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ARTICLE

Characterizing Downstream Migration Timing of American Eels Using Commercial Catch Data in the Penobscot and Delaware Rivers

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Abstract
Adult "silver-phase" American Eels *Anguilla rostrata* were a focus of commercial fisheries in the 1970s and 1980s, but stocks have been depleted due to many anthropogenic factors. One significant source of mortality occurs during the downstream migration of eels when passing through turbines at hydroelectric facilities. We sought to construct a model to predict eel migration timing to inform optimization of mitigation actions that might reduce mortality. We utilized commercial catch collected from 16 tributaries in the Penobscot River watershed, Maine (2–10 years), and the Delaware River, New York (31 years). A Bayesian hierarchical approach was used to model the relationship between the timing of silver eel capture and environmental conditions that are known to be related to their movements (i.e., river discharge, water temperature, and lunar cycle). Among river systems, daily catch was associated with higher-than-average flows, temperatures of 7–22°C, and new lunar phase cycles. A cross-validation approach to evaluate the ability of the models to make predictions for new data demonstrated a greater ability (higher R^2 values) to predict weekly eel catch (0.01–0.92) compared to daily eel catch (0.00–0.42). In addition, we examined the model's ability to forecast migration events by applying posterior simulations to make predictions of eel catch by ordinal date. Predicted daily eel catch generally followed the trend of observed daily catch and was stronger for the Delaware River ($R^2 = 0.67$) than for Souadabscook Stream, Maine ($R^2 = 0.07$). Sharp pulses in observed catch were not reflected by the predicted catch. Additionally, variability observed among rivers suggests that site-specific modeling may be advantageous (and necessary) to capture local conditions, thereby improving predictive power. More broadly, our work highlights a novel use of fishery-dependent data in a Bayesian modeling framework to predict intervals of risk for migrating fish.

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Historically, eels *Anguilla* spp. were targets for commercial fisheries; however, population recruitment has declined worldwide (Casselman 2003; Doyon 2015; Itakura et al. 2015; Aalto et al. 2016). From the 1970s to the mid-1980s, the American Eel *A. rostrata* supported significant commercial fisheries in both the United States and Canada, but currently this species is considered threatened in Canada (COSEWIC 2012) and is considered a depleted stock in Atlantic drainages of the United States (ASMFC 2012). Factors contributing to the decline of American Eels are shared with many commercial fish species: climate change, overfishing, pollution, and habitat loss (Castonguay et al. 1994; Wirth and Bernatchez 2003; Pierron et al. 2008; Machut et al. 2011; Drouineau et al. 2018).

American Eels and many other migratory fish have suffered from habitat loss and fragmentation brought on by the construction of dams over the last two centuries (Limburg and Waldman 2009). Despite impoundments and the variable (and often poor) success for upstream passage of migrating animals, eels persist in many upriver habitats because of their impressive migrating and climbing abilities as juveniles, although rearing habitat access remains a critical bottleneck (Feunteun et al. 1998; Briand et al. 2005; Laffaille et al. 2007). For downstream-migrating adults, dams—particularly large hydroelectric dams—may delay or preclude migration or contribute to the mortality of migrating individuals (Shepard 2015; Drouineau et al. 2018). Therefore, managing the conservation of eel populations concurrent with hydropower operations remains a challenge to population recovery and rebuilding of the fishery.

American Eels have a unique catadromous life history that includes long-distance movements among freshwaters, estuaries, and oceans. During fall, some American Eels residing in lakes and rivers undergo morphological, physiological, and behavioral changes associated with reproductive maturation, including an enlarging of the eye and silvering of the skin (i.e., "silver-phase" eels; Aida et al. 2003). These changes coincide with declining water temperatures, rising flows, new lunar cycles, and other factors that may serve as migratory cues to move downriver toward the ocean (Lowe 1952; Vøllestad et al. 1986; Haro 2003; Durif and Elie 2008; Sudo et al. 2017).

Some environmental conditions that prompt the downstream migration of maturing silver-phase American Eels are also optimal for hydroelectric power generation. Periods of high precipitation that increase river discharge are an exogenous environmental cue that triggers downstream-migrating silver American Eels (Haro 2003; Haro et al. 2003; Durif and Elie 2008). Tagging studies have demonstrated that a large proportion of eels pass through operating turbines at hydroelectric facilities (Winter et al. 2006). Consequently, hydropower turbines inflict substantial injury or mortality on migrating silver eels (EPRI 2001; McCleave 2001; Durif et al. 2003), with reported mortality rates commonly ranging from 10% to 50% (Winter et al. 2006; Jansen et al. 2007; Larinier 2008; Eyler et al. 2016; Mensinger et al. 2021). A loss of sexually mature adults directly impacts population recruitment and hinders the rebuilding of the fishery.

Mitigation strategies for existing hydroelectric facilities may necessitate engineered modifications and retrofitting. This may involve the addition of reduced rack gap and slope screenings and the installation of bypass systems that prevent or discourage downstream migration through turbines (Amaral et al. 2003; Calles et al. 2013). However, surface-oriented bypass facilities have demonstrated limited use by migrating eels (Carr and Whoriskey 2008; Debowski et al. 2016). Furthermore, these systems require substantial investment and maintenance costs that may not be feasible for some hydropower operations.

Given the relatively low efficacy of surface-oriented bypass systems, turbine shutdown may be another management option. However, the timing of downstream migration can be quite variable and protracted depending upon annual conditions (Haro 2003). Shutting down turbines during the entire migration period, which generally ranges from July to November, would likely reduce mortality and satisfy conservation goals but would be undesirable for power generation in terms of lost revenue. Because of this conflict between fisheries potential and energy production (sensu Song et al. 2019, 2020), the duration and timing of mandated shutdowns are increasingly considered in Federal Energy Regulatory Commission relicensing processes (Vogel and Jansujwicz, in press). Informed application of the timing and duration of operational changes is therefore desirable to minimize the negative impacts from competing conservation and societal needs (Roy et al. 2018).

Identifying and characterizing environmental variables that are conducive to silver eel migration may therefore be useful for predicting their movement and simultaneously re-evaluating anticipated hydropower operations. A number of studies have established relationships between exogenous variables and downstream migration of European Eels *A. anguilla* in rivers (Vøllestad et al. 1986; Durif and Elie 2008; Trancart et al. 2013; Drouineau et al. 2017), but comparatively less research effort has been conducted for American Eels (but see review by Haro 2003), creating a need for further research to establish the consistency of relationships (Eyler et al. 2016). In addition, many studies are short in duration (Boubee and Williams 2006; Eyler et al. 2016) or are restricted to one tributary (Haro et al. 2003) or one river basin (Durif and Elie 2008), although recent studies have been more comprehensive (Sandlund et al. 2017; Teichert et al. 2020). A robust assessment of predictive models based on environmental covariates and their ability to inform management decisions requires large-scale studies of multiple rivers over multiple years.

Collecting an adequate amount of data that can be useful in developing a predictive modeling framework can be a time-consuming and costly endeavor. The depleted status of catadromous eels worldwide (Drouineau et al. 2018) and American Eels specifically (ASMFC 2012) creates an urgent need for synthesizing and evaluating the currently available information. Fishery-dependent data can be a valuable source of needed information when scientific studies are lacking (Robertson and Midway 2019; Santos et al. 2019; Lin and Jessop 2020). Examples of using fishery-dependent data are more prevalent for data-limited marine species (Santos et al. 2019) but have also been used to inform eel management in rivers (Haro et al. 2003; Durif and Elie 2008; Lin and Jessop 2020). Although fishery-dependent data may suffer from a lack of quality when compared to rigorously collected scientific data, these studies demonstrate their usefulness to inform management and conservation goals in the absence of scientifically designed studies.

We assembled long-term data sets of commercial harvest of American Eels across multiple rivers and time periods (ranging from 3 to 31 years) and associated environmental covariates into a modeling framework to characterize and predict the timing of downstream migration of silver-phase eels. We sought to (1) identify and characterize the importance of environmental covariates for predicting the downstream migration of silver-phase American Eels across multiple river systems and (2) assess the ability of the resulting models to predict migratory events. A Bayesian hierarchical modeling framework was used to estimate parameters and quantify parameter uncertainty. We chose a Bayesian hierarchical approach because of its flexibility for incorporating data across spatial (sites) and temporal (years) scales.

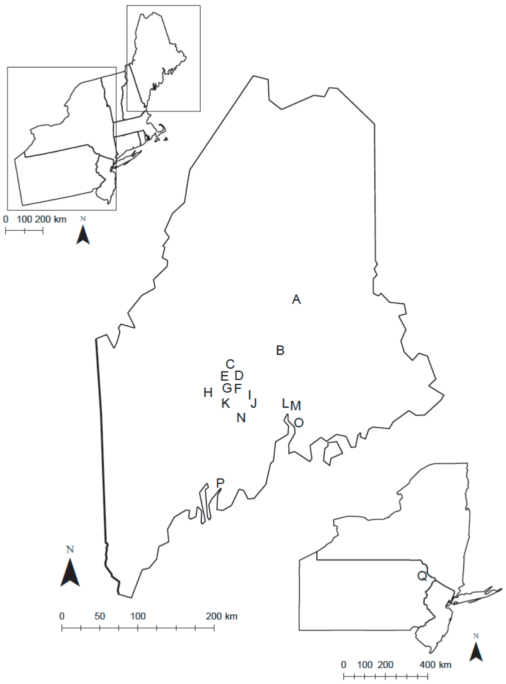
METHODS

Commercial harvest data.— American Eel catch data were compiled for 16 tributaries of the Penobscot River, Maine, and one location in the upper Delaware River (hereafter, "Delaware River"), New York (Figure 1; Supplement 1 available separately online). Data sets were comprised of daily American Eel catch collected by fishermen operating commercial fishing weirs. Generally, weirs consist of a series of panels staked into the river bottom that direct fish to a trap box and are deployed in a manner to catch fish moving downstream through the water channel (Gabriel and Wendt 2003). Commercial harvest for Souadabscook Stream, part of the Penobscot River watershed, was separated from the other Penobscot River sites ($n = 15$; hereafter, "Penobscot River tributaries") due to differing harvesting data time frames (1988–1998 for Souadabscook Stream versus 1997–1999 for the Penobscot River tributaries). Therefore, we present analyses for three data sets: Delaware River, Penobscot River tributaries, and Souadabscook Stream. Data were provided by The Nature Conservancy (Delaware River), by the Maine Department of Marine Resources (Penobscot River tributaries), and directly from the logbooks of commercial fishers Jim and Gloria Bennet (Souadabscook Stream). For the purposes of our models, we assumed that all eels caught by commercial harvesters were in the silver phase and were in the process of migrating to the ocean. Since commercial harvest coincided with summer and fall outmigration, we believe that this is a reasonable assumption.

Commercial American Eel catch data for the Delaware River were collected over a 31-year time span from 1977 to 2007 (Supplement 2), with data for 2003 missing. Dates of weir operation varied among years, with a median start date of July 21 and a median end date of October 22. Fishing effort ranged from 30 to 113 d, with annual catches ranging from 205 to 12,922 eels (Supplement 2; Figure 2). Harvest data for the Penobscot River tributaries were collected over a 1–3-year time span from 1997 to 1999 (Supplement 3). Weir operation began with a median start date of August 26 and a median end date of October 11. Fishing effort ranged from 10 to 92 d, with annual catches ranging from 14 to 5,383 eels (Supplement 3; Figure 2). Harvest data for Souadabscook Stream were collected from 1988 to 1998, with data for the years 1990 and 1996 missing. Weir operation began with a median start date of September 4 and a median end date of November 4. Total number of fishing days ranged from 15 to 73 d, with annual estimated catches ranging from 156 to 3,069 eels (Supplement 4; Figure 2).

Because of the nature of the data, eel catch was reported as an individual count, harvested weight (lb), or both. To compare data reported in disparate units, all data were converted to count data using the subset of eels (from all data sources) for which both harvest weight and count data were provided. This resulted in an average individual fish mass of 395 g (based on regression of data from 331 d when both counts and weights were reported from the Penobscot River tributaries and Souadabscook Stream data; $R^2 = 0.62$, $P < 0.001$). This conversion was required to estimate the eel count in 17% of the Penobscot River tributary data and 37% of the Souadabscook Stream data. Delaware River data were likewise reported as either eel count (64% of data) or weight (lb; 36%). Weight data were similarly converted to estimated count data using a river-specific conversion of 398 g (0.875 lb) per individual.

Environmental covariates.— Environmental variables were joined with corresponding eel catch during days of weir operation. Environmental variables considered in the analyses were average daily water temperature (°C),



Letter	River or Stream
A	Millinocket Stream
B	Piscataquis River
C	Ferguson Stream
D	Sebasticook River
E	Higgans Brook
F	Indian Stream
G	Withee Brook
H	Mill Stream
I	E. Branch Sebasticook River
J	Martin Stream
K	Carrabassett Stream
L	Souadabscook Stream
M	Sedgeunkedunk Stream
N	25 Mile Stream
O	Narramissic River
P	Sherman Lake
Q	Upper Delaware River

FIGURE 1. Locations of commercially operated weirs where American Eels were harvested. Catch data from 16 locations in the Penobscot River watershed, Maine, and one location in the upper Delaware River, New York, were synthesized and used in this study.

average daily river discharge (m^3/s), and lunar cycle, which have been demonstrated as important correlates for eel migration (Lowe 1952; Vøllestad et al. 1986; Haro 2003; Durif and Elie 2008) and were available for the Delaware and Penobscot rivers. Other environmental variables, such as wind speed, water conductivity, and dissolved oxygen, have also been shown to be important predictors of eel migration (Bultel et al. 2014; Sudo et al. 2017; Monteiro et al. 2020); however, these variables were not utilized for the systems we examined. Water temperature and river discharge data were collected primarily for nearby gauges operated by the U.S. Geological Survey (USGS), but these data were not always continuous or complete.

For analyses of the Penobscot River tributaries and Souadabscook Stream, we used the Penobscot River discharge at Eddington, Maine (USGS station 01036390), as directly measured or estimated from other sites. Eddington discharge was available for the years 1980–1996, but after 1996 no data were available, and discharge at Eddington was estimated from West Enfield discharge (USGS station 01034500) based on a linear regression of data when both sources were available ($R^2 = 0.967$, $P < 0.001$; Supplement 5). For the Delaware River, we used flow data from the Delaware River gauge at Trenton, New Jersey (USGS station 01463500).

Temperature for analyses of the Penobscot River tributaries and Souadabscook Stream was taken from the Penobscot River at Eddington (USGS station 01036390), as measured (only 17% of the data were available for the study period) or estimated from several sources. Temperature data from Milltown (USGS station 01021050) or Jay (USGS station 01055100) in Maine were used to generate linear regressions ($R^2 = 0.998$ and 0.997, respectively; Supplement 6) to estimate temperatures at Eddington (necessary for 72% of the temperature data). Temperature data were also provided by the Maine Department of Marine Resources (12%) and were collected daily at the upstream fishway at Veazie Dam, less than 1 km from the Eddington gauge site (Maine Department of Marine Resources, unpublished data; 9%). Less than 1% of temperature data was extrapolated from adjacent data to fill in gaps. For the Delaware River, we used temperature data from the Delaware River gauge at Trenton, New Jersey (USGS station 01463500). Missing data were interpolated or extrapolated from existing data within the series (5%). For 1979, in which a 52-d sequence of temperature data was missing, a daily average from all other years was substituted (3%).

Lunar cycle data were obtained from the U.S. Naval Observatory. We converted the lunar cycle into a continuous covariate by dividing the lunar phase cycle from a new moon to a full moon in equally spaced incremental steps, where 0.0 indicates the new moon and 1.0 indicates the full moon, and the first and last quarters were assigned a value of 0.5. Since the river systems that we were

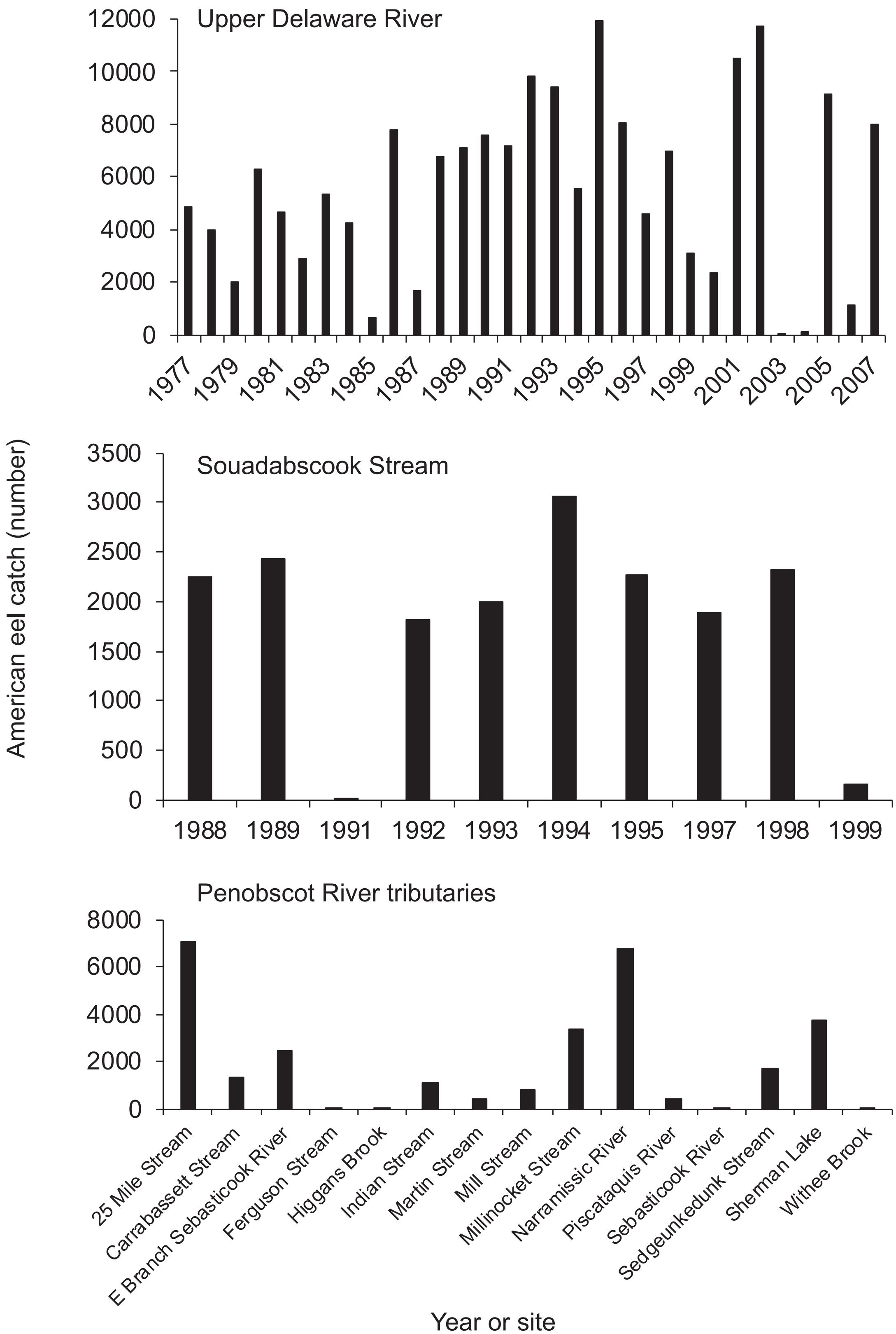


FIGURE 2. American Eel catch from commercially operated weirs by year for the upper Delaware River and Souadabscook Stream and by stream for the Penobscot River tributaries. Data for each tributary encompass total catch for 1–3 years.

comparing varied in size, we standardized river discharge. Standard daily discharge (SDD) was calculated as

$$\mathrm{SDD} = \frac{\text{Measured daily discharge}}{\text{Average discharge}},$$

where measured daily discharge is the discharge measured at the time of eel capture and average discharge is the 40-year average yearly discharge of the Penobscot and Delaware rivers. The Penobscot River SDD was used for the Souadabscook Stream analysis, as no discharge data were available for that stream. Values of SDD greater than 1 indicate discharge greater than the 40-year average, while values less than 1 indicate discharge less than the 40-year average.

Modeling of environmental relationships.— We modeled count data with generalized linear mixed modeling. Counts of eels tended to be highly skewed; therefore, a negative binomial likelihood was used to address possible overdispersion in the data (Smyth 1996; Lloyd-Smith 2007). We modeled all three data sets separately. A Bayesian hierarchical framework was employed to estimate parameters and measures of uncertainty (Gelman et al. 2013). The hierarchical structure of the models considered in the analyses allowed for spatial and temporal variability to be treated as random effects. The structure of the model can be written as

$$N_{i,j,t} \sim \mathrm{NB}(\lambda_{i,j,t}, \ \psi),$$

$$\log_{10}(\lambda_{i,j,t}) = \beta_0 + \gamma_{j,t} + \sum_{i=1}^{k} \beta_k \times Cov_{k,i,j,t},$$

$$\text{with}\, \gamma_{j,t} \sim \mathrm{Normal}(0, \ \sigma),$$

where $N_{i,j,t}$ is observed eel catch on day i at site j in year t, and ψ represents the overdispersion parameter of the negative binomial distribution. To model daily eel count ($\lambda_{i,j,t}$), a linear model was used, where β_0 is the intercept term, β_k is the kth coefficient in the model, and $Cov_{k,i,j,t}$-represents the kth environmental covariate (daily water temperature, average daily river discharge, and lunar cycle phase) for day i at site j in year t in the set of K covariates considered in the model. The term $\gamma_{j,t}$ is a normally distributed random effects term for site j in year t with a mean of zero and an SD of σ. For the Delaware River and Souadabscook Stream, there was only one site, so the random term could be reduced to a yearly random effect modeled as $\gamma_t \sim \mathrm{Normal}(0, \sigma)$.

Bayesian model selection was conducted for a series of candidate models to determine which one garnered the most support from the data. Linear relationships among environmental covariates and nonlinear relationships in the form of quadratic terms for temperature and flow (SDD) were included in the set of candidate models. Models were fitted using Markov chain–Monte Carlo (MCMC) using the program JAGS and the rjags package in R (Plummer et al. 2018; R Development Core Team 2019). Vague priors were used for all model parameters, where coefficients were modeled as Normal(0, 1,000), variance components were modeled as Uniform(0, 10), and the dispersion parameter of the negative binomial was modeled as Gamma(0.01, 0.01). For each model, five MCMC chains were constructed to establish the probability distribution. Each chain was run using a burn-in period of 30,000 iterations, followed by an adaptive phase of 10,000 iterations (sensu Gelman et al. 2013). Chains were not thinned. Candidate models were assessed with the deviance information criterion (DIC; Spiegelhalter et al. 2002). Models that received the lowest DIC value were identified as those that received the most support from the data. Chain convergence was assessed by visually examining MCMC trace plots and using the calculated Gelman–Rubin statistic (Gelman and Rubin 1992; Brooks and Gelman 1997).

Evaluation of model predictions.— We used posterior mean predictions to predict daily and weekly eel catch within river systems and to evaluate the ability of the model to make predictions for new data. We focused on the Delaware River and Souadabscook Stream because there were multiple years of data available from each of those systems. First, for each data set, we used a cross-validation approach in which we withheld 1 year of data and used the remaining data as a training data set to fit the model. We used the observed environmental covariates for the withheld year to predict mean eel catch for the withheld year. We repeated this process for each year in the respective data sets. To quantify prediction skill, we computed the R^2 value of the relationship between daily predicted catch and observed catch for each year.

In addition, as management decisions are often made on time scales greater than 1 d, we also looked at the relationship between weekly predicted and observed catch for each year. This larger temporal scale removed daily noise and allowed us to assess the ability of the model to capture coarser-scale patterns that may be relevant to managers. The years 1985, 2003, and 2004 for the Delaware River and the years 1990 and 1996 for Souadabscook Stream were not used—either because data were not available for those years or because too few data points were available to permit a sufficient analysis of weekly correlations (i.e., ≤1 week of eel catch data).

Next, because there was considerable noise in the data (Figure 2), we expected that daily catch predicted from the model would vary considerably from observed catch on any given day. Therefore, to smooth out the observed data, we calculated the mean observed catch for each ordinal date across all years in each data set. We next computed the mean predicted catch by averaging across all posterior predictions of daily catch from the previous cross-validation step. The overall mean prediction for a given ordinal date was compared to the mean eel catch observed on that same date.

Finally, to demonstrate the versatility of a Bayesian approach in forecasting migration events, we applied posterior simulations to make predictions. We simulated data from the posterior distribution and calculated the probability of above-average catch according to the model. In Supplement 7, we outline the method and demonstrate how results can be presented graphically to provide a visual assessment of predicted increases in catch probability that can be used as an informative tool to aid the management decision process.

RESULTS

Bayesian Model Results

Generally, across all systems, there was evidence that river discharge (SDD), water temperature, and lunar cycle were all important variables in predicting daily eel catch. Bayesian model selection results revealed that the model with linear terms for flow, temperature, and lunar cycle and quadratic terms for flow and temperature (i.e., the full model) was most supported by the data among the three river systems (Table 1). This model received the lowest DIC value among candidate models. Gelman–Rubin statistics were less than 1.1, indicating good convergence of all parameters (Brooks and Gelman 1997). Visual examination of MCMC trace plots also indicated convergence.

The posterior predictions of daily American Eel catch described negative quadratic relationships with temperature and river discharge among all systems (Figure 3). Median values for the β coefficients describing the quadratic terms of flow and temperature ranged from −0.30 to −2.86 and from −0.34 to −0.60, respectively (Table 2).

Environmental Relationships

American Eel movement occurred at elevated flows when river discharge was greater than average. Maximum daily eel catch occurred when the SDD was greater than 2 in the Delaware River and when the SDD was greater than 1 in Souadabscook Stream and the Penobscot River tributaries (Figure 3). In the Delaware River, the posterior median estimate of maximum daily eel catch was 1,431 (95% credible interval [CI] = 583–3,861). For Souadabscook Stream and the Penobscot River tributaries, posterior median estimates of maximum daily eel catches were 195 (95% CI = 144–1,055) and 109 (95% CI = 68–389), respectively.

TABLE 1. Model selection deviance information criterion (DIC) results, relative ranking, and R^2 values for model fit among 16 candidate models for the upper Delaware River, Souadabscook Stream, and the Penobscot River tributaries for the variables standard daily discharge (Flow), temperature (Temp), and lunar cycle (Moon). For brevity in labeling the table, candidate models that contained a quadratic term for a particular environmental variable are not labeled to display the linear term for the same variable. Values in bold indicate the lowest DIC value for the corresponding candidate model.

	Delaware River			Souadabscook Stream			Penobscot River tributaries		
Model	DIC	Rank	R^2	DIC	Rank	R^2	DIC	Rank	R^2
Null	15,971	16	<0.01	3,380	16	<0.01	6,108	16	<0.01
Moon	15,920	13	0.09	3,349	9	0.06	6,085	15	0.13
Flow	15,937	15	0.03	3,379	15	0.04	6,084	14	0.11
Temp + β.0	15,827	10	0.11	3,376	13	0.04	6,056	11	0.12
Flow + Moon	15,874	12	0.10	3,346	7	0.07	6,080	13	0.13
Temp + Moon	15,764	9	0.17	3,344	6	0.06	6,039	9	0.13
Flow + Temp	15,742	8	0.14	3,377	14	0.05	6,059	12	0.12
Flow + Temp + Moon	15,656	6	0.22	3,336	3	0.07	6,040	10	0.14
$Flow^2$	15,935	14	0.04	3,363	11	0.05	6,034	8	0.14
$Temp^2$	15,721	7	0.14	3,369	12	0.04	6,025	7	0.14
$Flow^2$ + Moon	15,869	11	0.10	3,330	2	0.06	6,003	6	0.15
$Temp^2$ + Moon	15,652	5	0.20	3,339	5	0.06	5,980	2	0.16
$Flow^2$ + Temp + Moon	15,625	3	0.22	3,337	4	0.07	5,999	4	0.16
$Temp^2$ + Flow + Moon	15,570	2	0.23	3,356	10	0.07	6,002	5	0.16
$Flow^2$ + $Temp^2$	15,642	4	0.16	3,348	8	0.07	5,988	3	0.15
$Flow^2$ + $Temp^2$ + Moon	**15,548**	**1**	**0.25**	**3,326**	**1**	**0.09**	**5,955**	**1**	**0.18**

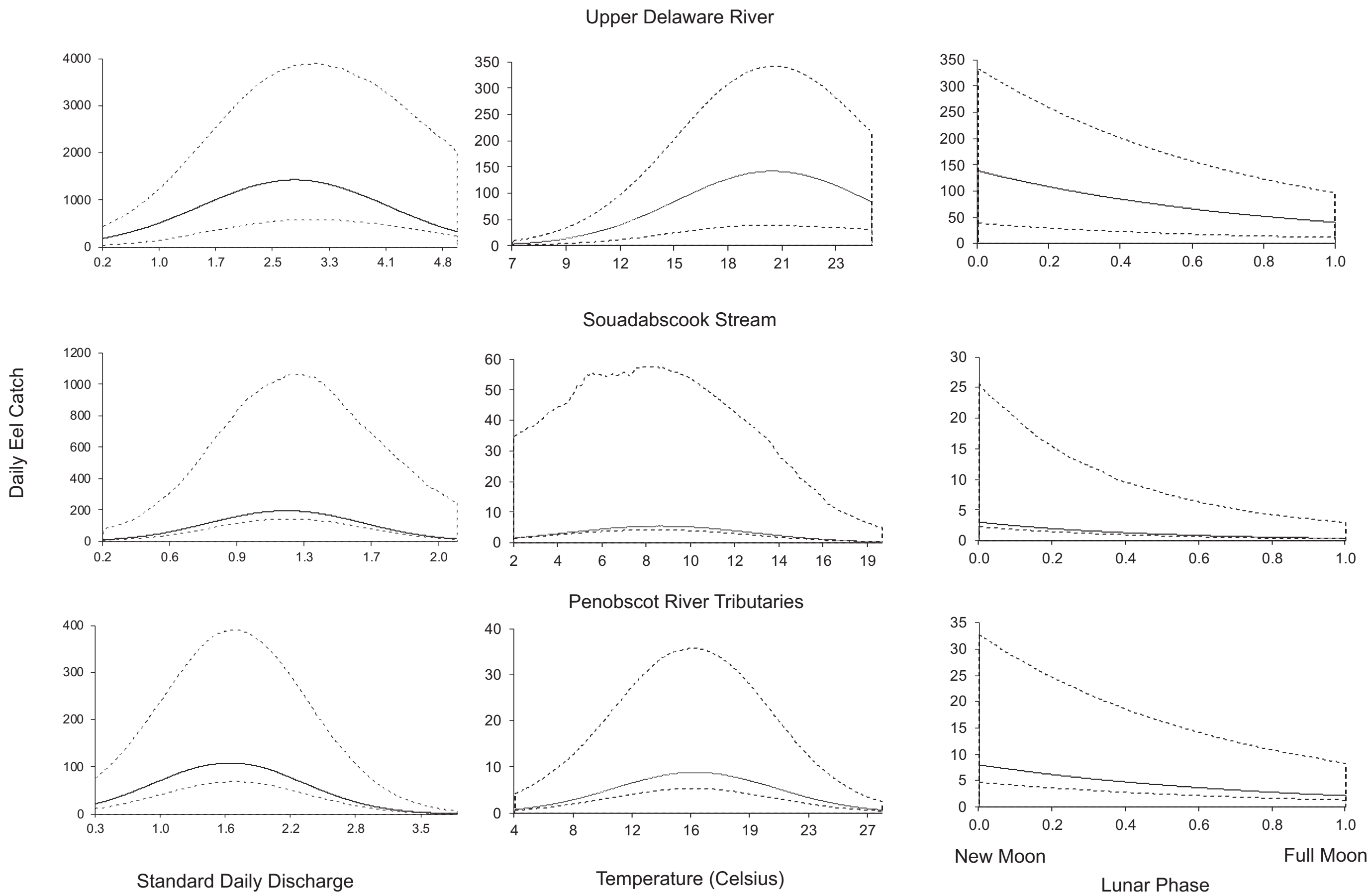


FIGURE 3. Predicted posterior median values (solid line) of daily American Eel catch in relation to standard daily discharge (proportion of 40-year average flow, m^3/s), water temperature (°C), and lunar phase cycle from the most supported models for the upper Delaware River, Souadabscook Stream, and the Penobscot River tributaries. Dashed lines represent 95% Bayesian credible intervals.

TABLE 2. Parameter estimates (median with SD in parentheses) and 95% credible intervals (CIs; lower limit, upper limit) from the best supported model among the three river systems for the variables standard daily discharge (Flow), temperature (Temp), and lunar cycle (Moon). Random variance component Year, referring to random year effects, applies to the upper Delaware River and Souadabscook Stream analyses, and Site × Year, referring to random site by year effects, applies to the analysis of Penobscot River tributaries. Psi (ψ) denotes the overdispersion parameter.

	Delaware River		Souadabscook Stream		Penobscot River tributaries	
Parameter	Median (SD)	95% CI	Median (SD)	95% CI	Median (SD)	95% CI
Null	4.93 (0.17)	4.60, 5.27	1.12 (0.94)	−0.30, 3.25	2.08 (0.50)	1.18, 3.20
Moon	−1.23 (0.12)	−1.47, −0.99	−2.12 (0.42)	−2.94, −1.29	−1.33 (0.25)	−1.83, −0.84
Flow	1.66 (0.21)	1.22, 2.06	6.84 (1.58)	3.72, 9.68	3.18 (0.53)	2.07, 4.16
$Flow^2$	−0.30 (0.06)	−0.39, −0.17	−2.86 (0.71)	−4.10, −1.42	−0.98 (0.14)	−1.24, −0.68
Temp	0.20 (0.07)	0.06, 0.33	−1.17 (0.29)	−1.72, −0.56	−0.42 (0.11)	−0.64, −0.20
$Temp^2$	−0.34 (0.04)	−0.42, −0.27	−0.60 (0.22)	−1.04, −0.17	−0.49 (0.08)	−0.65, −0.33
ψ	0.85 (0.03)	0.79, 0.91	0.21 (0.01)	0.18, 0.24	0.41 (0.02)	0.37, 0.46
Random term						
Year	0.74 (0.12)	0.55, 1.03	1.34 (0.60)	0.71, 2.83		
Site × Year					1.92 (0.32)	1.44, 2.70

Maximum daily eel catch occurred at a water temperature of 19.9°C for the Delaware River, which was higher than the temperatures of 8.9°C for Souadabscook Stream and 16.0°C for the Penobscot River tributaries. In the Delaware River, posterior predictions identified a maximum median daily eel catch of 142 (95% CI = 40–341). Similar to river discharge, maximum median daily eel catches in Souadabscook Stream and the Penobscot River tributaries were lower than that in the Delaware River at 5 eels (95% CI = 4–57) and 9 eels (95% CI = 5–36), respectively.

Model coefficients from the most supported models also suggested a negative curvilinear relationship between lunar cycle and eel catch. Eel catch was higher during new lunar cycles (i.e., when $x = 0.0$; Figure 3) and declined toward the full moon. This indicates that eel migration is more likely during new lunar cycles, potentially when ambient light is limited. Maximum median daily eel catch in the Delaware River was 139 (95% CI = 39–333), and like the other variables, maximum daily median catches were lower in Souadabscook Stream (3 eels; 95% CI = 2–26) and the Penobscot River tributaries (8 eels; 95% CI = 5–33).

Among the three river systems, there was substantial spatial and temporal variation, as indicated by the SD of the random effects of year and site × year (Table 2). This variation is not surprising, as there were large differences in annual counts among sites and years (Figure 2; Supplements 2–4). For example, annual catch ranged from less than 100 to nearly 12,000 eels in the Delaware River and from 8 to 3,000 eels in Souadabscook Stream. Among the Penobscot River tributaries, catch was also equally as variable and ranged from 14 to approximately 7,000 eels.

TABLE 3. Daily and weekly R^2 values from cross-validation analyses conducted for the upper Delaware River and Souadabscook Stream.

	Delaware River		Souadabscook Stream	
Year	Daily	Weekly	Daily	Weekly
1977	0.05	0.21		
1978	0.16	0.39		
1979	0.15	0.14		
1980	0.06	0.21		
1981	0.34	0.74		
1982	0.26	0.39		
1983	0.08	0.19		
1984	0.23	0.46		
1985				
1986	0.05	0.03		
1987	0.00	0.13		
1988	0.18	0.31	0.00	0.03
1989	0.40	0.43	0.00	0.01
1990	0.29	0.61		
1991	0.17	0.32	0.05	0.08
1992	0.37	0.70	0.24	0.40
1993	0.18	0.42	0.04	0.18
1994	0.26	0.33	0.01	0.02
1995	0.25	0.45	0.42	0.92
1996	0.15	0.39		
1997	0.05	0.15	0.02	0.20
1998	0.03	0.07	0.00	0.37
1999	0.08	0.22	0.26	0.73
2000	0.05	0.17		
2001	0.34	0.66		
2002	0.00	0.02		
2003				
2004				
2005	0.05	0.00		
2006	0.04	0.08		
2007	0.31	0.63		

Evaluation of Model Predictions

For both river systems, model prediction evaluations generally demonstrated a greater ability to predict weekly average eel catch estimates compared to daily eel catch estimates, as indicated by the cross-validation analysis. For Souadabscook Stream, R^2 values of observed and predicted eel catch ranged from 0.00 to 0.42 for daily estimates and from 0.01 to 0.92 for weekly estimates among years. For the Delaware River, R^2 values of observed and predicted eel catch ranged from 0.00 to 0.40 for daily estimates and from 0.00 to 0.74 for weekly estimates among years (Table 3). This result suggests greater accuracy in predicting eel catch over coarser time scales.

The prediction skill of our model for mean eel catch by ordinal date revealed trends in predicting eel catch across the fall migration season. For estimates of eel catch by ordinal date, the Delaware River model predicted a peak in mean eel catch early in the season, followed by a steady decline (Figure 4, left panels). The observed mean catch followed a similar pattern, albeit with pulses of high catches early in the season that were not reflected by the predicted mean catch. For Souadabscook Stream, higher mean eel catch was predicted for later in the season. Similar to the Delaware River, pulses of high observed catches in Souadabscook Stream were not reflected by the predicted mean catch. The relationship between observed average daily catch and mean predicted daily catch for a given ordinal date was much stronger for the Delaware River ($R^2 = 0.67$) than for Souadabscook Stream ($R^2 = 0.07$; Figure 4, right panels). This suggests that the model constructed for the Delaware River had greater accuracy in predicting daily eel catch over a season than the model constructed for Souadabscook Stream.

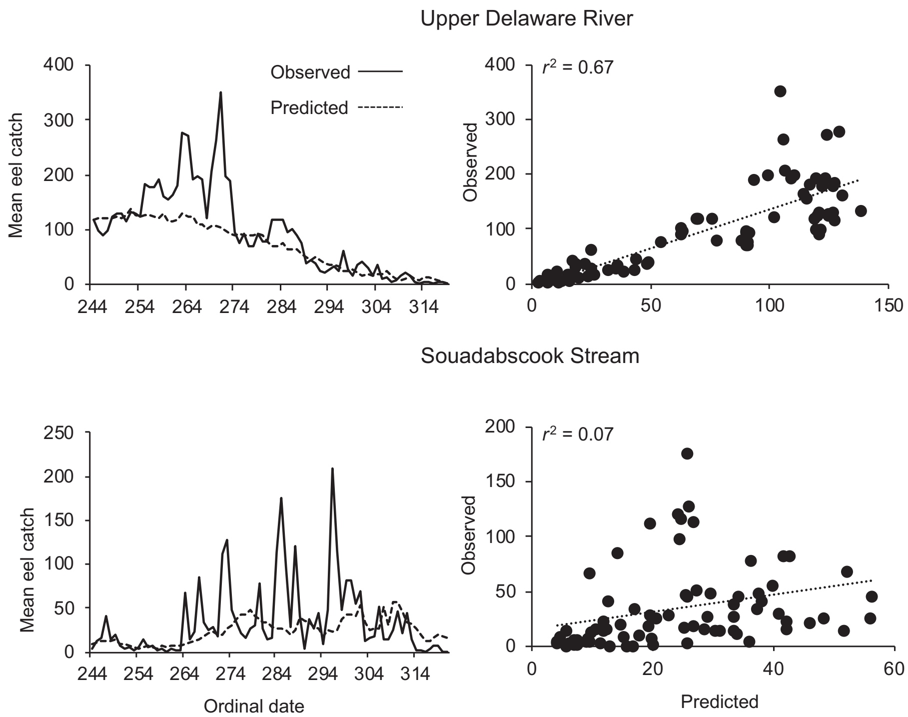


FIGURE 4. Mean observed American Eel catch (solid line) and mean predicted catch (dashed line) among ordinal dates averaged across all years for the upper Delaware River (upper left panel) and Souadabscook Stream (lower left panel). Mean observed American Eel catch for a given ordinal date regressed against the overall mean prediction for a given ordinal date averaged across all posterior predictions of daily catch from previous cross validation is also shown for the upper Delaware River (upper right panel) and Souadabscook Stream (lower right panel). Dashed lines indicate the linear trendlines and correspond to the r^2 value presented for each plot.

DISCUSSION

Our modeling exercise characterized the variability associated with commercial silver American Eel catch among environmental variables across multiple river systems. Our results identified significant parabolic relationships between eel catch and water temperature or river discharge and nonlinear relationships between eel catch and lunar cycle, which were consistent with the literature (Lowe 1952; Vøllestad et al. 1986; Haro 2003; Durif and Elie 2008). Across river systems, we generally found consistent patterns among environmental covariates, suggesting continuity in eel subpopulations among river systems. However, the differences we observed among parameter estimates across river systems—particularly with water temperature and river discharge—suggest that models parameterized for one system may not be directly transferable to other systems.

The environmental parameters we estimated from our models share some similarities with environmental parameter estimates from other published work. Our work suggests that in a system similar to the Delaware River, there is a high probability of eel migration during conditions characterized by higher-than-average river flows, water temperatures ranging from 18°C to 22°C, and lunar phases around the new moon that occur from September to mid-October. Additionally, our modeling suggests similar conditions for river discharge and lunar phase for migrating eels in Souadabscook Stream but with water temperatures ranging from 7°C to 11°C during a time frame of late September to late October. Other studies identified that water temperatures ranging from 8°C to 18°C triggered migratory behavior (Vøllestad et al. 1986; Tesch 1994; Durif et al. 2003). However, Haro (2003) suggested that periods of water temperature decline may be a more important cue than the actual temperature. The literature reports observed silver eel migrations at river discharge rates that were at or near average velocities (Tesch 1994; Haro 2003), while others observed migration pulses associated with precipitation events (Durif et al. 2003; Watene et al. 2003) or generally during periods of high rather than low river discharge (Frost 1950; Lowe 1952). Finally, studies have observed increased silver eel movement and higher catch associated with new moons (McGrath et al. 2003; Watene et al. 2003). Quantifying these relationships may inform management decisions concerning turbine shutdown by narrowing the migration window to discrete periods of high probability.

Our modeling is based on the observed interception of a migrating fish. This observation is the conditional probability of the fish initiating migration (a complex physiological and behavioral process; Shrimpton 2013) and the conditions that permit both migration and capture (e.g., enough flow for navigation and trap operation). Thus, the shared inclusion of predictive parameters among our three study data sets is congruent with shared biological processes among individual fish from each river. However, divergence among the data sets with regard to parameter magnitude is not an altogether surprising outcome. The location of a weir in a river system, the conditions under which the trap operates, and the physical differences among rivers are all likely to influence the timing and dynamics of the observed migrants. Similarly, Haro et al. (2003) and Trancart et al. (2013) concluded that site-specific information on run timing is likely necessary for modeling efforts to be successful.

A number of studies have evaluated the effectiveness of predicting eel migration from environmental cues (Durif and Elie 2008; Trancart et al. 2013), but few studies have evaluated the robustness over multiple years and rivers (although see Sandlund et al. 2017; Teichert et al. 2020). Our model's accuracy in making predictions greatly varied among rivers and among years within a river, as indicated by the widely ranging R^2 values from our cross-validation analysis. This result is not surprising, as ecological data are inherently noisy, thus complicating the ability of models to make consistently precise predictions (Dietz 2017). We found that broadening the temporal scale (i.e., from daily to weekly) smoothed some of the noise and provided better predictions while still being at a scale that was fine enough to be useful to management. Efforts to use models to forecast eel migration should carefully consider the objectives versus the constraints of the data and the chosen modeling framework. By focusing on a defined aspect of the migratory process, such as run timing, the use of correlative models may provide relatively accurate forecasts that are ultimately useful to management (Trancart et al. 2013).

Numerous different approaches have been used to model eel migration (Haro et al. 2003; Durif and Elie 2008; Trancart et al. 2013). We implemented a generalized linear mixed model within a Bayesian hierarchical framework to model variability among sites and years. The hierarchical structure accounts for some of the temporal and spatial variation in unmodeled population dynamics. This general framework can be built upon in future iterations by, for example, incorporating semi-parametric generalized additive models (Wood 2016), including prior information (McCarthy and Masters 2005), and modeling measurement error in the predictor and response variables (Hatch and Jiao 2016). Although our method appeared to capture relationships between environmental cues and eel catch, we also found some evidence of model misspecification late in the season, when the model tended to predict a high probability of migration, but the observed catch was relatively low (Supplement 7). Other modeling approaches could be explored, such as autoregressive models (Trancart et al. 2013) and modeling of cumulative distribution functions (Moravie et al. 2006), and their efficacy in forecasting could be evaluated through skill testing (Thorson 2019). A comparison of methods was not the goal of the present study but could be considered in the future when deciding on the most effective method to achieve management objectives.

A novel aspect of this study was the use of fishery-dependent data collected from commercial fishers as a source of data to inform our models. Such information, though limited, is critical for understanding silver eel migration (Durif and Eile 2008; Sandlund et al. 2017). These data sets encompass a long time series and broad spatial scale that may otherwise be unfeasible (economically or logistically) with a descriptive research study. However, fishery-dependent data sets may be biased in terms of the accuracy of reported catches, representativeness of sampling locations, yearly variability in fishing operation, and variation in the capture efficiency of the gear (Hilborn and Walters 1992). Despite these drawbacks, we were able to estimate significant environmental relationships that were consistent with the literature. Therefore, we highlight the resourceful use of commercial catch to construct models but caution the potential biases of nonstandard sampling effort associated with fishery-dependent data and capture efficiency. Future modeling efforts could consider adding complexity to the hierarchical framework to address these sources of uncertainty.

Management Implications

Broadly, our work highlights the novel use of fishery-dependent data to characterize fish movement and provides a framework with which to inform the development of prediction models and associated risk that may be applied to other migratory fish and river systems. Dams threaten ecosystem functions—notably populations of migratory fish that move between freshwater and saltwater habitats to fulfill life history requirements (Limburg and Waldman 2009; Hall et al. 2011). Strategies that incorporate dam removal could be beneficial for restoring watershed functions and diadromous fish populations, but the social (e.g., recreation) and economic (e.g., power generation) benefits are additional considerations (McShane et al. 2010; Brown et al. 2013; Fox et al. 2016). Our work can be used to inform decision making by natural resource managers and hydropower operators faced with conservation and societal objectives. A "win-win" solution may necessitate compromise among stakeholders with competing objectives (McShane et al. 2010). For example, temporarily suspending turbine activity at hydroelectric facilities during predicted periods of increased silver eel migration could minimize eel mortality and the potential loss of power generation from unnecessary shutdowns (Trancart et al. 2013; Smith et al. 2017). Additionally, our work may inform the consideration of alternatives to reduce eel mortality, such as engineering measures involving the modification of downstream bypass and physical screen systems (Calles et al. 2013; Baker et al. 2019; Pratt et al. 2021).

The environmental covariate relationships we modeled were initialized using fishery-dependent data. These relationships may be refined with the addition of newer data (i.e., independent data). For example, results from our models could be combined with information from telemetry studies (e.g., Bultel et al. 2014) to construct a more comprehensive modeling framework that assesses eel transit and behavioral interactions at dams. The flexibility of the Bayesian hierarchical modeling approach readily permits the incorporation of new data.

Diadromous fish, including American Eels, represent an important link between marine and freshwater ecosystems and have significant commercial value (Limburg and Waldman 2009; Weaver et al. 2018). Thus, our work may be utilized in broader decision-making frameworks that consider multiple diadromous fish species, those that employ ecosystem-based management (Pikitch et al. 2004), and those that incorporate social and economic aspects of fisheries (i.e., hydropower operation; Fletcher et al. 2010). Management decisions informed by biological data could be better positioned to conserve and restore wild fisheries populations and aquatic ecosystems.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.