the gate valve and allowed the eel 5min to leave the refuge. We recorded whether an individual emerged (*binary emergence*), and for those that did emerge, we recorded emergence latency (*emergence time*) and the time to cross the dashed line opposite the refuge door (*exploration time,* Figure 1.1B).

Climbing Test

Three weeks after personality assays, we subjected eels to a climbing test designed to measure propensity to move between tanks through an irrigated ramp similar to the eel ladders employed at dams. This assay consisted of two, adjacent 375L tanks connected by an opaque, PVC tube (1.2m long, 10cm diameter) at a 32° incline (Figure 1.1C). The tube was lined with 2.5cm polypropylene netting, and some material extended beyond the openings of the tube. A pipe at the top of the tube supplied filtered, recirculated water at a rate of $67cm^3 \cdot s^{-1}$; enough to create an attractant flow yet maintain a constant water level in the starting tank. All fish were placed in the starting tank simultaneously within 1h of beginning of the 12h daylight cycle and allowed to volitionally move to the neighboring tank over 8h. To limit disturbance from observers, successful climbers were identified each hour, and the start tank was screened while testing. We performed the climbing test for all fish three times over 10d, allowing at least 36h between trials.

Data analysis

Assessment of repeatability

We estimated the repeatability of each response variable in open field and emergence tests, and all analysis was conducted in Program R (R Core Team 2013). We used the *lme4* package (Bates et al. 2015) to create a linear mixed effect model for each focal personality metric (dependent variable), and treated fish ID as a random intercept. We controlled for testing order (1–31), open field tank/emergence apparatus, and fish length by including these variables as fixed effects in each model. To determine if individuals behaved consistently through time (i.e., personality), we estimated the adjusted repeatability (R; referred to as repeatability hereafter), by dividing the variance between individuals by the total variance (between individual variance combined with marginal variance associated with fixed effects; Dingemanse and Dochtermann 2013). We used *rptR* package (Stoffel et al. 2017) to generate 95% confidence intervals around repeatability estimates by performing 1000 parametric bootstrap iterations. Variables were considered highly repeatable if $R > 0.5$ or at least marginally repeatable if $R > 0.2$, and the lower bound of the confidence interval (CI) was > 0.0 in both scenarios (Dzieweczynski and Crovo 2011; Aplin et al. 2015; Baker et al. 2018).

For each continuous behavioral variable, we visually inspected Q-Q and residual vs fit plots to check for normality and homoscedasticity. This revealed that proportional response variables in the open field (i.e., time spent in different sections) and emergence variables (*emergence time*, *exploration time*) were highly skewed. To meet normality assumptions, we applied the optimal Box-Cox power transformation for these variables using the *EnvStats* package (Millard 2013) and then re-inspected plots to verify an appropriate application of a gaussian error distribution. For personality variables that were inherently non-gaussian (*binary emergence*, *escape attempts*), we used the link-scale approximation of R (Stoffel et al. 2019).

Relationship between personality and climbing

Three different climbing outcomes were used to assess climbing propensity and each were treated as dependent variables in generalized linear and linear mixed-effect models. We first considered whether each fish did or did not climb during any of the trials (*climb ever*) or within a trial (*climb binary*). Both assessments were modeled as binomial responses and fish ID was treated as random intercept in the *climb binary* analysis. For all fish that successfully climbed during a climbing trial, we also assessed the time taken to climb (h, *climbing time*) and treated fish ID a random effect to control for multiple observations for some individuals. Although we measured climbing time in discrete, 1h intervals, a relatively modest sample size (n=29) of climbing observations led to poor model convergence using a Poisson error distribution. Instead, we $\log_{10}$ transformed climbing time and assumed a gaussian error term, which improved model fit and increased homoscedasticity.

To determine if personality was a predictor of climbing propensity, we incorporated repeatable personality variables as fixed effects in climbing outcome models. For all continuous, repeatable behaviors, we estimated the best linear univariate predictor (BLUP) for each individual as has frequently been employed in recent personality studies (Dingemanse et al. 2020; Gharnit et al. 2020). Using repeated observations of each fish across multiple personality trials, BLUPs represent the mean response variable (or mean optimal Box-Cox transformation if used in the repeatability assessment), controlling for tank, testing order, and fish length for each individual following 1000 simulations using the *arm* package (Gelman and Hill 2007). Distinct from the repeatably models, we only considered fish length as a controlling covariate in this assessment as all eels started the trial simultaneously in the same tank.

Since, proportional responses in the open field were highly correlated with each other ($r > 0.8$) we used the proportion of time spent along the edge of the tank (*time along edge*, Figure 1.1A) in the climbing analysis because it was the only proportional variable that was nonzero for all fish and therefore most reflective of an individual's behavior (i.e., fish spent most of the trial around the edges of the tank). We then tested for correlations between all combinations of personality BLUPs (*time along edge*, *mean speed*, *exploration time*, *escape attempts*) and a fish length covariate. These variables were not highly correlated with each other ($|r| < 0.3$) except for *time along edge* and *exploration time* which were marginally correlated ($r = -0.46$). Since these behaviors were repeatable, we decided to consider both in the climbing analysis because they were measured in different assays, suggesting fundamentally different behaviors. Variables were z-standardized to directly compare effect sizes among independent variables.

For each climbing outcome, we used Akaike's Information Criterion (AICc) adjusted for small sample size to evaluate the relative support for competing models using ΔAICc < 2.00 as a threshold for model support. We first evaluated the support for fish length, which was retained in personality models if it improved by >2.00 AICc against the null model. Each repeated behavior was then incorporated into the climbing model in a univariate framework (or with fish length, if supported), and we retained personality variables if they improved support by > 2.00 AICc. We also tested for non-linear responses (quadratic, exponential, logarithmic) for each behavior, which we considered to be more supported if they outperformed a linear response by > 2.00 AICc. For all supported models, we validated support by analyzing the effect sizes for each behavior (*β*) and those with 95% confidence intervals not overlapping zero were considered to significantly influence the climbing outcome.

Results

We assessed the repeatability of behaviors for 61 individuals in open field and emergence assays. Two observations were removed from open field Trial 1 and one observation was removed from emergence Trial 1 due to protocol error. We evaluated the climbing propensity of 60 fish as one individual died before the start of trials. Additionally, one fish (that did not exhibit climbing behavior during Trial 1), died before the second climbing trial. This fish was included in the *climb binary* but excluded from the *climb ever* assessment. A summary of the observations is shown in Table 1.1

Table 1.1. Overview of observations used to evaluate American eel behavior in personality and climbing assays. Observations reflect the number of samples per individual that we used to estimate repeatability of behaviors in open field and emergence assays or assess one of three climbing responses[1].

Assay	Observations per fish			Total fish[2]
	3	2	1	
Open field	59	2	0	61
Emergence	60	1	0	61
Climb ever	59	0	0	59
Climb binary	59	0	1	60
Climbing time	2	6	11	19

[1] *Climb ever* = a binary response describing if an individual successfully climbed at least once during three climbing trials. *Climb binary* = a binary response describing if an individual successfully climbed within a trial. *Climbing* time = for successful climbers within a trial, the time taken to reach (h) the adjacent tank

[2] We tested 63 fish in total. Two fish were removed prior to analysis because a marking failure did not allow consistently ID them between trials. An unequal number of observations per fish between open field and emergence assays reflect protocol errors. Two fish died before completing all three climbing trials, absent observations were excluded from the climbing analysis.

Personality Assays

We found evidence of repeatable behavior in both open field and emergence trails (Table 1.2). Most variables measured in the open field showed significant repeatability and *mean speed* was highly repeatable (R = 0.54 ± 0.07 SE). On average, fish traveled at 0.091m·s^{-1} (range = 0.041–0.145) and spent the majority of the trial swimming along the perimeter of the tank (mean = 0.92, range = 0.50–1.00), and only entered the center-most area on 37.6% of all observations across trials. There was high variation in the number of *escape attempts* (ranging from 0–33 unique attempts across all trials), which likely explains the relatively larger confidence intervals around this repeatability estimate.

Table 1.2. Repeatability of behaviors measured in the open field and emergence assays of juvenile American eel). R = repeatability; highly repeatable variables are bolded and highlighted and moderately repeatable behaviors are highlighted only. SE = standard error. CI = confidence interval.

Behavior	Assay	R	SE	95% CI
mean speed	Open field	**0.537**	0.072	(0.397–0.671)
time along edge	Open field	0.433	0.082	(0.272–0.587)
escape attempts	Open field	0.292	0.106	(0.061–0.478)
binary emergence	Emergence	0.215	0.107	(0.000–0.415)
emergence time	Emergence	0.168	0.123	(0.000–0.443)
exploration time	Emergence	0.294	0.134	(0.034–0.561)

We found that *exploration time* was significantly repeatable in the emergence test (R= 0.29 ± 0.13 SE). Once fish exited the refuge, fish reached the back of tank relatively quickly (mean = 29s, range= 6–75s). Over three emergence trials, fish emerged from the refuge in 56% of all observations and 82% of fish emerged at least once. The occurrences of emergences increased from 35% of observations in the first trial to 64% and 69% in Trials 2 and 3, respectively, which suggests that fish may have become acclimated the apparatus following initial exposure. Given the increase in emergences after Trial 1, it is unsurprising that we did not find significant repeatability for *binary emergence.* Any acclimatization to the assays that occurred may have also prevented us from detecting repeatability in *emergence time* which averaged 106s (range = 9–290s), but the mean *emergence time* decreased by >30s after Trial 1.

Climbing Test

Individuals varied in climbing propensity. Over three climbing trials, 32% of fish climbed at least once and fish climbed successfully (i.e., reached adjacent tank within 8h) in 16% of all observations (Table 1.1). The most climbing observations occurred in Trial 2 (n=15). Of the 19 individuals that climbed, 8 fish climbed at least twice and 2 climbed during all three trials.

When we assessed the relationship between climbing outcomes, repeatable behaviors, and fish length, there was support for both fish length and *mean speed*, but predictors varied among the three climbing outcomes (Table 1.3). First, we found support for both quadratic and exponential effect of *mean speed* on both *climb ever* and *climb binary.* Both models improved supported by > 9.00 AICc (*climb ever*) and > 5.00 AICc (*climb binary*) against the null model. Upon closer examination of the slope coefficients from these models, there was a support for a negative exponential relationship ($\beta = -1.24 \pm 0.64$ SE) of *mean speed* in the *climb ever* model which suggests that we were less likely to observe climbing behavior for faster moving fish (Figure 1.2). Coefficients from the other supported models also reflect this trend (where faster individuals were the least likely to climb), but the upper confidence limits of these effects include 0.00. Relationships between the most supported model for other repeatable behaviors in the *climb ever* assessment are show in Figure 2.

Table 1.3. Relative performance of models used to assess climbing propensity of American eel. Variable = response variable in climbing model[1]. Model = independent variables used in in climbing model[2]. ΔAICc = difference in AICc from most supported model. R^2 = variance described by fixed effects. β = effect size for the univariate effect (i.e. quadratic effect for quadratic model, for models with fish length and personality variable, β =effect size of personality variable).

Assessment	Model	ΔAICc	R^2	β	SE	95%CI
Climb ever	(*mean speed*)^2	0.00	0.19	-1.24	0.64	(-2.49 – 0.01)
	exp(*mean speed*)	0.34	0.15	-1.16	0.54	(-2.22 – -0.10)
Climb binary	exp(*mean speed*)	0.00	0.04	-0.95	0.51	(-1.95 – 0.05)
	(*mean speed*)^2	0.54	0.05	-1.08	0.63	(-2.31 – 0.16)
Climbing time	fish length	0.00	0.27	-0.17	0.06	(-0.28 – -0.06)
	(*time along edge*)^2 + fish length	0.27	0.42	0.10	0.04	(0.03 – 0.17)
	exp(*escape attempts*) + fish length	0.79	0.32	-0.06	0.04	(-0.15 – 0.02)
	log(fish length)	0.99	0.26	-0.33	0.11	(-0.55 – -0.11)
	exp(*time along edge*) + fish length	1.19	0.33	0.05	0.04	(-0.02 – 0.12)
	exp(fish length)	1.33	0.20	-0.05	0.02	(-0.09 – -0.01)
	exp(*mean speed*) + fish length	1.80	0.31	-0.04	0.04	(-0.11 – 0.03)
	log(*exploration time*) + fish length	1.96	0.30	-0.17	0.17	(-0.49 – 0.16)

[1] *Climb ever* = binary response describing whether an individual ever climbed during three climbing trials, *climb binary* = mixed effect model describing whether an individual climbed within a climbing trial with fish ID treated as a random effect, *climbing time* = mixed effect model where the time taken (h) to move through eel ladder to adjacent tank with fish ID treated as a random effect

[2] *mean speed* = the average swimming speed in the open field, *time along edge* = the proportion of time spent along the edge of the open field (Figure 1.1B), *escape attempts* = number of wall-climbing attempts in open field, *exploration time* = time to fully explore emergence tank.

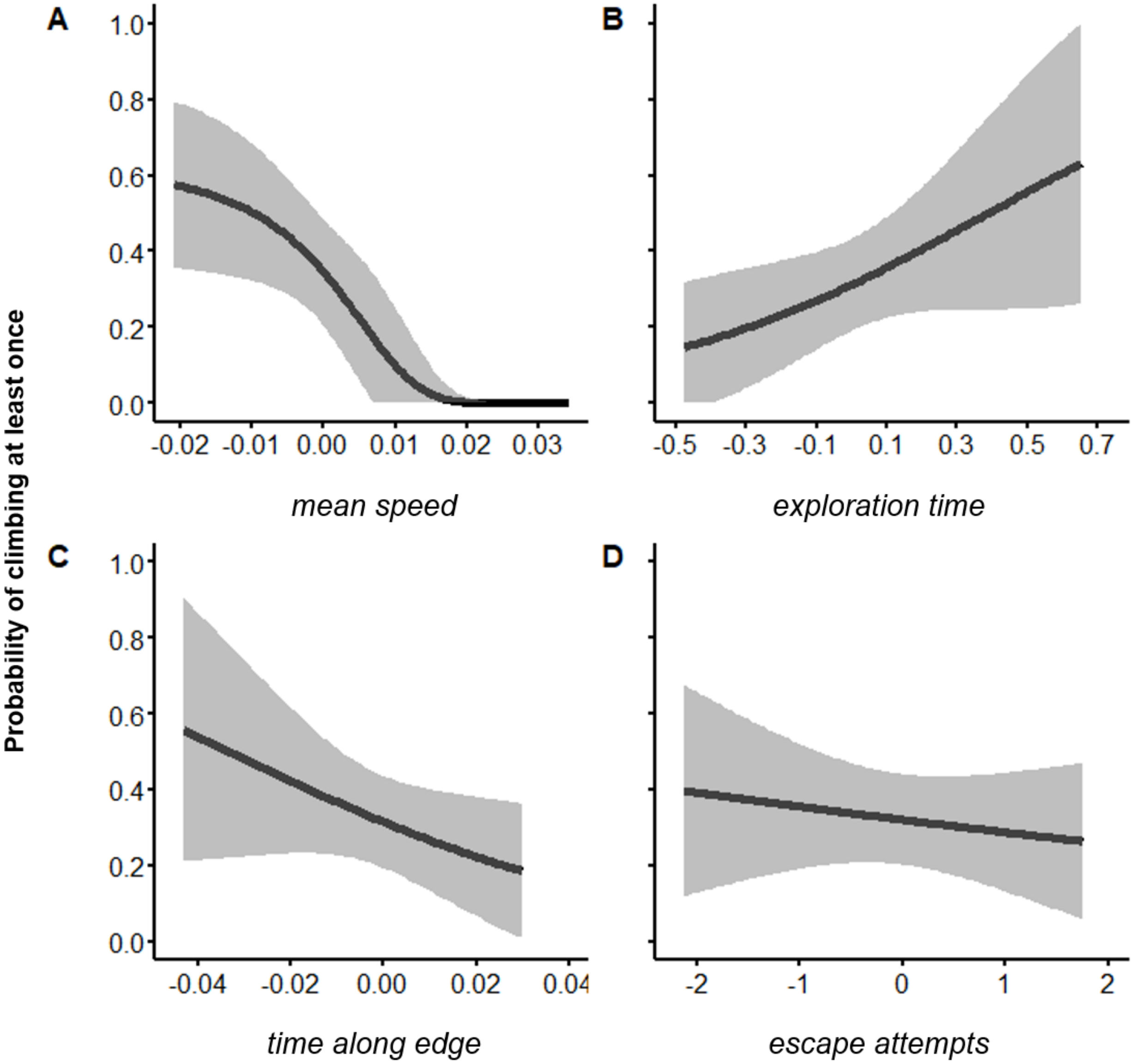

Figure 1.2. Probability of fish successful climbing at least once (*climb ever*) in climbing trial for each repeatable behavior in the personality assessment. Univariate personality models were used to predict the probability of climbing at least once across four repeatable behaviors and the most supported relationships for each behavior are represented here . The horizontal axis represents the best linear univariate predictor for each variable. Panel A is an exponential response, while Panels B–D are linear responses.

When assessing the time taken to climb into the adjacent tank ($\log_{10}$ transformed), including a linear effect of fish length improved model support by > 4.00 ΔAICc against the baseline. The coefficients from this model reflect a negative relationship between fish length and climbing time (β = -0.17 ± 0.06 SE), which suggests that the largest individuals ascended the apparatus quicker than smaller individuals (Figure 1.3). Adding behavior variables to the fish length model did not improved model support which indicates that the behaviors measured in personality assays were not good predictors of climbing time. When contrasted with the lack of support for fish size in the *climb ever* and *climb binary* assessments, this result suggests that larger fish may not have a greater motivation to climb, but rather a greater climbing ability relative to smaller conspecifics.

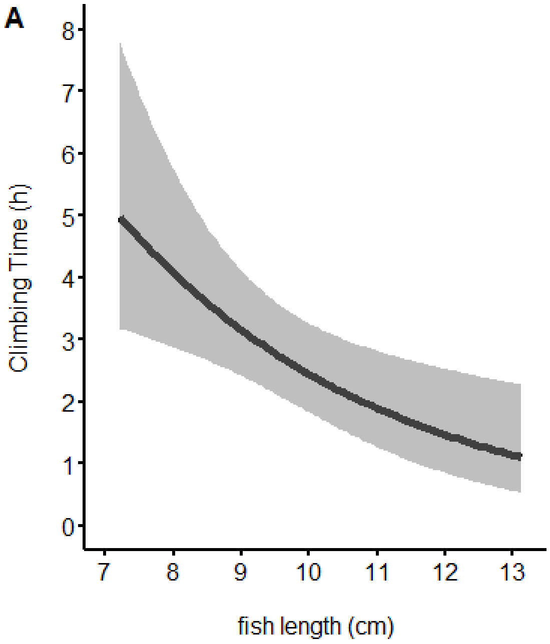

Figure 1.3. Predicted climbing time by fish length. Fish were afforded 8h to volitionally move through simulated fishway into an adjacent tank, and successful climbers were identified every 8h. Since this analysis was performed in a mixed-effect framework (i.e. random intercept), the mean intercept is represented here.

Discussion

Evidence for Personality

We observed repeatable behaviors of response variables in two classic personality tests which provides evidence for variation in individual behavior for juvenile American eel. Among behaviors tested, *mean speed* in the open field was the most repeatable (R= 0.54), which suggests high variation in individual activity levels and swimming speed during this life stage. Our results are consistent with Geffroy et al.'s (2015) study on young European eels which also found high repeatability (R=0.71) in activity level, and our results are within the ranges of estimates (R= 0.40– 0.73) from other fish species (Dzieweczynski and Crovo 2011; Baker et al. 2018). Repeatability of *time along edge* was the next most repeatable behavior (R=0.43) which we suggest offers evidence for variation in both boldness and exploratory behavior among individuals. Fish that spent less time along the edge of the open field also spent more time in the middle two sections (r = -0.84). These sections may be perceived as risky environments for eels given their distance from tank walls and shallowness relative to the edges of the arena. Our results are corroborated by other fish personality studies which found significant repeatability in the time spent in different sections of the open field (Boulton et al. 2014; Baker et al. 2018)

We expected to observe significant repeatability in emergence latency given its support in other fish personality studies (Mazue et al. 2015; Polverino et al. 2016; Coates et al. 2019). Point estimates of repeatability for both *binary emergence* and *emergence time* were relatively low (R < 0.25), and high within individual variation resulted in 95% confidence intervals that included 0. Given the large difference in the number of individuals that emerged between Trial 1 (n= 23) and Trials 2 and 3 (n= 40, n=44), we suspect that individuals became acclimated to the either the emergence apparatus or the handling procedure. The first emergence trial occurred two days after the first open field trial (following 2 weeks without handling), so stress induced by the first open field trial may have carried over to the initial emergence trial. While we did not observe significant repeatability in either emergence variable, once fish left the refuge there was moderate repeatability (R=0.29) in time to reach the back of the emergence tank (*exploration time*). This result provides further evidence for differences in exploratory behavior among individuals, and here we consider that fish that took longer to reach the back of the emergence tank to be more interested in exploring a novel environment.

Variation in Climbing and Ecological Applications

Slower swimming fish in the open field were less likely to climb. This result was unexpected given the demonstrated relationship between boldness and movement propensity in other fish species (Fraser et al. 2001; Chapman et al. 2011; Myles-Gonzalez et al. 2015). We propose two potential hypotheses for this outcome. First, more exploratory fish may have been more likely to locate and climb through the tube. In the open field trials, slower moving fish appeared more methodical and there was a negative correlation between *mean speed* and time spent in the middle three sections (r = -0.35) of the open field. This suggests that on average, slower moving fish explored more of the open field. The trends, although not statistically significant, between both *exploration time* and *time along edge* and climbing propensity support this hypotheses as more exploratory fish (i.e., less *time along edge*, increased *exploration time*) were, on average, more likely to initiate climbing (Figure 2).

As we argue for the above scenario, we cannot ignore the possibility that faster moving fish may have outcompeted slower individuals for space within the starting tank. While we removed all structure from the start tank, some shelter was available underneath the climbing tube, in the overhanging mesh, and around the tank standpipe. Throughout the study, fish were frequently seen entangled with each other, which may suggest potential social structure within the study group. Geffroy et al.'s (2014) research on juvenile European eels observed high sociability during this life stage in the laboratory, so position on a social-asocial behavioral axis (which was not tested in our study) may have influenced the decision to use the passage device. Previous research suggests that asocial individuals are more likely to disperse (Blumstein et al. 2009; Cote et al. 2010). Either hypothesis, however, is congruent with the idea that individual differences in behavior influenced climbing propensity within the trial, and these same socio-behavioral factors would also be present in a field setting.

For fish that demonstrated high climbing propensity, there was negative relationship between climbing time and fish size, where larger fish reached the adjacent tank sooner. Since an effect of fish length was unsupported in the *climb ever* or *climb binary* analyses, support for length in the *climbing time* assessment indicates that larger fish were faster climbers, but climbing motivation was not influenced by fish size. This result provides evidence that size-selectivity in passage efficiency may occur at eel ladders, especially when scaling our study to conditions encountered by fish in the field.

Size selection is observed in numerous fishways and can favor individuals of a specific size range (Mallen-Cooper and Stuart 2007; Haugen et al. 2008; Maynard et al. 2017). We note that our passage device was similar to some eel ladder conditions at dams (Solomon and Beach 2004), but we did not replicate the scale of these fishways in the laboratory. Of the 892 hydropower dams in U.S. states where American eels are regulated by the Atlantic States Marine Fisheries Commission, 623 (~70%) exceed 5m in height (U.S. Army Corps of Engineers 2020). Therefore, most eel ladders will need to be at least this long to allow eels to move upstream of dams, and we would expect any selection that occurs during upstream passage to be greater in functioning fishways. Previous research show increased energy expenditure for fish moving under increased flows and slope (Standen et al. 2002; Wang and Chanson 2018). Given the steepness of many eel ladders, we assume climbing activity to be energetically demanding for young eels, so longer climbing times for smaller individuals may result in lower body condition for successful climbers or cause fish to abandon climbing behavior. This hypothesis is supported by Podgorniak et al. (2017) who found evidence for potential size selectivity in eel ladders during this life stage, where fish upstream of multiple ladders were ~10cm larger than those found downstream of these obstacles.

Implications for American eel Conservation

Freshwater systems across the Atlantic coast receive marine-derived nutrients from diadromous fish which are then integrated throughout aquatic food webs (West et al. 2010; Guyette et al. 2014; Weaver et al. 2018). Most species embark on seasonal migrations into freshwater to spawn (anadromy), which constrains the range and frequency of these contributions. However, American eels may spend decades in freshwater and travel hundreds of kms upriver before returning to the marine environment during adult spawning migrations (Oliveira 1999; Jessop 2010). As the only catadromous species found throughout eastern North America, their ability to occupy a range of freshwater habitats (Wiley et al. 2004; Johnson and Nack 2013) may offer an infrequent link to the marine environment in systems and that are otherwise absent of catadromous imports (Gross et al. 1988). Dams limit eel establishment in upstream habitat (Wiley et al. 2004; Machut et al. 2007; Hitt et al. 2012), which may disrupt the natural flow of nutrients within these systems. While extensive effort has been dedicated to restoring the historical connectivity of impounded watersheds thorough the implementation of fish passage systems, most of these structures suffer from poor passage efficiencies (Noonan et al. 2012)

Our findings provide evidence for differences in climbing propensity among individual fish which may be related in innate behavioral characteristics. Eel ladders are engineered to facilitate the movement of juvenile eels when small body mass allows fish to overcome the force of gravity. Following the juvenile migratory stage, American eel continue growing and metamorphose into a sub-adult (yellow) eels, where they can reach lengths upwards of 1m (Jessop 2010). While yellow eels have been observed using eel ladders, most fish that use these systems are < 20cm (Schmidt et al. 2009). Upstream movement is not only associated with the juvenile migratory stage, as some yellow eels undergo extensive movement between freshwater and saline habitats in unobstructed rivers systems (Jessop et al. 2006; Lamson et al. 2006). Since fish personalities, especially activity level, are plastic through time and across contexts (Frost et al. 2007; Biro et al. 2010; Polverino et al. 2016), eel personality, and any underlying relationship to climbing propensity may also change through time. Therefore, individuals that choose to move upstream during this yellow stage, or fish that were unable to pass dams successfully as juveniles, may develop climbing motivation later in life but when they are at suboptimal size to use these existing passage systems. Additionally, research on the European river lamprey (*Lampetra fluviatilis*), another anguilliform, show that few fish can effectively pass more conventional fishways (Foulds and Lucas 2013). Therefore, despite multiple options for upstream passage (through fishways or eel ladders), opportunities to access upstream reaches may occur in a short time window when fish have both climbing motivation and are small enough to utilize eel ladders.

Selection at fishways may have unrecognized consequences at the population level. These costs are clearer for anadromous species (e.g. salmonids) that must pass dams to reach upstream spawning habitat, and where the exclusion of some proportion of the population limits the spawning stock biomass and reduces the phenotypic and genetic variation contributed by those individuals (Caudill et al. 2007; Lundqvist et al. 2008; Maynard et al. 2017). Although catadromous species do not necessarily need to access reaches upstream of dams to complete their life cycles, suboptimal performance of eel passage systems that prevent a subset of individuals from reaching rearing habitat may have indirect effects.

First, limiting access to upstream habitat may increase intraspecific competition downstream, especially in smaller, resource limited tributaries. Second, American eel are found throughout watersheds and contribute substantial biomass to aquatic systems (Ogden 1970; Hitt et al. 2012; Kiraly et al. 2015). Selection against some individuals at dams may ultimately limit eel establishment in upstream reaches, with the potential for ecosystem-wide implications for fish communities (Hitt et al. 2012). Third, fish that spend their lives in higher reaches after successful upstream migration face major challenges while passing dams during their eventual downstream spawning migration where passage is known to increase mortality and migratory delays (Norrgård et al. 2013; Stich et al. 2014; Nyqvist et al. 2016; Eyler et al. 2016). In aggregate, selectivity at juvenile eel ladders may have the potential for individual, population, and ecosystem-wide implications. While this study does not provide direct evidence for selection in the field, we demonstrate a link between eel personality and climbing behavior. These results would be complimented by additional research that characterizes variability in behavioral traits and climbing activity at the watershed-level. Collectively, we hope this information will be useful to dam operators, fisheries managers, and fishway engineers and that fish personality merits consideration when discussing methods to improve fish passage.

CHAPTER 2

THE CONSEQUENCES OF DAM PASSAGE FOR MIGRATING AMERICAN EEL IN THE PENOBSCOT RIVER, MAINE

Abstract

American eel (*Anguilla rostrata*) often pass hydropower dams during adult spawning migrations. We conducted a four-year acoustic telemetry study that characterized passage risks through two dams (West Enfield and Milford) in the Penobscot River, Maine, USA. We released tagged fish (n=355) at two sites, estimated survival and delay under variable river conditions, and compared performance among dammed and free-flowing river sections. Survival rates (standardized per river km) were lower at West Enfield ($\Phi_{rkm} = 0.984 \pm 0.006$ SE) and Milford ($\Phi_{rkm} = 0.966 \pm 0.007$ SE), compared to undammed River sections ($\Phi_{rkm} = 0.998 \pm 0.0003$ SE). This accounted for 8.7%, 14.2%, and 8.7% cumulative mortality through sections classified as West Enfield (4.4km), Milford (5.5km), or River (58.1km) respectively. Fish that already passed an upstream dam incurred higher downstream mortality compared to individuals without passage experience. Additionally, fish endured long delays at dams, and >10% of fish were delayed >24h. Low flows exacerbated the risk of mortality and delay. These results offer evidence for direct, latent, and sub-lethal consequences of dam passage for migrating eels.

Introduction

Diadromous fish species have experienced substantial population declines over the last 200 years, with many Atlantic stocks currently < 10% of historic estimates (Limburg and Waldman 2009). These losses are attributed to anthropogenic stressors fueled by industrialization, pollution, climate change, overfishing, and reduced habitat connectivity caused by hydroelectric dams (Hall et al. 2011). Among these species, the American eel (*Anguilla* *rostrata*) stock has seen declines range-wide and the population remains near historic lows (Haro et al. 2000; ASMFC 2017). Commercial harvest occurs across all three continental American eel life stages. Fueled by Maine's lucrative glass eel fishery, the U.S. eel fishery has evolved into a multimillion-dollar industry which peaked at >$40million (USD) in 2012 (Brust et al. 2017). Low recruitment has led to conservation concern, emphasized by 2004 and 2010 petitions to the United States Fish and Wildlife Service (USFWS) to list American eel for protection under the Endangered Species Act (Bell 2007; Shepard 2015). Although the USFWS determined that protection was unwarranted, the complex American eel life cycle presents major challenges for the conservation and management of this species.

After beginning life in the Sargasso Sea, American eel larvae are dispersed across the eastern coast of North America (Tesch 2004). They eventually transition to a translucent, "glass" stage near coastal waters and begin actively swimming upriver, and many encounter dams in pursuit of freshwater lakes, rivers, and streams. Although these barriers delay movement and limit eel establishment in headwater reaches (Hitt et al. 2012), many dam structures have been retrofitted with juvenile eel ladders that offer upstream passage opportunities (Schmidt et al. 2009; Welsh and Liller 2013). Once in freshwater, eels may spend more than 20+ years before beginning a transoceanic spawning migration and return to the Sargasso Sea (Oliveira 1999; Jessop et al. 2008; Jessop 2010), during which they must pass the same dams ascended as juveniles. Such late-life mortality in this long-lived, semelparous fish is likely to have disproportionate consequences for populations trajectories, and the risks associated with downstream passage through hydropower facilities is considered one of many stressors contributing to population declines (Castonguay et al. 1994).

Migrating American eel face two major challenges when navigating hydropower dams. First, eels must locate a downstream passage route, which may occur through spillways, downstream fishways, or turbine intakes, depending on specific facilities and river conditions. Some individuals spend hours or even days searching for passage routes, drawing on energy stores reserved for migration (Carr and Whoriskey 2008; Piper et al. 2013; Eyler et al. 2016). Anguillid eel migrations are also synchronized with environmental cues (river flow, water temperature, lunar phase, tidal cycles) which are presumed to promote successful migration, and long delays at dams may cause fish to miss an optimal migratory window (Barbin et al. 1998; Durif et al. 2008; Acou et al. 2008). When routes are selected, eels risk impingement on dams structures, impact-related injuries from falling overtop spillways, and lethal strikes by turbine blades in power generating stations (Piper et al. 2013; Eyler et al. 2016). Even when direct mortality is avoided, salmonid research showed that non-lethal injuries sustained during dam passage may result in mortality downstream (Mathur et al. 2000; Ferguson et al. 2006; Stich et al. 2015). Despite the mounting evidence attesting to the negative interaction between eels and hydropower, the most recent USFWS American eel biological assessment concluded that "*turbine mortality is not considered a significant stressor to the American eel at a population level*" (Shepard 2015). However, relatively few studies have fully described mortality and delays at dams during outbound migration, and the net reduction in survival associated with dam passage remains unknown in many systems or under variable river conditions

American eel are ubiquitous throughout the Penobscot River watershed (Kiraly et al. 2015; Watson et al. 2018), which is the largest river drainage in Maine, USA. The river harbors 14 federally regulated hydropower projects within its main stem and tributaries. By 2030, eight of these dams will undergo relicensing by the Federal Energy Regulatory Commission (FERC) and licenses can last anywhere from 30–50 years (Maine DEP 2014). Fish passage is among the criteria discussed throughout the relicensing process, which offers an infrequent opportunity to make federally mandated improvements to promote the safe movement of fish through dam structures.

The co-occurrence of American eels and dams within the watershed makes the Penobscot River a convenient system to study the interactions between fish and hydropower generation. Our primary goals with this research were to: 1) characterize mortality and delays experienced by migrating eels at two hydroelectric projects, and 2) understand the effect of passing multiple dams during adult spawning migration. We conducted a four-year acoustic telemetry study to track eel movement through West Enfield and Milford Dams in the Penobscot River to more broadly understand the risks of dam passage for migrating eels under varying river conditions, while also offering site-specific information ahead of impending relicensing decisions

Methods

Study Site

The Penobscot River runs 175km through Maine's interior before entering Penobscot Bay at 0 river kilometers ("rkm" hereafter; relative to the upstream distance from the river's terminus). Recently, the lower river has undergone major changes in connectivity through the removal of two dams in 2012 and 2013, which left West Enfield Dam (101rkm) and Milford Dam (62rkm) as the final dams encountered by migrating eels each fall. At both projects, dam structures extend across the entire river and downstream fish passage is available via spillways (under high flows), sluiceways, power generating facilities, and fish-specific passages which are intended to prevent detour fish around turbine intakes and guide them to alternative passage routes. Downstream fish passage at West Enfield consists of five surface bypasses positioned above turbine intakes while Milford Dam has a vertical bar system with a gated, bottom intake designed for adult eel passage. West Enfield has two turbines (13MW total capacity), while Milford has four (8MW total capacity). Operations at both dams are regulated by FERC and existing licenses expire in 2024 at West Enfield and 2038 at Milford (Gallagher 2005; Kleinschmidt Group 2015; Dorman 2019)

Fish Collection and Tagging

We collected fish from Souadabscook Stream in Hampden, Maine, U.S.A, using a weir located 3km upstream from the stream's confluence with the Penobscot River (31rkm). Downstream movement in this tributary is unimpeded by anthropogenic barriers, and we assumed fish experienced similar migration histories prior to sampling. Since American eel migrate throughout the fall (Parker and McCleave 1997; Verreault et al. 2012), we operated the trap nightly from September–November and selected eels for further processing that were >40cm and exhibited clear characteristics of adult metamorphosis (i.e., enlarged eyes, dark dorsal surface; Pankhurst and Lythgoe, 1982).

Eels were anesthetized in a cold-water tricaine methanesulfonate (MS-222, 250mg/L) bath for approximately 10min prior to surgery. We surgically implanted each fish with an acoustic transmitter (InnovaSea, V9-2x) through a small incision in the peritoneal cavity and secured the wound with 2-3 braided, absorbable sutures (Ethicon Inc., VICRYL 3-0). These transmitters had an estimate tag life of 649d and were programed to emit a 69kHz signal (once every 3–60s for the first 90d, 150–250s for 210d, 30–60s for 150d, and 150–250s for 200d, before the cycle repeated, given enough battery life). We programed this sequence to maximize detection efficiency throughout the fall migration, but also have the ability to detect individuals that remained in the system for subsequent seasons (i.e., fish that abandoned migration, but survived). After surgery, eels recovered in aerated, 100L coolers for at least 1h during transport to release sites. We tagged and released 100 fish/year from 2016–2018, and 55 fish in 2019.

Release Sites

We transported eels to one of two release sites in the Penobscot River (Figure 2.1A). In 2017 and 2019, all fish were released in South Lincoln, Maine, 12km upstream of West Enfield Dam ("Upstream release", 113rkm). In 2016 and 2018, we released approximately half of tagged fish at this upstream release site and the remaining fish were released in Passadumkeag, Maine, 9km downstream of West Enfield Dam ("Downstream release", 92rkm). These paired releases were used to understand the relative risk for fish that pass multiple dams during migration.

Acoustic Array

Eel movements were tracked from release sites to the Penobscot River estuary with an array of >60 acoustic receivers (InnovaSea, VR2W). Receivers were moored to the river bottom and multiple receivers were clustered near dams or in areas where detection efficiency was compromised due to high flows or in-river obstructions. Each receiver (or group of receivers) was assigned to 1 of 15 unique receiver Stations (Figure 2.1A, 2.11C), and detections were pooled for stations that consisted of multiple receivers. The tidal section of the river ends at 48rkm, below receiver Station 14. Since the primary objective of this study was to compare passage through dams with free-flowing river sections, we pooled all tidal receivers into a single receiver station (Station 15). We considered all fish detected at least once from 44.6–17.3rkm (site of most downstream estuary receiver) to have survived to the estuary. The array was deployed prior to tagging and retrieved from the river before ice-in (Nov 16–Dec 9) to allow

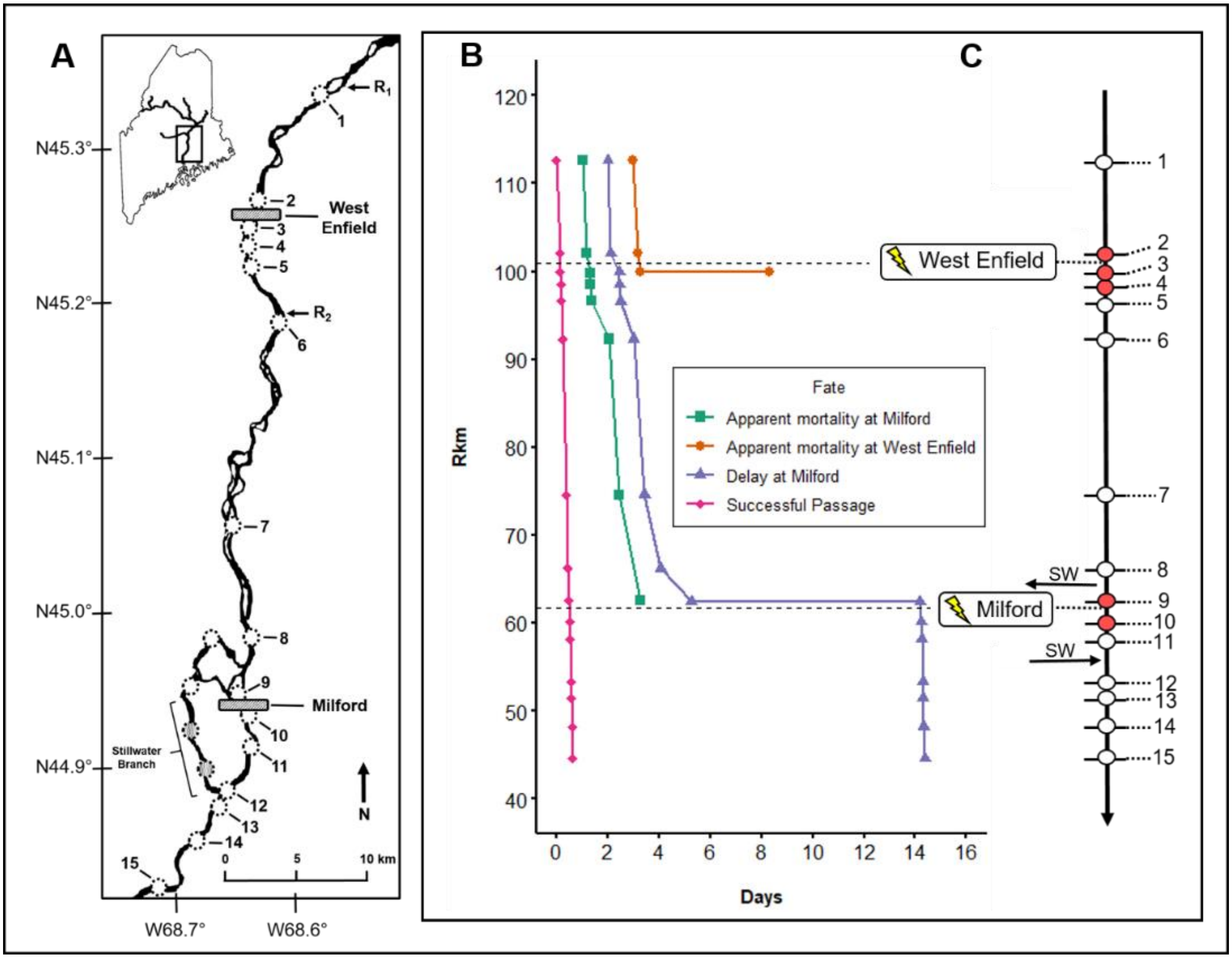

Figure 2.11. A) Overview of study area. Open circles and corresponding numbers represent receiver stations and capture occasions in the main stem of the Penobscot River. Open circles without numbers represent additional receiver stations. Shaded circles are receivers in the Stillwater Branch. R_1 = Release site upstream of West Enfield Dam in South Lincoln (Upstream release), ME. R_2 = Release site downstream of West Enfield Dam in Passadumkeag, ME (Downstream release). B) Potential fates of individual fish following post-release. Telemetry tracks were extracted from four fish released upstream of West Enfield in 2017 (pink diamonds, purple triangles, and orange circles) and 2018 (green squares). Days represent the relative time spent in the river post-release. C) Conceptual model of acoustic array. Red circles represent receiver stations where mortalities in the next downstream reach were attributed dam passage and SW arrows represent potential exit and re-entrance of the main stem through the Stillwater River.

enough time for fish to move through the study area. A subset of receives were deployed through the winter each year so that any fish moving would still be detected.

Survival Analysis

All survival analysis was performed using a Cormack-Jolly-Seber (CJS) mark-recapture framework (Pollock et al. 1990) in Program R (R Core Team 2013) using the *RMark* package (Laake 2013). We created capture histories for each fish contingent on if individuals were detected (1) or not detected (0) at each receiver station. This approach allowed us to estimate apparent survival (Φ; "survival" hereafter) in the intervals between receiver stations and also estimate the probability of detecting a fish (p) at each station, given that the fish was still alive to be detected. We assumed fish movement was unidirectional, which allowed us to create a space-based analysis similar to time-based models in a traditional CJS framework, such that Φ represented the survival between receiver stations corrected for imperfect detection, as is frequently employed in fish movement studies (Halfyard et al. 2013; Michel et al. 2015; Zydlewski et al. 2017; Hawkes et al. 2017). Fish entered the capture history at the time of first detection, which usually occurred at Station 1 (Upstream release) or Station 6 (Downstream release).

Each interval between receiver stations was categorized as either "River", "West Enfield" or "Milford", referencing the type of river section that eels moved through. Dead fish are known to drift considerable distances in rivers (Calles et al. 2010; Havn et al. 2017), and some eels may suffer sub-lethal injuries during passage, potentially leading to mortality further downstream (Besson et al. 2016). To capture both direct and latent mortality during passage, we classified intervals between Stations 2–5 (102.1 – 96.6rkm) as "West Enfield", Stations 9–11 (62.5 – 58.1rkm) as "Milford", and all other intervals were classified as "River" reaches. Unless explicitly mentioned, survival was scaled to units of rkm^{-1} (Φ_{rkm}; “relative survival” hereafter) to account for differences in reach length among reach type. To estimate cumulative survival through dammed and undammed reaches, we back-transformed the relative survival estimates by raising them to the power of the length of the focal river section. Additionally, dynamic river conditions prevented complete recovery and deployment of the receiver array each season, resulting in an inconsistent number of receiver stations per year. Therefore, to maintain the same number of capture occasions across all years, we fixed $p = 0$ for “missing” receiver stations during years in which data were not available (0–3 stations/year).

Near 62rkm, the Stillwater River branches from the main stem before rejoining the river 11km downstream, circumnavigating Milford Dam (Figure 2.1A, 2.1C). Previous research on juvenile Atlantic salmon (*Salmo salar*) has shown that a minor proportion ($\leq$ 26% annually) of fish select this alternative route (Holbrook et al. 2011; Stich et al. 2014). In our study design, fish that survived until Station 9 and moved through the Stillwater River were temporarily unavailable for detection at Stations 10 and 11. We first explored constructing a multistate framework to address this problem (where use of the Stillwater River constituted an alternative state) similar to Holbrook et al. (2011) and Stitch et al. (2014). However, the added complexity of the multi-state model, coupled with the modest sample size of eels that we observed using the Stillwater Branch, compromised our ability to produce robust survival and detection estimates under the multi-state framework (as evidenced by poor model convergence). Instead, fish that were detected in the Stillwater Branch were censored from Stations 10 and 11, but contributed to parameter estimation in all other reaches.

Comparison of dammed and undammed river

One objective of this study was to estimate the total mortality attributed to dam passage throughout the study area. To distinguish dam-related mortality from background river mortality, we compared cumulative survival from our observed estimates to a hypothetical "dam-free" scenario. We estimated cumulative survival through the study area using results from our 4-year aggregate, reach-dependent model, which generated different relative survival estimates for each reach (*i*) that were aggregated across study years. Cumulative survival throughout the study area is given as:

$$\Phi_{cumulative} = \prod_{i=1}^{14} (\Phi_i)^{L_i}$$

Equation 2.1

where $\Phi_{\text{cumulative}}$ is the product of all reach-specific estimates raised to the power of their respective lengths (*L* ; km). In the "dam free" counterfactual, we substituted the aggregate relative survival estimates of "River" section, for reaches classified as either "West Enfield" (*i* = 2–4) or "Milford" (*i* = 9,10) in the previous framework. The resulting estimate of $\Phi_{\text{cumulative}}$ provided an approximation of the expected survival through the system if it was comprised entirely of free-flowing River reaches. In both scenarios, all eels were theoretically released at the Upstream release site, and we assumed perfect survival until Station 1. We derived standard errors (SE) for all cumulative survival estimates using the Delta method (Powell 2007) to propagate variance via the *deltavar()* function offered through the *emdbook* package (Bolker 2020).

Assessment of environmental factors on survival

To better understand the relationship between survival and environmental conditions, we included river flow as a continuous, reach-dependent covariate. Flow data was obtained from the United States Geological Survey's (USGS) stream gage (hydrological unit 01020005) located at 98.5rkm, 3.5km downstream of West Enfield Dam. Both river discharge ($m^3 \cdot s^{-1}$) and river stage (m) are available in 15min intervals, and since both measurements are highly correlated ($r > 0.99$), we used river discharge in this analysis ("flow" hereafter). For all detections, we used the last detection time for each fish at each Station and assigned a flow measurement using the most proximate gage reading. We also included fish length as a continuous, individual covariate to investigate potential size-dependent mortality during dam passage (Calles et al. 2010).

Assessment of passing multiple dams

We included an additive, group effect of release site in the survival analysis that described whether eels were released upstream of 1 or 2 dams. While only the Upstream release group passed West Enfield, both groups traveled through Milford Dam and free-flowing River sections. Therefore, an additive effect of release group described the overall effect of release site through Milford and River sections combined, but was limited in its ability to detect differences in survival between release groups at Milford Dam specifically. We considered adding an interaction between release group and reach type, but annual variation in survival within the system complicated this assessment. Instead, we conducted a *post-hoc* analysis to evaluate the effect of the release group Milford Dam survival. Using only data from years with paired releases (2016 and 2018), we implemented a "virtual release" for all fish detected in the Milford Dam headpond (Station 9; similar to Skalski et al. 2009), and classified whether fish were (1) or were not (0) detected at any point downriver from the Milford section. Because the cumulative detection probability for all receivers in the estuary was essentially 1.00, this simple binomial trial provides a proxy for the probability of survival through this section of the study area. We then used a generalized linear model with a binomial error distribution a fixed effect of release group to assess whether previous dam passage influenced survival at Milford Dam.

Survival model interpretation

We used Akaike's Information Criterion (AICc) adjusted for small sample size to evaluate relative support for competing survival models using ΔAICc < 2.00 as a threshold for model support. Starting from the null model, we first added single, categorical covariates (reach number, reach type) and assessed if they improved model fit. We then incorporated spatially-independent covariates (release site, fish length) as additive terms to base models and retained supported covariates. Lastly, we included space-dependent (flow) and time-dependent (year) covariates as interactive terms to supported models, which allowed for categorical and group effect sizes to vary among seasons and river sections. All continuous covariates were z-standardized, which allowed us to directly compare effect sizes among competing variables. Coefficients (β) from supported models were further assessed to understand their effect on survival estimates, and those with 95% confidence limits not overlapping zero were considered to differ from a slope of 0.0. Since we were most interested in estimating p at all receiver stations each year, we only considered a station-year interaction for this parameter (i.e., the most general form of the detection model) and used this structure in all analyses. A preliminary analysis validated that this model configuration as it consistently outperformed models with more constrained detection structures (e.g., constant or aggregated p)

Delay Analysis

Delays experienced during dam passage were assessed by calculating passage times (h) between receiver stations using the time of first detection at each station. If fish were not detected at the next downstream receiver station, they were removed from the analysis for that reach, and fish that were not detected in the estuary were removed from the analysis for reaches downstream of their last detection. To ensure that potential “holding” patterns post-release, (described by Carr et al. 2008), were not reflected in passage times for the first reach, we used the last detection at Station 1 to calculate the time to move between Stations 1 and 2. Passage time through West Enfield was calculated from the headpond (Station 2) to the confluence of the Piscataquis River (Station 4) because of consistently lower p in the tailrace (Station 3). Time to pass Milford Dam was calculated from the headpond (Station 9) through the tailrace (Station 10). Passage times were scaled (i.e., $h \cdot km^{-1}$) which allowed us to directly compare migration time among different reach lengths. Detections at Station 12 (53.3rkm) were removed from the delay analysis because its proximity to Station 13 (51.4rkm) resulted in overlapping detection ranges that sometimes produced unrealistic passage times (i.e., < 0h). We also removed one observation at Milford Dam that estimated passage time at 0.00h. Since this approach lead to multiple observations for each individual in undammed reaches, we applied a general linear mixed effect model using the *lmer()* function in the *lme4* package (Bates et al. 2015) to compare delays in different sections of river. Passage times were $\log_{10}$-transformed to meet the assumption of normally distributed residuals and Fish ID was treated as random intercept to account for inherent differences in mean passage time among individuals and address the issue of repeated measures as fish moved through multiple free-flowing river reaches within the system. We used a similar tiered approach to model selection as described in the survival analysis, where we first started with a categorical effect of reach type (again classified as “West Enfield”, “Milford” and “River”). We then added spatially-independent covariates (fish length, release site) before integrating interaction terms of release year and river flow. We used ΔAICc < 2.00 as a threshold for model support in conjunction with an evaluation of β coefficients to assess the effect of covariates on passage time.

Results

Of the 355 fish tagged and released, we included capture histories from 343 in the survival and delay analysis (Table 2.1). Migratory status was verified by observing sustained, downstream movement post-release, and individuals were excluded from analysis if they did not meet this criterion. Specifically, we removed fish that were not detected post-release (n=5) or did not move through the study area during the release year and were detected in subsequent seasons (n=6). The six fish that overwintered in the system had a variety of fates: i) Two were detected in the West Enfield headpond the following spring and then initiated downstream movement (one with an apparent mortality at West Enfield Dam, while the other survived to the estuary). ii) One was detected in the West Enfield headpond during the release year but was last detected below the dam the following fall. This behavior is characteristic of a mortality event but we were unable to conclusively determine if the fish moved through the dam during the release year. iii) Two fish passed West Enfield and were last detected in the Milford headpond in December of the release year, but were later detected in the estuary the next spring. iv) One fish moved past West Enfield during the release year, but then appeared to abandon migratory behavior before reaching Milford Dam and was last detected at a receiver, supplementary to the array, between Stations 8 and 9. In addition to the fish detected the following seasons, we also removed one 2016 fish because it was only detected at Station 4 (98rkm) before being detected by an estuary receiver (24rkm) three days later (likely caused by a tag malfunction or avian predation). Telemetry tracks representative of some potential fates are shown in Figure 2.1B. Of the 313 fish that were detected above Milford Dam, 41 (13.1%) moved through the Stillwater River. Across all study years, we detected 282 fish in the Penobscot River estuary, which represents 82.2% of all fish included in the analysis.

Table 2.1. Summary of releases by year. Eels were released at one of two sites in the Penobscot River relative to West Enfield Dam (Upstream = released upstream of West Enfield at 113rkm, Downstream= released downstream of West Enfield at 92rkm; Figure 2.1A). N = number of fish released. Fish length = mean total length (cm) of each release group with ranges in parentheses.

Year	Release site	N	Fish length
2016	Upstream	45	59.2 (48.0-74.0)
	Downstream	50	61.0 (45.5-78.9)
2017	Upstream	100	63.3 (51.0-90.2)
2018	Upstream	46	64.1 (51.0-89.5)
	Downstream	49	61.4 (43.5-83.5)
2019	Upstream	53	60.2 (48.5-86.0)

Survival

We found that eels had lower survival when moving through dammed reaches compared to the free-flowing river sections. Over four years, relative survival was lowest for fish passing Milford Dam ($\Phi_{rkm} = 0.966 \pm 0.007$ SE), and survival at both Milford and West Enfield ($\Phi_{rkm} = 0.984 \pm 0.006$ SE) was lower than free-flowing River sections ($\Phi_{rkm} = 0.998 \pm 0.0003$ SE; Figure 2.2). When we used the reach-dependent estimates (Table A.1) to propagate survival throughout the study area, cumulative survival was estimated at 0.795 ± 0.023 SE, which was lower than the theoretical undammed scenario (Φ = 0.930 ± 0.014 SE; Figure 2.3).

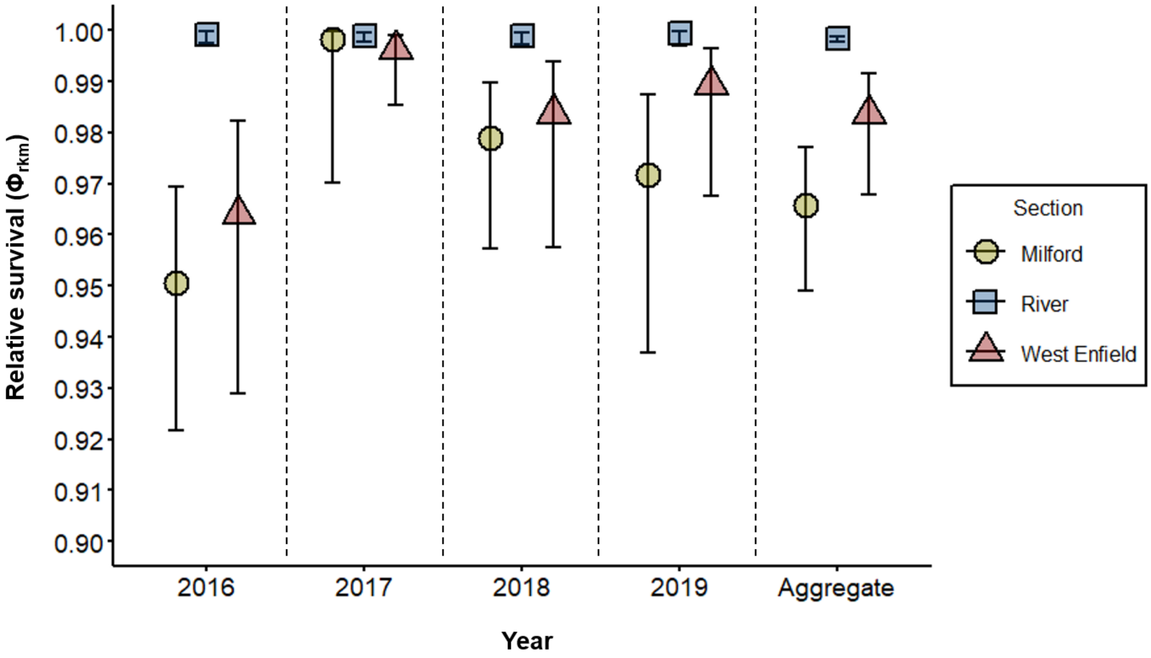

Figure 2.2 Relative survival in each section of the study area. Yearly estimates were pulled from the reach type survival model with a year interaction and aggregate estimates reflect the mean survival in each river section aggregated across all four years. Error bars represent 95% CIs.

Survival varied across study years (Figure 2.2; A.2). Incorporating a year interaction to the reach type model improved support by > 15 ΔAICc from the reach type model alone, and the year interaction was included in the most supported survival model (Table 2.2). Cumulative survival through dammed sections was lowest in 2016 for both West Enfield (Φ = 0.818 ± 0.059 SE) and Milford (Φ= 0.800 ± 0.044 SE) and highest in 2017 for both dams (West Enfield: Φ = 0.980 ± 0.014 SE, Milford: Φ = 0.993 ± 0.011 SE; complete breakdown in Table A.2). Survival in free-flowing River sections was consistently high, and the cumulative survival throughout the

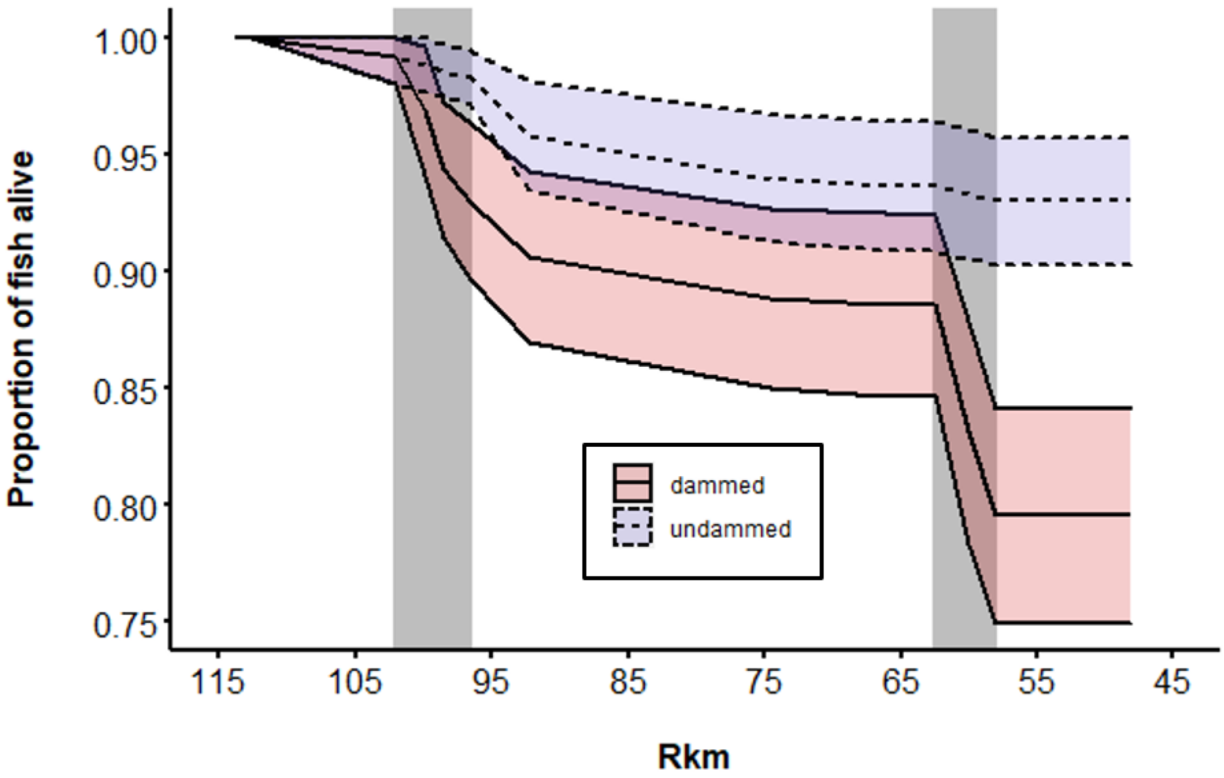

Figure 2.3. Cumulative survival from the upstream release site to the Penobscot River estuary using reach-specific survival estimates in the current (dammed) and theoretically dam-free (undammed) study area. Survival in the current, dammed scenario (solid line, red-shaded region) was propagated using relative (Φ_{rkm}) reach-dependent survival estimates aggregated across all four years (Table A.1). Grey rectangles represent river sections where we attributed mortality to passing West Enfield Dam (left) and Milford Dam (right). Dashed lines and blue-shaded regions represent the expected survival if both dams were removed from the river, which was estimated by replacing the aggregate Φ_{rkm} associated with passing West Enfield and Milford Dam with the aggregate Φ_{rkm} in free-flowing River sections. In this simulation, all fish were released at the upstream release site. Shaded regions represent 95% CIs.

Table 2.2 Relative performance of CJS mark-recapture models to evaluate American eel relative survival during outbound migration. Φ_{rkm} = structure of survival parameter*. Structure of detection parameter (*p*) was kept constant with independent estimates for each receiver station/year. K = number of parameters used in each model, AICc = Akaike's Information Criterion adjusted for small sample size, ΔAIC_c = difference in AICc from most supported model, weight = relative support for each model.

Φ_{rkm}	*p*	K	AIC_c	ΔAIC_c	weight
reach type × year + release	year × station	64	1976.69	0.00	0.77
reach type × year	year × station	63	1979.74	3.05	0.17
reach type × year + fish length	year × station	64	1981.83	5.14	0.06
reach type × river discharge	year × station	57	1990.27	13.58	0.00
reach type	year × station	54	1994.09	17.40	0.00
reach type + fish length	year × station	55	1995.68	18.99	0.00
reach type + release	year × station	55	1995.98	19.29	0.00
reach	year × station	65	2001.15	24.46	0.00
reach × river discharge	year × station	79	2001.16	24.47	0.00
reach × year	year × station	107	2041.09	64.40	0.00
null	year × station	52	2089.58	112.89	0.00
fish length	year × station	53	2091.20	114.51	0.00

*reach = reach-dependent survival estimates for intervals between each receiver station, reach type = intervals were classified as free-flowing River, West Enfield Dam or Milford Dam, year = group effect of release year, release = group effect of release site, river discharge = river flow ($m^3 \cdot s^{-1}$) treated as a continuous, reach-specific variable for each fish, fish length = total fish length.

entire 58.1km of free-flowing River sections varied between 0.944–0.976 depending on year, consistent with the near perfect River Φ_{rkm} (0.999–1.000) throughout the study. We did not find support for an effect of fish length on survival ($\beta_{length} = 0.001 \pm 0.016$ SE).

Survival through dams increased under high flow conditions. Tagged fish appeared to experience the most favorable conditions when passing dams in 2017 when maximum daily flow was consistently > $300 m^3 \cdot s^{-1}$ (Figure 2.4) and survival was at a four-year high (Figure 2.2). In other years, flow generally fell between 100–300 $m^3 \cdot s^{-1}$ when eels passed West Enfield and Milford Dam. We assessed the effect of flow on survival in each reach type using β estimates

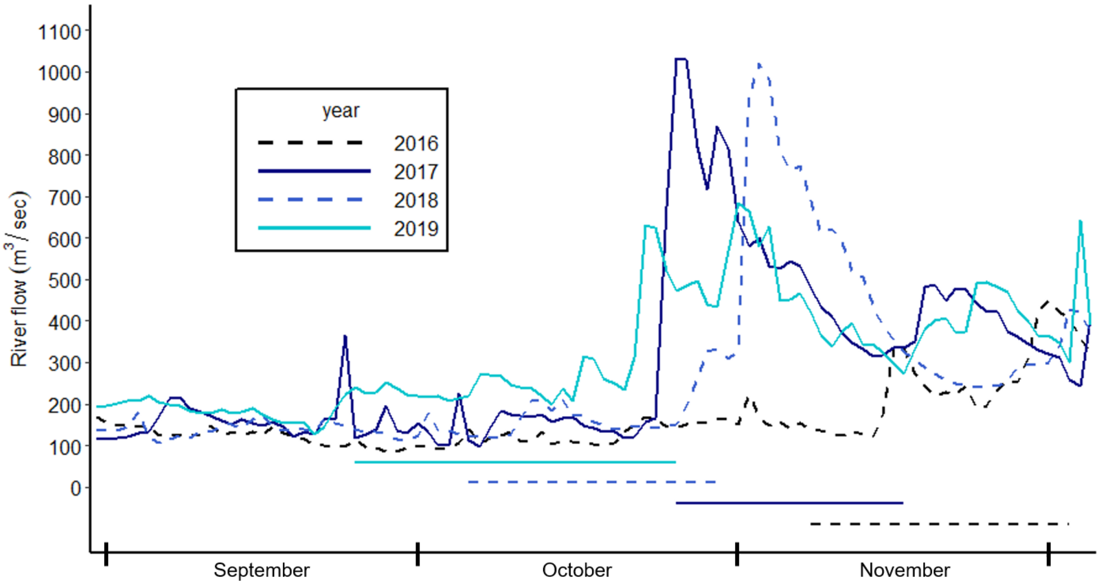

Figure 2.4. Variation in seasonal river discharge across sampling years. Flow data was downloaded from the USGS hydrologic unit deployed downstream of West Enfield Dam near receiver Station 4. Flow represents the maximum daily river discharge. Horizontal lines represent the range of dates when tagged fish had the potential to pass West Enfield or Milford Dam each season.

from a model where the reach type interacted with flow; a configuration that improved support by > 4.00 ΔAICc over the effect of reach type alone (Table 2.2). Upon closer examination of β coefficients from this model, we found a positive relationship between flow and survival at Milford (β_{flow} = 0.969 ± 0.431 SE), but the effect size was not demonstrated to be different than 0.00 when passing West Enfield (β_{flow} = 0.291 ± 0.327 SE) or free-flowing River sections (β_{flow} = -0.183 ± 0.271 SE; Figure 2.5).

Fish in the Upstream release group had lower survival than those in the Downstream release group (Figure 2.6; Table A.3). Adding release site as an additive, group effect (β_{upstream} = -0.829 ± 0.373 SE) was also included in the top model and improved support by >3.00 ΔAICc over the same model without release group (Table 2.2). Cumulative survival through Milford was estimated to be lowest for the upstream group in 2016 (Φ = 0.715 ± 0.069 SE), which was 14.6% (± 8.1%) lower than the downstream group (Φ = 0.861± 0.042 SE). When the effect of release group was applied to 43.3rkm of River sections shared by both release groups (Stations 6–9 and 11–15), we estimated cumulative survival to be lower for the upstream group in 2016 (Φ = 0.951 ± 0.028 SE) and 2018 (0.944 ± 0.028 SE) when contrasted with the downstream group during both years (2016: Φ = 0.978 ± 0.014 SE; 2018: Φ = 0.975 ± 0.014 SE).

When we considered a virtual release immediately upstream of Milford Dam in 2016 and 2018, we did not find support for an effect of release site on survival at Milford Dam (β_{upstream} = -0.141 ± 0.535 SE, $p = 0.792$). When combined with the larger CJS framework, the results from the post-hoc analysis suggest that while the Upstream release group experienced higher downstream mortality, the data do not allow us to disentangle the effect size at downstream dams from free-flowing river sections.

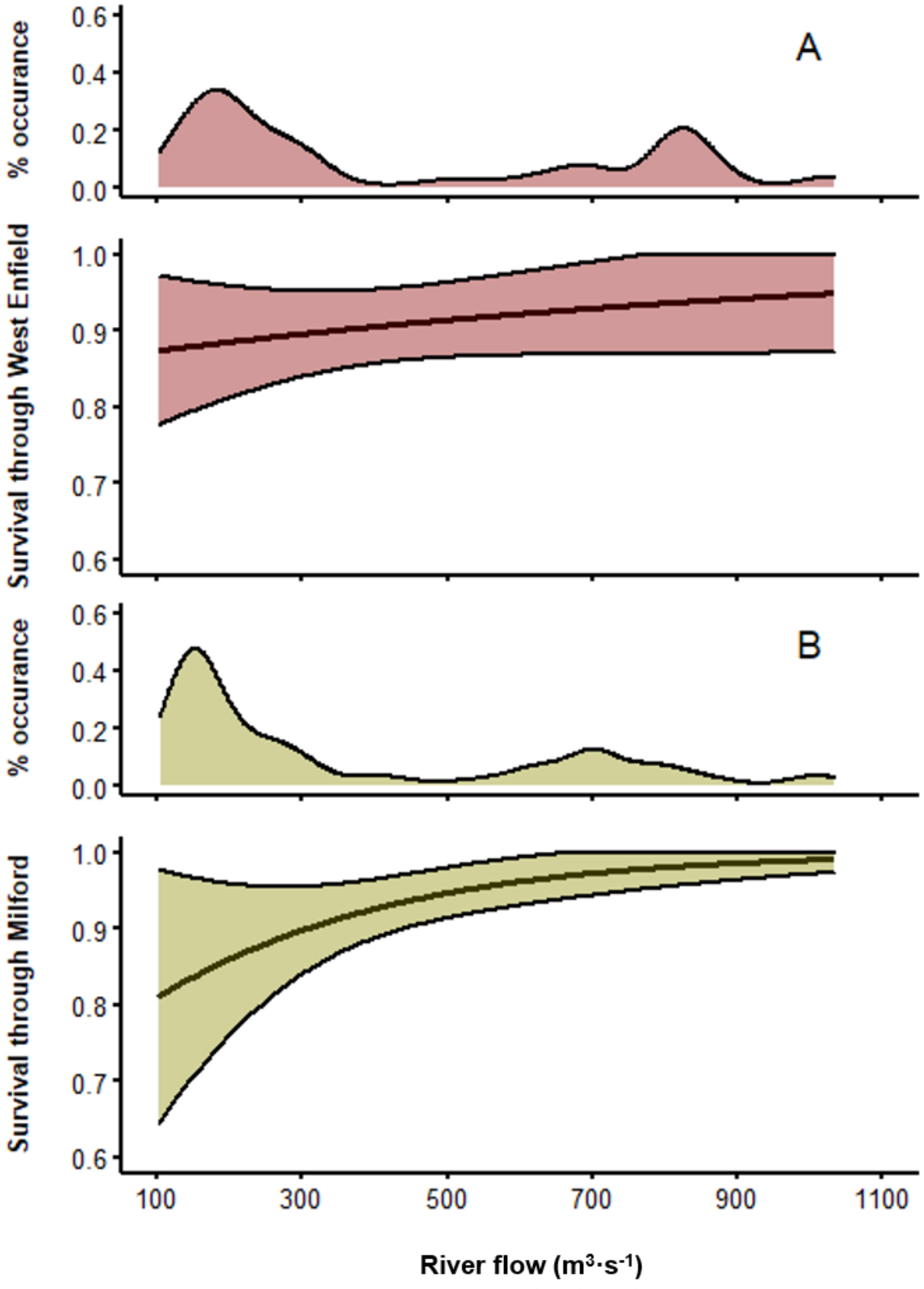

Figure 2.5. Predicted survival under changing flow conditions at West Enfield (A) and Milford (B) Dams juxtaposed with density plots representing the percent of observations across a range of river flows experienced by fish during the last detection at reach receiver station. Predictions were generated from β coefficients that allowed for the effect of flow on survival to vary for each section type. Shaded regions represent 95% CI's.

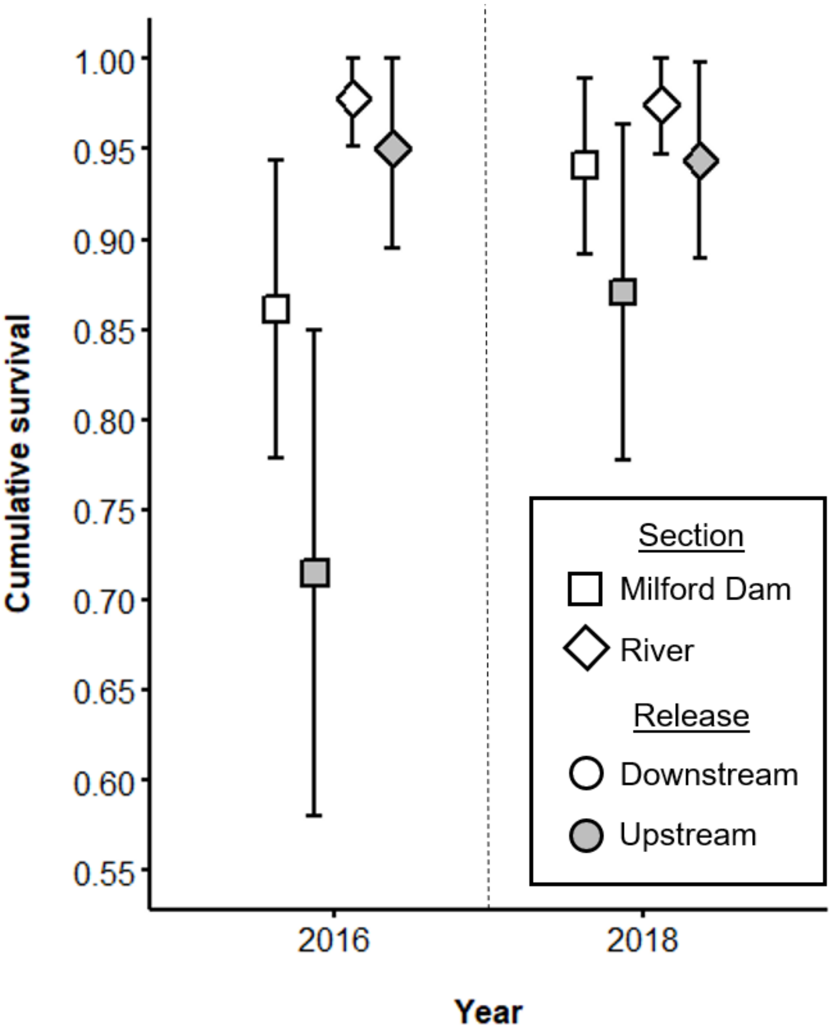

Figure 2.6. Cumulative survival through Milford Dam and free-flowing River sections by release group. Fish in the Upstream group (shaded shapes) were released upstream of West Enfield Dam, so Milford Dam was the second dam encountered during spawning migrations. The Downstream group (unshaded shapes) was released downstream of West Enfield Dam and Milford Dam was the first and only dam encountered when moving downstream. Estimates reflective a single, additive, effect of release group when applied to River (triangles) and Milford Dam (squares) sections. Cumulative survival through River sections was truncated for the upstream group to reflect survival through 43.3km of river shared by both release groups. Error bars reflect 95% CIs. Specific estimates are offered in Table A.3.

Detection probability

Overall, *p* at each receiver station was high throughout the study (mean $p = 0.871$, median $p = 0.983$; Table A.4). Detection probabilities were lowest in 2017 when river flows were highest (Figure 2.4), which likely lowered detection efficiency by increasing acoustic "noise" and reducing the amount of time fish were within detections areas of each station. Stations 3 and 10 had relatively low detection efficiency ($p < 0.500$) in 2016 and 2017. In effort to increase *p* in the following seasons, we deployed additional receivers at these stations in 2018 and 2019, which likely contributed to higher detection efficiencies during subsequent seasons.

Delay

Fish moved slower in dammed than free-flowing reaches (Figure 2.7). On average, fish spent 5.2-fold longer passing West Enfield (mean=11.80h, median = 1.42h) and 5.9-fold longer passing Milford (mean=13.30h, median = 0.98h) compared to free-flowing River sections (mean=2.25h, median = 0.38h). Throughout the study, there was high variation individual passage time at both West Enfield (0.13h – 170h) and Milford (0.21h – 457h). Of the fish detected immediately above each dam, at least 28 fish at West Enfield (16%) and 15 fish at Milford (10%) were delayed >24h. Of the 15 fish that spent more than one day upstream of Milford, all but two fish survived until the estuary, which suggests that passive carcass drift was not a major influence on these passage times.

Adding an interactive effect of release year improved support by >14 ΔAICc over the effect of reach type alone, but annual variation in passage efficiency was most likely explained by inter- and intra-seasonal changes in river conditions (Table 2.3). Passage times through dammed sections were faster under high flow conditions (Figure 2.8), where there was a strong, negative relationship between flow and log passage time at West Enfield (β_{flow}= -0.607 ± 0.046 SE) and Milford (β_{flow} = -0.430 ± 0.081 SE) compared to weak relationship in free-flowing River sections (β_{flow} = -0.147 ± 0.062 SE). These effects were substantial enough that predicted passage time at West Enfield decreased from nearly 8h to < 15min when river stage rose from $100\text{m}^3\cdot\text{s}^{-1}$ to $1000\text{m}^3\cdot\text{s}^{-1}$

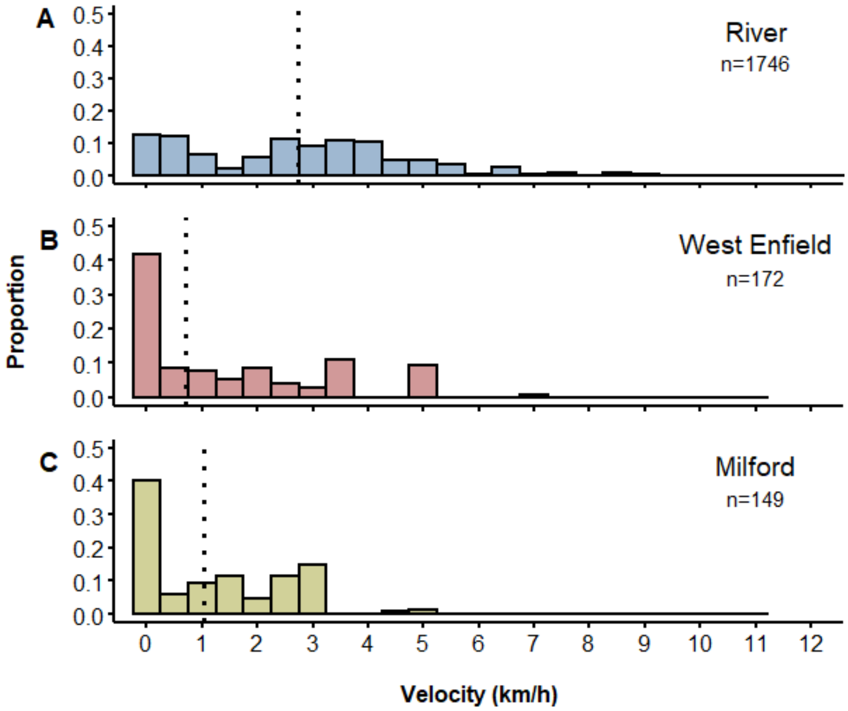

Figure 2.7. Fish velocities by river section. Histograms represent the proportion of observations of each velocity across all years through river (A) and dammed (B, C) reaches. Dotted lines represent the median velocity in each section and the number of observations for each section are listed below labels.

Poor detection efficiency (p= 0.201 ± 0.050 SE) below Milford Dam in 2016 resulted in small sample of passage times this season, which forced us to assess a combined effect of release group for 2016 and 2018. Given the effect of river conditions on passage time, we excluded years without two release groups (2017, 2019) from this analysis, and used a general linear model to isolate the effect of release group on passage time only at Milford Dam. We did not find support for an effect of previous dam passage on log passage time in this river section ($\beta_{upstream}$ = -0.103 ± 0.169 SE, p-value = 0.546).

Table 2.3. Relative performance of generalized linear mixed models to characterize fish passage time (h·km^{-1}) through different river sections. Model = parameter structure for fixed effects*, fish ID was treated as a random effect for all models. K = number of parameters used in each model, AICc = Akaike's Information Criterion adjusted for small sample size, ΔAIC_c = difference in AICc from most supported model, weight = relative support for each model, R^2 = reflects the variance described by fixed effects

Model	K	AICc	ΔAIC_c	weight	R^2
reach type × flow	8	3600.09	0.00	0.60	0.21
reach type × flow + fish length	9	3600.91	0.82	0.40	0.21
reach type × year + fish length	15	3626.23	26.14	0.00	0.21
reach type × year	14	3626.59	26.51	0.00	0.21
reach type × flow	6	3677.86	77.78	0.00	0.18
reach type × fish length	6	3817.38	217.29	0.00	0.10
reach type	5	3819.89	219.81	0.00	0.09
reach type × fish length	8	3821.20	221.11	0.00	0.10
length	4	4027.76	427.68	0.00	0.00
null	3	4029.38	429.30	0.00	0.00

*reach type = intervals were classified as free-flowing river, West Enfield Dam or Milford Dam. year = group effect of release year, river discharge = river flow (m^3·s^{-1}) as a continuous, reach-specific variables for each fish, length = total fish length (cm).

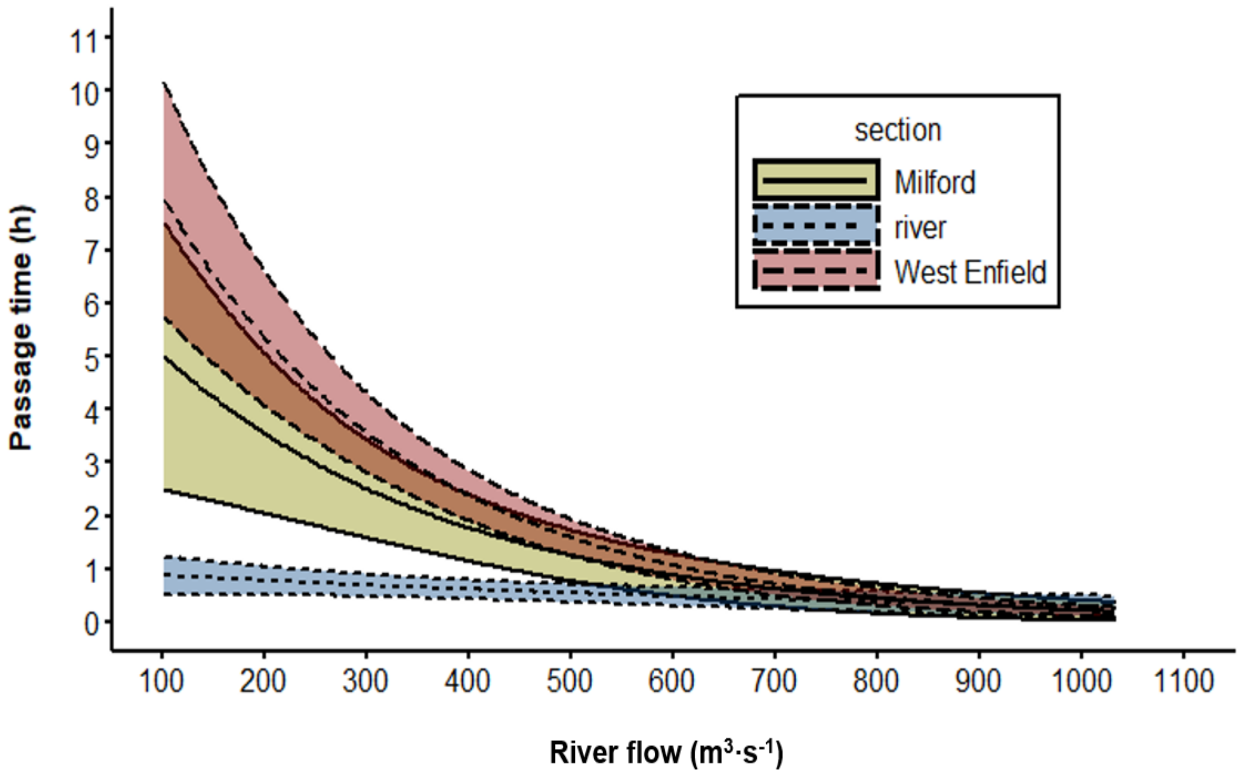

Figure 2.8. Predicted passage times through West Enfield (dashed line), Milford (solid line) and free-flowing River reaches (dotted line), under different river flow. Flow data was downloaded from the USGS hydrological unit deployed downstream of West Enfield Dam near receiver Station 4. Passage time are scaled to reflect the number of hours for fish to move 1km in each river section. Shaded regions represent 95% CI's.

Discussion

Survival through dams

Migrating American eels experienced lower survival through dams compared to free-flowing river sections. Relative survival probabilities varied each year at West Enfield (96.4–99.6%) and Milford (95.1–99.8%), but were substantially lower when compared to free-flowing River sections where survival was consistently high throughout the study (99.9–100.0%). In aggregate, this resulted in 1.4% and 3.2% lower Φ_{rkm} at West Enfield and Milford Dam respectively, relative to River section. While these differences may seem trivial, when we consider the total length of impounded river section, the two dams in our study resulted in removal of > 13% of fish, on average, compared to the expectation under a totally free-flowing river. Furthermore, our analysis was conducted in a system where fish encountered only two hydropower dams during outbound migration, and we would expect even greater losses in system with additional dams. For this long-lived, semelparous fish species, we anticipate any additional, unnatural mortality on reproductively mature individuals to adverse consequences for at the population level.

Despite the inherent differences in dam structures encountered by migrating Anguillid eels across the globe, these survival estimates generally fell within the range of other eel passage studies where dam-specific mortality ranged between 6–42% (Winter et al. 2006; Calles et al. 2010; Eyler et al. 2016). Our results further illustrate the potential for high variability in survival. In 2016, cumulative mortality was substantial through West Enfield (18%) and Milford (20%), compared with 2017 when mortality was ≤ 2% through both dams. Since eels were released under a range of river conditions (Figure 2.4), we suspect the majority of variation in passage success is attributed to inter-seasonal changes in environmental conditions rather than the inherent stochasticity of risk imposed by each dam.

Seasonal changes in river flow likely afford eels different migration routes through dam structures during fall migration. When survival at both dams was nearly perfect in 2017, river flows were consistently high. Survival through Milford was positively influenced by river discharge, and we predicted cumulative survival to exceed 95% when flows were $>520 m^3 \cdot s^{-1}$. While survival at West Enfield was highest in the high flow year, β_{flow} was not exclusive of 0.00. This result was unexpected because the downstream fish passage facility does not have an eel-specific bypass system. However, generally higher survival at West Enfield (relative to Milford) may have made it more difficult to detect the interaction because there was less room for high flows to increase survival relative to the baseline.

While we were unable to specify passage route in this study, previous work observed near perfect survival for fish passing through spillways, suggesting that most dam passage mortalities are turbine-related (Muir et al. 2001; Skalski et al. 2002; Eyler et al. 2016). Therefore, increased survival under high flow conditions observed in this study is likely the result of passing over spillways at Milford and West Enfield, effectively lowering the probability of passing through power stations. Our results are corroborated by Wertheimer and Evans (2005) study on steelhead (*Oncorhynchus mykiss*) where migratory success was reduced by 11.5% during non-spill years. Given the relationship between flow and survival observed in this study, adult American eels would benefit from dam operations that maintain spillway passage that is well synchronized with fall migration.

Although we found a generally negative effect of dams on survival, it is likely we underestimated the full scope of mortality associated with West Enfield. First, two fish that likely died when passing West Enfield were excluded from the analysis because we were unable to confirm migratory status during the release year. Additionally, we suspect that natural mortality in the freshwater-phase of adult eel migrations in the Penobscot River is negligible given a lack of large piscivores (Kiraly et al. 2015; Watson et al. 2018) and limited fishing activity, which are known to cause mortality in estuarine and marine phases of eel spawning migrations (Aarestrup et al. 2009; Béguer-Pon et al. 2012). Since adult eels can survive turbine strikes (Saylor et al. 2019; Heisey et al. 2019), injured eels may continue migration (or be transported during high flow events), but succumb to injuries further downstream. In our study, all apparent losses in River sections below dams (n=10) occurred downstream of West Enfield before fish reached Milford. We assume that these disappearances are reflective of delayed mortalities related to passing West Enfield, but we cannot definitively distinguish these losses from natural mortality, tag loss, or failed detections. While these individuals only represented 4% of all fish released upstream of West Enfield, we expect aggregate, cumulative mortality at West Enfield would increase to 13.5% if these losses were attributed to dam passage. Our conclusions are supported by a Ferguson et. al (2006) study which estimated that 46–70% of all dam-related mortalities of migrating Pacific salmon smolts (*Oncorhynchus tshawytscha)* were indirect, occurring downstream of dam infrastructure.

Although we may not have characterized the latent mortality attributed to West Enfield in the survival estimates, these effects may be imbedded within the model that included an additive, effect of release group. This effect suggests that previous dam passage experience increased mortality as eels continued downstream migration. However, we were unable to disentangle whether the previous passage experience resulted in lower survival at downstream dams or free-flowing sections of river. Either scenario implies a complex system-wide influence of dam passage that can be well-removed from hydropower facilities. We assume that latent mortality is the result of severe, turbine-related injuries (e.g. bruises, lacerations, fractured vertebrae, severed tails) as evidenced by other studies that have recaptured eels following dam passage (Besson et al. 2016; Heisey et al. 2019). Fish may die further downstream as a result, or these injuries may compromise swimming ability limit their capacity to locate safe passage alternatives at downstream dams. Research tracking the downstream movement of adult steelhead (*Oncorhynchus mykiss*) and juvenile Atlantic salmon (*Salmo salar*) characterized the severe implications for fishing pass multiple dams as few fish (0–16%) survived eight, consecutive passage events (Wertheimer and Evans 2005; Norrgård et al. 2013; Nyqvist et al. 2016). Given the evidence of direct and latent mortality found in this study, we expect eels that begin migration upstream of multiple dams to have a relatively low probability of surviving to the marine environment.

Delays at dams

Overall, eels moved slower in impounded than free-flowing sections of river (Figure 2.7). We offer evidence for high variation in individual passages times where some navigated dams in minutes while others spent days delayed in dam headponds before passing successfully. The high variability in delay aligns with other eel passage studies which also showed similar variation in site-specific passage efficiencies (Carr and Whoriskey 2008; Piper et al. 2013; Eyler et al. 2016). The magnitude of delays were exacerbated under low flow conditions (Figure 2.8). For example, passage times at both dams were not predicted to be comparable to free-flowing river reaches until flow exceeded $800 m^3 \cdot s^{-1}$, a condition that occurred in < 17% all dam passage observations. These long passage times suggest that when eels encounter dams under low flow conditions, passage routes are limited or difficult to locate. Our results are not surprising, given the demonstrated influence of increased flow on downstream migration rates in other fish species (Smith et al. 2002; Wertheimer and Evans 2005; Norrgård et al. 2013). Some delays at dams, especially those delayed < 11h (approximately the average duration of daylight during eel migration) may reflect individual differences in arrival time at dam structures. American eel are largely nocturnal (Hedger et al. 2010; Aldinger and Welsh 2017), and downstream movements by adults occur at night (Béguer-Pon et al. 2014). Therefore, fish that arrive in dam headponds near sunrise, may discontinue movement until sunset, which would elongate passage times for reasons mostly independent of dams. This constraint of migration is likely also experienced by fish moving through free-flowing River sections and may explain why some migration speeds that were slower than otherwise expected in this region of the study area. Nevertheless, we found strong differences in passage times between Dam and River sections (Figure 2.7), highlighting the overall negative effect of dams on the speed of eel spawning migrations.

In combination with increased mortality, long delays during passage events may have further consequences for spawning success. Studies using three-dimensional telemetry reveal that eels exhibit extensive searching behavior in headponds and some individuals may briefly move upstream before making additional passage attempts at dams (Brown et al. 2009; Trancart et al. 2020). Downstream eel movements through the river and into the marine environment are highly synchronized with environmental triggers (flow, lunar cycle, tides) that are assumed to promote migratory success (Barbin et al. 1998; Durif et al. 2008; Acou et al. 2008; Béguer-Pon et al. 2014; Verhelst et al. 2018). The extensive delays experienced by migrating eels may prevent fish from moving under ideal conditions and may ultimately limit spawning potential, as excessive swimming associated searching activity may deplete energy stores reserved for migration (van Ginneken 2005). However, given the sparse information about American eel spawning activity, we know little about the reproductive consequences of migratory delays. Salmonid research has demonstrated that inefficient barrier passage during adult spawning migrations limit reproduction and are an impediment to population recovery (Caudill et al. 2007; Lundqvist et al. 2008). Given the length and timing of American eel spawning migrations, we assume that extensive delays have sub-lethal consequences on eel populations of which the severity remains unknown.

Implications for eel conservation

In aggregate, our results offer compelling evidence for direct mortality, latent mortality, and sub-lethal consequences of dam passage for migrating adult eels. While many eel passage studies are limited to one season, our four-year study allowed us to track fish movement under a variety of conditions, and demonstrate that survival is conditional river flow and previous passage experience. Nightly turbine shutdowns and downstream, eel-specific bypass mechanisms are proven to be effective measures to mitigate the risk associated with hydropower dam passage (Eyler et al. 2016; Baker et al. 2019). Our results support implementing these strategies, especially under low flow conditions, to maximize both safe and efficient passage. However, we recognize both the physical and opportunity costs incurred by dam operators that implement these solutions, so a mitigation approach that considers in-river conditions may be an effective, interim solution. When river flows crest, usually after the cumulative response to frequent and heavy precipitation events throughout fall migration, we estimated the risks associated with dam passage to be relatively low. Therefore, fish that migrate during high flow events may benefit from more favorable migratory conditions and pass dams via spillways, which effectively reduces the probability of encountering turbine blades and increases passage efficiency. Until these flow thresholds are reached each year, our results suggest that eels are at serious risk of mortality and delay at dams.

These findings would be most informative when paired with eel forecasting data that allows both fisheries managers and dam operators to predict when eels are moving through the system and modify dam operations accordingly. While, the ASMFC American eel benchmark stock assessment and 2015 USFWS American eel biological report recognize the effectiveness of turbine shutdowns, they lament on the challenges of predicting downstream eel movement (Limburg et al. 2012; Shepard 2015). Despite the demonstrated relationship between Anguillid eel migration and high flow events (Durif et al. 2008; Acou et al. 2008), turbine shutdowns that are synchronized with large pulses in eel movement may simultaneously occur when passage conditions are most favorable and the risks of passage are naturally mitigated. Although these efforts are intended to protect large proportions of the population, they may neglect periods when eels are most vulnerable. Therefore, careful consideration of flow regimes may be beneficial when implementing mitigations strategies to balance losses of American eels and hydropower production.

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APPENDIX A

Table A.1. Relative survival estimates (annual and aggregate) of each reach throughout the study. Length = reach length (km). Estimated were extracted from stand-alone reach survival model. SE = standard error. CI = confidence interval. Length = length of each interval.

Year	Reach	Φ_{rkm}	SE	95% CI	Length
2016	1	0.996	0.003	(0.983–0.999)	10.5
	2	0.946	0.075	(0.498–0.997)	2.2
	3	0.999	0.118	(0.000–1.000)	1.4
	4	1.000	0.000	(1.000–1.000)	1.9
	5	0.981	0.011	(0.943–0.994)	4.3
	6	0.999	0.001	(0.995–1.000)	17.7
	7	1.000	0.000	(1.000–1.000)	8.4
	8	1.000	0.000	(1.000–1.000)	3.7
	9	1.000	0.000	(1.000–1.000)	2.4
	10	0.893	0.025	(0.835–0.933)	2
	11	1.000	0.000	(1.000–1.000)	4.8
	12	1.000	0.000	(1.000–1.000)	1.9
	13	1.000	0.000	(1.000–1.000)	3.2
	14	1.000	0.000	(1.000–1.000)	3.6
2017	1	1.000	0.000	(1.000–1.000)	10.5
	2	0.997	0.005	(0.940–1.000)	2.2
	3	1.000	0.000	(1.000–1.000)	1.4
	4	0.994	0.007	(0.944–0.999)	1.9
	5	0.993	0.004	(0.976–0.998)	4.3
	6	0.999	0.001	(0.995–1.000)	17.7
	7	1.000	0.000	(1.000–1.000)	8.4
	8	1.000	0.000	(1.000–1.000)	3.7
	9	0.996	0.004	(0.969–0.999)	2.4
	10	1.000	0.000	(1.000–1.000)	2
	11	1.000	0.000	(1.000–1.000)	4.8
	12	1.000	0.000	(1.000–1.000)	1.9
	13	1.000	0.000	(1.000–1.000)	3.2
	14	1.000	0.000	(1.000–1.000)	3.6
2018	1	1.000	0.000	(1.000–1.000)	10.5
	2	0.993	0.011	(0.867–1.000)	2.2
	3	0.980	0.021	(0.860–0.997)	1.4
	4	0.975	0.017	(0.906–0.994)	1.9

Table A.1 continued

	5	1.000	0.000	(1.000–1.000)	4.3
	6	0.998	0.001	(0.994–0.999)	17.7
	7	1.000	0.000	(1.000–1.000)	8.4
	8	0.997	0.003	(0.978–1.000)	3.7
	9	0.968	0.013	(0.930–0.985)	2.4
	10	0.991	0.009	(0.942–0.999)	2
	11	1.000	0.000	(1.000–1.000)	4.8
	12	1.000	0.000	(1.000–1.000)	1.9
	13	1.000	0.000	(1.000–1.000)	3.2
	14	1.000	0.000	(1.000–1.000)	3.6
2019	1	1.000	0.000	(1.000–1.000)	10.5
	2	0.983	0.012	(0.933–0.996)	2.2
	3	0.985	0.015	(0.903–0.998)	1.4
	4	1.000	0.000	(1.000–1.000)	1.9
	5	0.995	0.005	(0.968–0.999)	4.3
	6	1.000	0.000	(1.000–1.000)	17.7
	7	1.000	0.000	(1.000–1.000)	8.4
	8	1.000	0.000	(1.000–1.000)	3.7
	9	0.975	0.017	(0.909–0.994)	2.4
	10	0.965	0.031	(0.819–0.994)	2
	11	1.000	0.010	(0.000–1.000)	4.8
	12	1.000	0.000	(1.000–1.000)	1.9
	13	1.000	0.000	(1.000–1.000)	3.2
	14	1.000	0.000	(1.000–1.000)	3.6
Aggregate	1	0.999	0.001	(0.997–1.000)	10.5
	2	0.989	0.006	(0.968–0.997)	2.2
	3	0.981	0.010	(0.948–0.993)	1.4
	4	0.992	0.005	(0.973–0.998)	1.9
	5	0.994	0.003	(0.985–0.998)	4.3
	6	0.999	0.000	(0.998–1.000)	17.7
	7	1.000	0.001	(0.995–1.000)	8.4
	8	1.000	0.001	(0.000–1.000)	3.7
	9	0.974	0.008	(0.953–0.985)	2.4
	10	0.978	0.009	(0.953–0.990)	2
	11	1.000	0.000	(1.000–1.000)	4.8
	12	1.000	0.000	(1.000–1.000)	1.9

Table A.1. continued

	13	1.000	0.000	(1.000–1.000)	3.2
	14	1.000	0.000	(1.000–1.000)	3.6

Table A.2. Relative (Φ_{rkm}) and cumulative survival (Φ) by river section each year. Yearly estimates were extracted from model with reach-type and release year interaction, while aggregated estimates were extracted from reach-type model alone. Φ = Φ_{rkm} raised to the length of the section. SE = standard error. CI = confidence interval. Length = length of each river section (km)

Year	Section	Φ_{rkm}	SE	95% CI	Φ	SE	95% CI	Length
2016	River	0.9992	0.0005	(0.9975–0.9997)	0.953	0.026	(0.902–1.000)	58.1
	West Enfield	0.9641	0.0127	(0.9290–0.9822)	0.818	0.059	(0.702–0.934)	5.5
	Milford	0.9507	0.0118	(0.9216–0.9693)	0.800	0.044	(0.715–0.886)	4.4
2017	River	0.9990	0.0004	(0.9977–0.9996)	0.945	0.024	(0.898–0.992)	58.1
	West Enfield	0.9964	0.0026	(0.9854–0.9991)	0.980	0.014	(0.953–1.000)	5.5
	Milford	0.9983	0.0025	(0.9703–0.9999)	0.993	0.011	(0.971–1.000)	4.4
2018	River	0.9990	0.0005	(0.9974–0.9996)	0.944	0.027	(0.892–0.997)	58.1
	West Enfield	0.9838	0.0081	(0.9576–0.9939)	0.914	0.041	(0.833–0.995)	5.5
	Milford	0.9790	0.0077	(0.9574–0.9897)	0.911	0.031	(0.849–0.972)	4.4
2019	River	0.9996	0.0004	(0.9971–0.9999)	0.976	0.023	(0.930–1.000)	58.1
	West Enfield	0.9893	0.0061	(0.9675–0.9966)	0.943	0.032	(0.880–1.000)	5.5
	Milford	0.9717	0.0118	(0.9369–0.9875)	0.881	0.047	(0.789–0.973)	4.4
Aggregate	River	0.9984	0.0003	(0.9977–0.9989)	0.913	0.016	(0.881–0.945)	58.1
	West Enfield	0.9836	0.0056	(0.9679–0.9917)	0.913	0.029	(0.857–0.970)	5.5
	Milford	0.9657	0.0070	(0.9490–0.9771)	0.858	0.027	(0.804–0.911)	4.4

Table A.3. Relative (Φ_{rkm}) and cumulative (Φ) survival through Milford Dam and free-flowing River sections. Φ = Φ_{rkm} raised to the length of the section (Milford = 4.4km, River = 43.3km), and River estimates Φ reflect cumulative survival through river sections navigated group. SE = standard error. CI = confidence interval

Year	Section	Release site	Φ_{rkm}	SE	95% CI	Φ	SE	95% CI
2016	Milford	Downstream	0.9666	0.0108	(0.9377–0.9823)	0.861	0.042	(0.778–0.944)
		Upstream	0.9266	0.0202	(0.8758–0.9576)	0.715	0.069	(0.580–0.850)
2018	Milford	Downstream	0.9862	0.0059	(0.9681–0.9941)	0.941	0.025	(0.892–0.990)
		Upstream	0.9690	0.0120	(0.9347–0.9855)	0.870	0.047	(0.778–0.963)
2016	River	Downstream	0.9995	0.0003	(0.9983–0.9999)	0.978	0.014	(0.952–1.000)
		Upstream	0.9988	0.0007	(0.9963–0.9996)	0.951	0.028	(0.895–1.000)
2018	River	Downstream	0.9994	0.0003	(0.9982–0.9998)	0.975	0.014	(0.948–1.000)
		Upstream	0.9987	0.0007	(0.9964–0.9995)	0.944	0.028	(0.889–0.998)

Table A.4. Annual detections probabilities (*p*) at each receiver station. * indicate stations where we fixed *p*= 0.00. SE = standard error. CI = confidence interval.

Receiver station	Year	*p*	SE	95% CI
2	2016	1.000	0.000	(1.000–1.000)
3	2016	0.000	0.000	(0.000–0.000)
4	2016	1.000	0.000	(1.000–1.000)
5*	2016	0.000	0.000	(0.000–0.000)
6	2016	1.000	0.000	(1.000–1.000)
7	2016	1.000	0.000	(1.000–1.000)
8	2016	1.000	0.000	(1.000–1.000)
9	2016	1.000	0.000	(1.000–1.000)
10	2016	0.201	0.050	(0.120–0.317)
11	2016	0.733	0.057	(0.608–0.830)
12	2016	0.940	0.029	(0.851–0.977)
13	2016	0.985	0.015	(0.902–0.998)
14	2016	0.955	0.025	(0.870–0.985)
15	2016	1.000	0.000	(1.000–1.000)
2	2017	1.000	0.000	(1.000–1.000)
3	2017	0.261	0.044	(0.184–0.356)
4	2017	0.682	0.047	(0.584–0.767)
5	2017	0.949	0.022	(0.883–0.979)
6	2017	0.925	0.027	(0.851–0.964)
7	2017	0.968	0.018	(0.904–0.990)
8	2017	0.978	0.015	(0.918–0.995)
9	2017	1.000	0.000	(1.000–1.000)
10	2017	0.380	0.053	(0.283–0.487)
11	2017	0.298	0.050	(0.210–0.403)
12	2017	0.239	0.044	(0.163–0.337)
13	2017	0.880	0.034	(0.797–0.933)
14	2017	0.522	0.052	(0.420–0.622)
15	2017	1.000	0.000	(1.000–1.000)
2	2018	1.000	0.000	(1.000–1.000)
3	2018	0.752	0.065	(0.606–0.857)
4	2018	0.977	0.023	(0.854–0.997)
5	2018	1.000	0.000	(0.000–1.000)
6	2018	1.000	0.000	(0.000–1.000)
7	2018	0.989	0.011	(0.923–0.998)
8*	2018	0.000	0.000	(0.000–0.000)
9	2018	1.000	0.000	(1.000–1.000)
10	2018	0.940	0.029	(0.852–0.977)
11*	2018	0.000	0.000	(0.000–0.000)
12*	2018	0.000	0.000	(0.000–0.000)

Table A4. continued

13	2018	0.937	0.027	(0.857–0.973)
14	2018	0.987	0.013	(0.916–0.998)
15	2018	1.000	0.000	(1.000–1.000)
2	2019	1.000	0.000	(1.000–1.000)
3	2019	0.959	0.028	(0.851–0.990)
4	2019	1.000	0.000	(1.000–1.000)
5	2019	1.000	0.000	(0.000–1.000)
6	2019	1.000	0.000	(1.000–1.000)
7	2019	0.980	0.020	(0.869–0.997)
8	2019	1.000	0.000	(0.000–1.000)
9	2019	1.000	0.000	(1.000–1.000)
10	2019	0.948	0.035	(0.816–0.987)
11*	2019	0.000	0.000	(0.000–0.000)
12*	2019	0.000	0.000	(0.000–0.000)
13	2019	0.558	0.076	(0.409–0.698)
14	2019	0.884	0.049	(0.749–0.951)
15	2019	1.000	0.000	(1.000–1.000)

BIOGRAPHY OF THE AUTHOR

Matthew Allen Mensinger was born in Nashville, Tennessee on October 22, 1993. He grew up near Duluth, Minnesota, but spent his first 22 summers in Woods Hole, Massachusetts where he grew interested in fish and science. Matt graduated from Hermantown High School in 2012 and went to play football and study biology at Carleton College. After earning his Bachelor of Arts in 2016, he moved to East Greenwich, Rhode Island where he worked commercial fisheries observer across southern New England and coached high school lacrosse. Eager to return to school, Matt joined the Maine Cooperative Fish and Wildlife Research Unit and Department of Wildlife, Fisheries, and Conservation Biology at the University of Maine in August 2018. Matt is a candidate for the Master of Science degree in Wildlife Ecology from the University of Maine in December 2020.