The consequences of dam passage for downstream-migrating American eel in the Penobscot River, Maine

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Abstract: American eel (Anguilla rostrata) often pass hydropower dams during adult spawning migrations. We conducted a 4-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 kilometre, rkm) were lower at West Enfield (\( \Phi_{\text{rkm}} = 0.984 \pm 0.006 \) SE) and Milford (\( \Phi_{\text{rkm}} = 0.966 \pm 0.007 \) SE) compared with undammed River sections (\( \Phi_{\text{rkm}} = 0.998 \pm 0.0003 \) SE). Cumulative mortality was 8.7% (4.4 km) and 14.2% (5.5 km) through dammed sections and 8.7% throughout the rest of the river (58.1 km). Fish that already passed an upstream dam incurred higher downstream mortality compared with individuals without passage experience. Additionally, fish endured long delays at dams, and >10% of fish were delayed >24 h. Low flows exacerbated the risk of mortality and delay. These results offer evidence for direct, latent, and sublethal consequences of dam passage for migrating eels.

Résumé : Des anguilles d’Amérique (Anguilla rostrata) adultes passent souvent à travers de barrages hydroélectriques durant leurs migrations de frai. Nous avons mené une étude de télemétrie acoustique de quatre ans qui a permis de caractériser les risques associés au passage à travers deux barrages hydroélectriques (West Enfield et Milford) sur le fleuve Penobscot (Maine, États-Unis). Nous avons relâché des poissons étiquetés (n = 355) en deux sites, estimé la survie et le retard dans des conditions variables du fleuve et comparé les performances entre des tronçons du fleuve endigués et à écoulement libre. Les taux de survie (normalisés par kilomètre de cours d’eau, rkm) étaient plus faibles à West Enfield (\( \Phi_{\text{rkm}} = 0.984 \pm 0.006 \) ET) et Milford (\( \Phi_{\text{rkm}} = 0.966 \pm 0.007 \) ET) que dans les tronçons non endigués du fleuve (\( \Phi_{\text{rkm}} = 0.998 \pm 0.0003 \) ET). La mortalité cumulative était de 8.7 % (4.4 km) et 14.2 % (5.5 km) dans les tronçons endigués et de 8.7 % dans tout le reste du fleuve (58,1 km). Les anguilles qui étaient déjà passées par un barrage en amont présentaient une mortalité plus forte en aval que les spécimens sans expérience de passage. En outre, les poissons subissaient de longs retards aux barrages, ce retard étant de >24 h pour >10 % des anguilles. De faibles débits exacerbéraient le risque de mortalité et la durée des retards. Ces résultats témoignent de conséquences directes, latentes et sublétales du passage de barrages pour les anguilles en migration. [Traduit par la Rédaction]

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, such as 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 United States eel fishery has evolved into a multimillion-dollar industry, which peaked at >$40 million (USD) in 2012 (ASMFC 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 by ocean currents 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, when many encounter dams in pursuit of freshwater lakes, rivers, and streams. Because 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 to offer upstream passage opportunities (Schmidt et al. 2009; Welsh and Liller 2013). Once in fresh water, eels may reside in these systems for more than 20 years before beginning a transoceanic spawning migration to return to the Sargasso Sea (Oliveira 1999; Jessop et al. 2008; Jessop 2010), during which they must pass the same dams they ascended as juveniles. The risks
associated with downstream passage through hydropower facilities is considered one of many stressors contributing to population decline (Castonguay et al. 1994).

Downstream-migrating American eel face two major challenges when navigating hydropower dams. First, eels must locate a passage route, which may occur through spillways, fish bypasses, 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 (Castonguay and Wernham 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). During passage, eels risk impingement on dam structures, impact-related injuries from falling over the top of 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 shows that nonlethal injuries sustained during dam passage may result in mortality later 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.

Like many systems across the Atlantic coast of the US, American eel are ubiquitous throughout the Penobscot River watershed (Kiraly et al. 2015; Watson et al. 2018). This 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, and licenses can last anywhere from 30 to 50 years (Maine DEP 2014). Fish passage is regulated by the Federal Energy Regulatory Commission, and licenses can last anywhere from 30 to 50 years (Maine DEP 2014). Fish passage is among the criteria discussed throughout the relicensing process, which presents 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. Our primary goals with this research were to (i) characterize mortality and delays experienced by downstream-migrating eels at two sequential hydroelectric projects and (ii) understand the effects of passing multiple dams during adult spawning migrations. We conducted a 4-year acoustic telemetry study to track adult eel movement through West Enfield and Milford dams in the Penobscot River. We hypothesized that migrating eels will incur higher mortality and passage times through dams relative to free-flowing river sections. Ultimately, we hoped 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 main stem of the Penobscot River runs 175 km through Maine’s interior before entering Penobscot Bay at 0 river kilometres (“rkm” hereinafter; 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 (101 rkm, 45.25°N, 68.65°W) and Milford Dam (62 rkm, 44.94°N, 68.65°W) as the final dams encountered by migrating eels on the river’s main stem. Both run-of-the-river projects are regulated by Federal Energy Regulatory Commission, and existing licenses expire in 2024 at West Enfield and 2038 at Milford.

West Enfield Dam has a height of 11.9 m and has two Kaplan turbines (86 rpm, 191 m3·s−1 per unit) and a maximum generating capacity of 13 MW. Turbine intakes are guarded by racks with 7.6 cm vertical bar spacing. Above these intakes, there are five 1.2 m × 4.3 m surface-level fish bypasses that discharge into the tailrace (area directly downstream of dam). Potential downstream passage routes for eels at West Enfield include the spillway (110 m wide), three radial spillgates (7.6 m × 7.9 m), turbine intakes (30 m wide), surface-level bypasses, or through an upstream vertical slot fishway.

Milford Dam has a height of 6.1 m and has six turbines with an 8 MW maximum generating capacity: two vertical propellers (257 rpm, 16 m3·s−1 per unit), one fixed blade propeller (120 rpm, 39 m3·s−1), and three Kaplan turbines (120 rpm, 40 m3·s−1 per unit). Turbine intakes are guarded by an outer and inner rack with 10 cm (outer) and 2.5 cm (inner) vertical bar spacing. At the bottom of the inner rack, there is a low-level (1.2 m × 1.2 m) entrance to an eel-specific bypass to facilitate passage to the tailrace through a 0.6 m diameter pipe. There are also two 2.7 m wide surface-level bypasses above turbine intakes that discharge into the tailrace. Potential downstream passage routes at Milford Dam include the spillway (250 m wide), sluiceway (8 m wide), turbine intakes (60 m wide), or fish passage facilities described above (Jeff Murphy, NOAA – Fisheries, personal communication).

Fish collection, tagging, and release

We collected silver-phase eels from the Souradabscook Stream in Hampden, Maine, USA (44.76°N, 68.86°W) using a weir located 3 km upstream from the stream’s confluence with the Penobscot River (31 rkm). Downstream movement in this tributary is unimpeded by anthropogenic barriers, and we assumed fish experienced similar migration histories prior to capture. Because American eel migrate throughout the fall (Parker and McCleave 1997; Verreault et al. 2012), we operated the trap nightly from September to November and selected eels for further processing that were >40 cm and exhibited clear characteristics of adult metamorphosis (e.g., enlarged eyes, dark dorsal surface; Pankhurst and Lythgoe 1982).

Eels were anesthetized in a cold-water tricaine methanesulfonate (MS-222, 250 mg·L−1) bath for ~10 min 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 two to three braided, absorbable sutures (Ethicon Inc., VICRYL 3-0). These pulse position modulation transmitters had an estimated tag life of 649 days and were programmed to emit a 69 kHz signal at varying intervals (once every: 3–60 s for the first 90 days, 150–250 s for 210 days, 30–60 s for 150 days, and 150–250 s for 200 days, before the cycle repeated, given enough battery life). We programed this sequence to maximize detection efficiency throughout the fall migration, but also to have the ability to detect individuals that remained in the system for subsequent seasons (i.e., fish that terminated migration, but survived). After surgery, eels recovered in aerated, 100 L coolers filled with ambient river water. Once all eels collected during the previous night were tagged (~10 h after sunrise), we transported fish (in coolers) to one of two release sites in the Penobscot River (1–2 h transit time; Fig. 1A). All fish tagged on the same day were released at the same release site. In 2017 and 2019, all fish were released in South Lincoln, Maine, 12 km upstream of West Enfield Dam (“Upstream release”, 113 rkm). In 2016 and 2018, we released approximately half of tagged fish at this release site, and the remaining fish were released in Passadumkeag, Maine, 9 km downstream of West Enfield Dam (“Downstream release”, 92 rkm). In 2016, we released fish at the Downstream site before releasing fish at the Upstream site, and we released fish evenly between sites in 2018, alternating between locations as necessary.
These paired releases were used to understand the relative risk for fish that pass multiple dams during migration. In total, we released 100 fish per year from 2016 to 2018 and 55 fish in 2019.

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 in dam headponds (reservoirs immediately upstream of dams where natural flows are directly influenced by dam presence), dam tailraces, or in areas where detection efficiency was otherwise compromised due to high flows or in-river obstructions. Each receiver (or group of receivers) was assigned to 1 of 15 unique receiver stations (Figs. 1A, 1C), and detections were pooled for stations that consisted of multiple receivers. The tidal section of the river begins at 48 rkm, below receiver Station 14. To minimize the influence of tidal cycles on migration rates, we pooled all tidal receivers into a single receiver station (Station 15). We considered all fish detected at least once from 44.6 to 17.3 rkm (site of the most downstream estuary receiver) to have migrated to the estuary. The array was deployed prior to tagging and retrieved from the river before ice-in (16 November – 9 December) to allow enough time for fish to move through the study area. A subset of receivers was deployed through the winter each year so that any fish moving would still be detected.

Analysis of survival

All analysis of survival 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 whether individuals were detected (1) or not detected (0) at each receiver station. This approach allowed us to estimate apparent survival (Φ; “survival” hereinafter) in the intervals between receiver stations and estimate the probability of detecting a fish (p) at each station, given that the fish was still alive to be detected.

We assumed that fish movement was downstream and unidirectional. We validated this assumption by visually inspecting migration histories for each fish (e.g., Fig. 1B) and confirmed that no fish returned to upriver receiver stations after having been detected further downstream. This 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 (e.g., Halfyard et al. 2013; Michel et al. 2015; Zydlewski et al. 2017; Hawkes et al. 2017). Fish entered the capture history at their first detection, which usually occurred at Station 1 (Upstream release) or Station 6 (Downstream release). For 1 – Φ to represent true mortality under the CJS framework, we assumed that all detections reflected living fish and that no ecological processes other than failed detection caused marked eels to permanently disappear from the

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Fig. 1. (A) Overview of study area in the Penobscot River, Maine, USA (inset). Open circles and corresponding numbers represent receiver stations and capture occasions, respectively, in the main stem of the Penobscot River. Open circles without numbers represent additional receiver stations. Shaded circles are receivers in the Stillwater Branch. R1 = release site upstream of West Enfield Dam in South Lincoln (Upstream release). R2 = release site downstream of West Enfield Dam in Passadumkeag (Downstream release). Map was produced by hand using Google Earth imagery as a reference layer. (B) Potential fates of individual fish. Telemetry tracks were extracted from four fish released upstream of West Enfield in 2017 (pink triangles, purple diamonds, and orange squares) and 2018 (green circles). Days represent the relative time spent in the river after release. (C) Conceptual model of acoustic array. Red circles represent receiver stations where mortalities in the next downstream reach were attributed to dam passage, and “SW” arrows represent potential exit and re-entrance of the main stem through the Stillwater River. [Colour online.]
encounter history. We may have sometimes violated the first assumption given that dead fish can drift considerable distances in rivers (Calles et al. 2010; Havn et al. 2017). While this may have caused some uncertainty in the specific timing of mortality, any effect on the overall system mortality is likely to be negligible, and we specifically grouped receiver stations to account for potential latent mortality at dams (described below). The second assumption may have been violated if fish experienced nonniethal migratory failure after initiating downriver migration and then remained stationary in the river thereafter. Therefore, we excluded fish from the analysis that were detected in the system during subsequent sessions (i.e., individuals that appeared to terminate migration, but survive).

Each interval between receiver stations was categorized as either “River”, “West Enfield”, or “Milford”, referencing the type of river section that eels moved through. In an effort to capture both direct and latent mortality during passage, we classified intervals between Stations 2 and 5 (102.1 rkm) as “River”, Stations 2 and 5 (102.1–96.6 rkm) as “West Enfield”, Stations 9 and 11 (62.5–58.1 rkm) as “Milford”, and all other intervals were classified as “River” reaches. Unless explicitly mentioned, survival was scaled to units of rkm⁻¹ (Φ_km; “relative survival” hereinafter) to account for differences in 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. 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 annually (of ~3 stations-year⁻¹) 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. 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 annually, we fixed p = 0 for “missing” receiver stations during years in which data were not available (0–3 stations-year⁻¹). Near 62 rkm, the Stillwater River branches from the main stem before rejoining the river 11 km downstream, circumnavigating Milford Dam (Figs. 1A, 1C). Past research on juvenile Atlantic salmon (Salmo salar) has shown that a small proportion (~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 Stich et al. (2014). However, the added complexity of the multistate 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 this framework (as evidenced by model poor 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 with 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

\[
\Phi_{\text{cumulative}} = \prod_{i=1}^{14} (\Phi_i)^{l_i}
\]

where \(\Phi_{\text{cumulative}}\) is the product of all reach-specific estimates raised to the power of their respective lengths (\(l_i\); km). In the “dam-free” counterfactual, we substituted the aggregated relative survival estimates of “River” sections, 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 100% survival until Station 1. We derived standard errors (SEs) for all cumulative survival estimates using the Delta method (Powell 2007) to propagate variance via the deltavar function offered through the emdback 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 were obtained from the US Geological Survey’s (USGS) stream gauge (hydrological unit 01020005) located at 98.5 rkm, 3.5 km downstream of West Enfield Dam. Both river discharge (m³·s⁻¹) and river stage (m) are available in 15 min intervals, and since both measurements are highly correlated (\(r > 0.99\)), we used river discharge in this analysis (“flow” hereinafter). This is the only stream gauge in the study area, and therefore we assumed that flow data were directly correlated with river conditions experienced by eels moving between all receiver stations. For all detections, we used the last detection time for each fish at each station and assigned a flow measurement using the most proximate gauge 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 assessment that described whether eels were released upstream of one or two 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 on survival at Milford Dam. 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; sensu Skalski et al. 2009) and classified whether fish were (i) 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 and 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 the relative support for competing survival models using ΔAICc < 2.00 as a threshold for model support (Burnham and Anderson 2002). Starting from the null model, we first added single, categorical covariates (reach number, reach type) and assessed whether 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 conditions. All continuous covariates were z-standardized, which allowed us to directly compare effect sizes among competing variables. Coefficients ($\beta$) from supported models were further assessed to understand their effect on survival estimates, and those with 95% confidence intervals (CI) not overlapping zero were considered to differ from a slope of 0.0. Because 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 (i.e., lack of immediate downstream movement after release; Carr and Whoriskey 2008) were not reflected in passage times for the first reach, we used the last detection at Station 1 (Upstream release) or Station 6 (Downstream release) to calculate the time to move between Stations 1 and 2 or Stations 6 and 7, respectively. 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 (h·km$^{-1}$), which allowed us to directly compare migration time among different reach lengths. Detections at Station 12 (53.3 rkm) were removed from the delay analysis because its proximity to Station 13 (51.4 rkm) resulted in overlapping detection ranges that sometimes produced unrealistic passage times (i.e., $< 0$ h). We also removed one observation at Milford Dam that estimated passage time at 0 h. Because 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 a 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 assessment, 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 for release year and river flow (using the most proximate gauge reading to the last detection time at each receiver station). We used $\Delta$AIC$_c < 2.00$ as a threshold for model support in conjunction with an evaluation of $\beta$ coefficients to assess the effect of covariates on passage time.

Results

Of the 355 fish tagged and released, 341 fish sustained downstream movement through the study area during the release year and were included in the analysis of survival and delay (Table 1). Some of these fish ($n = 12$) remained near release sites for $>24$ h, before moving downstream. Two fish in the Upstream release group were only detected by receiver Station 1 and were included in the survival assessment but were not included in the delay analysis because passage times could not be calculated from a single detection. The fish excluded from both analyses were not detected after release ($n = 4$), did not move through the study area during the release year ($n = 7$), or experienced apparent avian predation ($n = 1$; refer to online Supplementary Material S1$^1$). Telemetry histories representative of some potential fates are shown in Fig. 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.

Detection probability

Overall, $p$ at each receiver station was high throughout the study (mean $p = 0.871$, median $p = 0.983$; Supplementary Table S2$^1$). Detection probabilities were lowest in 2017 when river flows were highest (Fig. 2), which likely lowered detection efficiency by increasing acoustic “noise” and reducing the amount of time fish were within detection areas of each station. Stations 3 and 10 had relatively low detection efficiency ($p < 0.500$) in 2016 and 2017. In an 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.

Survival

We found that eels had lower survival when moving through dammed reaches compared with free-flowing river sections. Over 4 years, relative survival was lowest for fish passing Milford Dam (mean $\pm$ SE: $\Phi_{\text{Rkm}} = 0.966 \pm 0.007$), and survival at both Milford and West Enfield ($\Phi_{\text{Rkm}} = 0.984 \pm 0.006$) was lower than free-flowing River sections ($\Phi_{\text{Rkm}} = 0.998 \pm 0.0003$; Fig. 3). When we used the reach-dependent estimates (Supplementary Table S3$^1$) to propagate survival throughout the study area, cumulative survival was

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Table 1. Summary of American eel releases for fish used in analyses.

<table>
<thead>
<tr>
<th>Year</th>
<th>Release site</th>
<th>Releases</th>
<th>$N_{\text{release}}$</th>
<th>Dates</th>
<th>Fish length (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2016</td>
<td>Upstream</td>
<td>9</td>
<td>45</td>
<td>1–21</td>
<td>59.2 (48.0–74.0)</td>
</tr>
<tr>
<td></td>
<td>Downstream</td>
<td>7</td>
<td>50</td>
<td>1–19</td>
<td>61.0 (45.5–78.9)</td>
</tr>
<tr>
<td>2017</td>
<td>Upstream</td>
<td>3</td>
<td>100</td>
<td>12–72</td>
<td>63.3 (51.0–90.2)</td>
</tr>
<tr>
<td></td>
<td>Downstream</td>
<td>5</td>
<td>46</td>
<td>1–40</td>
<td>64.1 (51.0–89.5)</td>
</tr>
<tr>
<td>2018</td>
<td>Upstream</td>
<td>8</td>
<td>49</td>
<td>1–15</td>
<td>61.4 (43.8–83.5)</td>
</tr>
<tr>
<td></td>
<td>Downstream</td>
<td>10</td>
<td>53</td>
<td>1–16</td>
<td>60.2 (48.5–86.0)</td>
</tr>
</tbody>
</table>

Note: Eels were released at one of two sites in the Penobscot River relative to West Enfield Dam (Upstream = released upstream of West Enfield at 113 rkm, Downstream = released downstream of West Enfield at 92 rkm; Fig. 1A). All eels captured during a given night were released at the same location. Releases = aggregate number of release dates at each release site; $N_{\text{release}}$ = aggregate number of fish released; Dates = range of fish released per release date; Dates = range of release dates; Fish length = mean total length (cm) of each release group, with ranges in parentheses.

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$^1$Supplementary material is available with the article at https://doi.org/10.1139/cjfas-2020-0402.
estimated at 0.795 ± 0.023, which was lower than the theoretical undammed scenario ($\Phi = 0.930 \pm 0.014$; Fig. 4).

Survival varied across study years (Fig. 3; Supplementary Table S4†). Incorporating a year interaction to the reach type model improved support by $>15$ $\Delta$AIC, from the reach type model alone, and this interaction was included in the most supported survival model (Table 2). Cumulative survival through dammed sections was lowest in 2016 for both West Enfield ($\Phi = 0.818 \pm 0.059$) and Milford ($\Phi = 0.800 \pm 0.044$) and highest in 2017 for both dams (West Enfield: $\Phi = 0.980 \pm 0.014$, Milford: $\Phi = 0.993 \pm 0.011$; complete breakdown in Supplementary Table S4†). Survival in free-flowing River sections was consistently high, and the cumulative survival throughout the entire 58.1 km of free-flowing River sections varied between 0.944 and 0.976 depending on year, consistent with the near-100% River $\Phi_{\text{Rkm}}$ (0.999–1.000) throughout the study. We did not find support for an effect of fish length on survival ($\beta_{\text{length}} = 0.001 \pm 0.016$).

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 $>300$ $\text{m}^3\text{s}^{-1}$ (Fig. 2) and survival was at a 4-year high (Fig. 3). In other years, flow generally fell between 100 and 300 $\text{m}^3\text{s}^{-1}$ when eels passed both dams. We assessed the effect of flow on survival in each reach type using $\beta$ estimates from a model where reach type

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Fig. 2. Variation in seasonal river discharge across sampling years. Flow data were 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. [Colour online.]

Fig. 3. Relative survival in each section of the study area. Yearly estimates were derived from the survival model with a reach type–year interaction, and aggregate estimates reflect the mean survival in each river section aggregated across all 4 years. Error bars represent 95% CIs. [Colour online.]
interacted with flow, a configuration that improved support by 3.82 ΔAICc over the effect of reach type alone (Table 2). Upon closer examination of β coefficients from this model, we found a positive relationship between flow and survival at Milford (βflow = 0.969 ± 0.431), but the effect size was not demonstrated to be different than 0.00 when passing West Enfield (βflow = 0.291 ± 0.327) or free-flowing River sections (βflow = −0.183 ± 0.271; Fig. 5).

Fish in the Upstream release group had lower survival than those in the Downstream release group (Fig. 6; Supplementary Table S5). Adding release site as an additive, group effect (βupstream = −0.829 ± 0.373) was also included in the top model and improved support by > 3.00 ΔAICc over the same model without release group (Table 2). Cumulative survival through Milford was estimated to be lowest for the Upstream group in 2016 (Φ = 0.715 ± 0.069), which was 14.6% (±8.13%) lower than the Downstream group (Φ = 0.861 ± 0.042). When the effect of release group was applied to 43.3 km 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) and 2018 (0.944 ± 0.028) when contrasted with the downstream group during both years (2016: Φ = 0.978 ± 0.014; 2018: Φ = 0.975 ± 0.014).

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 (βupstream = −0.141 ± 0.535, 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, these data do not allow us to disentangle the effect size at downstream dams from free-flowing river sections.
free-flowing sections of river. Over four field seasons, we tracked >350 fish across a range of environmental conditions and demonstrate that passage risks are exacerbated under low flows, which likely increased the probability of eels passing through turbines. Additionally, our results suggest that mortality can occur far downstream from dam structures, which emphasizes the importance of system-wide monitoring for fish passage studies. Given the pervasiveness of hydropower production throughout the American eel range, a large proportion of mature eels may face similar challenges during downstream spawning migrations. Based on these observations, we anticipate any unnatural mortality on reproductively mature individuals to have adverse consequences 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% and 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 (Fig. 2), we suspect the majority of variation in passage success is attributed to interseasonal changes in environmental conditions rather than the inherent stochasticity of risk imposed by each dam.

Survival through dams
Migrating American eels experienced lower survival through dams compared with 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 consistently lower when compared with free-flowing River sections where survival was high throughout the study (99.9%–100.0%). In aggregate, this resulted in 1.4% and 3.2% lower φ_{αm} at West Enfield and Milford Dam respectively, relative to the River section. While these differences may seem trivial, the two dams in our study resulted in the loss of >13% of fish annually, compared with the expectation under a totally free-flowing river. Furthermore, our study only considered passage through two hydropower dams during outbound migration, and we would expect even greater losses in systems with additional dams. For this long-lived, semelparous fish species, we anticipate any unnatural mortality on reproductively mature individuals to have adverse consequences at the population level.

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Seasonal changes in river flow likely afford eels different routes through dam structures during fall migration. When survival at both dams was nearly 100% 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$^3$s$^{-1}$ (Fig. 5). While survival at West Enfield was highest in this high flow year, $\beta_{\text{flow}}$ was not exclusive of 0.00. This result was unexpected because there is not an eel-specific downstream passage at this dam, which mostly restricts passage options to turbine intakes and surface-level bypasses. However, generally higher survival at West Enfield (relative to Milford) may have made it more difficult to detect the interaction because there was less scope for high flows to increase survival relative to the baseline.

While we were unable to specify passage route in this study, previous research has shown near-100% survival for fish ID was treated as a random effect for all models; $R_m^2$ = marginal $R^2$; $R^2$ = for the entire model; $K$ = number of parameters used in each model; $\Delta$AICc = difference in Akaike’s information criterion (adjusted for small sample size) from most supported model; $\beta_{\text{flow}}$ = river water flow (m$^3$s$^{-1}$) as a continuous, reach-specific variables for each fish; fish length = total fish length (cm).

**Table 3.** Relative performance of generalized linear mixed models to characterize fish passage time (h·km$^{-1}$) through different river sections.

<table>
<thead>
<tr>
<th>Model</th>
<th>$K$</th>
<th>$\Delta$AICc</th>
<th>$R_m^2$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reach type x flow</td>
<td>8</td>
<td>0.00</td>
<td>0.60</td>
<td>0.21</td>
</tr>
<tr>
<td>Reach type x flow + fish length</td>
<td>9</td>
<td>0.83</td>
<td>0.40</td>
<td>0.21</td>
</tr>
<tr>
<td>Reach type x year + fish length</td>
<td>15</td>
<td>26.31</td>
<td>0.00</td>
<td>0.21</td>
</tr>
<tr>
<td>Reach type x year</td>
<td>14</td>
<td>26.47</td>
<td>0.00</td>
<td>0.21</td>
</tr>
<tr>
<td>Reach type + flow</td>
<td>6</td>
<td>77.81</td>
<td>0.00</td>
<td>0.18</td>
</tr>
<tr>
<td>Reach type + fish length</td>
<td>6</td>
<td>217.37</td>
<td>0.00</td>
<td>0.10</td>
</tr>
<tr>
<td>Reach type</td>
<td>5</td>
<td>219.67</td>
<td>0.00</td>
<td>0.09</td>
</tr>
<tr>
<td>Reach type x fish length</td>
<td>8</td>
<td>220.99</td>
<td>0.00</td>
<td>0.10</td>
</tr>
<tr>
<td>Fish length</td>
<td>4</td>
<td>427.62</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Null</td>
<td>3</td>
<td>429.23</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

**Note:** Model = parameter structure for fixed effects; fish ID was treated as a random effect for all models; $R_m^2$ = marginal $R^2$; $R^2$ = for the entire model; $K$ = number of parameters used in each model; $\Delta$AICc = difference in Akaike’s information criterion (adjusted for small sample size) from most supported model; Weight = weighted Akaike support for each model; reach type = intervals between receiver stations were classified as free-flowing River, West Enfield Dam, or Milford Dam; year = group effect of release year; flow = river flow (m$^3$s$^{-1}$) as a continuous, reach-specific variables for each fish; fish length = total fish length (cm).

**Fig. 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. [Colour online.]

**Fig. 8.** Predicted passage times through West Enfield (dashed line), Milford (solid line), and free-flowing River reaches (dotted line) under different river flows. Flow data were obtained from the USGS hydrological unit deployed downstream of West Enfield Dam near receiver Station 4. Passage time is scaled to reflect the number of hours for fish to move 1 km in each river section. Shaded regions represent 95% CIs. [Colour online.]

While adult eels can survive turbine strikes (Saylor et al. 2019; Heisey et al. 2019), injured fish may continue migration (or be transported under high flows), 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, migration termination, 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 about latent mortality 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 expect that any latent mortality is the result of severe, turbinedirected 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 have sublethal consequences (i.e., those that ultimately result in migratory failure), by compromising swimming ability, impairing navigation, or increasing susceptibility to predation and disease. Research tracking the downstream movement of adult steelhead and juvenile Atlantic salmon (Salmo salar) characterized the severe implications for fishing passing 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 (Fig. 7). We offer evidence for high variation in individual passage times where some navigated dams in minutes while others spent days delayed in dam headpools before passing successfully. The high variability in delay aligns with other eel passage studies that also showed similar variation in site-specific passage efficiencies (Carr and Whoriskey 2008; Piper et al. 2013; Elyer et al. 2016). The magnitude of delays was exacerbated under low flow conditions (Fig. 8). For example, passage times at both dams were not predicted to be comparable to free-flowing river reaches until flows exceeded 800 m³ s⁻¹, a condition that occurred in <17% of all dam passage observations. These long passage times suggest that when eels encounter dams under low flow conditions, passage routes may be limited and 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 <1 h (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 (Bégueur-Pon et al. 2014). Therefore, fish that arrive in dam headpools near sunrise may discontinue movement until sunset, which would increase 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 were slower than otherwise expected in this region of the study area. Nevertheless, we found strong differences in passage times between dammed and undammed sections (Fig. 7), highlighting the overall negative effect dams have on the rate of eel migration.

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 headpools, and some individuals may briefly move upstream before making additional passage attempts at dams (Brown et al. 2009; Trancart et al. 2020). Excessive swimming when searching for passage routes may deplete energy stores reserved for migration (van Ginneken 2005), which may lead to migratory failure. Additionally, downstream migration is highly synchronized with environmental cues (flow, lunar cycle, tides) that are assumed to promote migratory success (Barbin et al. 1998; Durif et al. 2008; Acou et al. 2008; Bégueur-Pon et al. 2014; Verhelst et al. 2018). Therefore, delays may prevent fish from moving under favorable conditions during future dam passage events or elsewhere during migration. 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 could have similar consequences for eels, of which the severity remains unknown.

Implications for eel conservation

In aggregate, our results offer compelling evidence for direct mortality, latent mortality, and sublethal consequences of dam passage for migrating adult eels. While many eel passage studies are limited to one season, our 4-year study allowed us to track fish movement under a variety of conditions and demonstrate that survival is influenced by 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 (Elyer et al. 2016; Baker et al. 2019). Our results support implementing these solutions to maximize both safe and efficient passage. However, we recognize both the physical and opportunity costs incurred by dam operators that apply such strategies, so a mitigation approach that considers real time river conditions may be an effective, interim solution. When river flows crest, usually after frequent and heavy precipitation events, 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. Our data suggest that below these flow thresholds, without effective downstream passage, hydropower operation poses a serious risk of mortality and delay for migrating eels.

These findings would be most informative when paired with forecasting data that can accurately predict downstream eel migrations. This approach would allow dam operators to curtail hydropower output. However, the effectiveness of this mitigation strategy is conditional on the establishment of operational cut-offs that may vary between systems and hydropower projects (Smith et al. 2017). Recent Atlantic States Marine Fisheries Commission and USFWS American eel assessments acknowledge the effectiveness of turbine shutdowns, but lament on the challenges of predicting downstream eel movement (Limburg et al. 2012; Shepard 2015). Such uncertainty may prevent range-wide implementation of this technique, which requires the development of reliable forecasting models. Although eel migrations are synchronized with high flow events (Durif et al. 2008; Acou et al. 2008), turbine shutdowns synchronized with flow alone may occur during conditions when passage risks are naturally mitigated. Therefore, careful consideration of flow regimes, together with other predictive forces, may be beneficial to balance losses of American eels and hydropower production.

Acknowledgements

Financial support for this research was provided by The Nature Conservancy, University of Maine, and the National Science Foundation’s Research Infrastructure Improvement NSF No. IIA-1539071. Field and logistic support was provided by the University of Maine Department of Wildlife, Fisheries, and Conservation.
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Hitt, N.P., Eyler, S., and Wofford, J.E.B. 2012. Dam removal increases American eel survival in downstream hydraulic structures and two anonymous reviewers for providing helpful comments on earlier drafts of the manuscript. This project was greatly supported by the help of many field technicians, including Cory Gardner, Josh Kocik, Evan Dunn, Jordan Goodstein, and numerous volunteers. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. This work was done in coordination and cooperation with NOAA Fisheries Northeast Fisheries Science Center and conducted under the University of Maine Institutional Animal Care and Use Committee (IACUC) protocol A2018-07-03. This project was supported by the USDA National Institute of Food and Agriculture, McIntire-Stennis project No. ME0-41602 through the Maine Agricultural and Forest Experiment Station. This is Maine Agricultural and Forest Experiment Publication No. 3804.

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Can. J. Fish. Aquat. Sci. Downloaded from cdnsciencepub.com by UNIVERSITY OF MAINE on 09/21/21

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