SPECIAL SECTION: 4TH MISSISSIPPI–YANGTZE RIVER BASINS SYMPOSIUM

Modeling Larval American Shad Recruitment in a Large River

Elizabeth A. Marschall (iD)

Aquatic Ecology Laboratory, Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, 1314 Kinnear Road, Columbus, Ohio 43212, USA

David C. Glover (iD)

Aquatic Ecology Laboratory, The Ohio State University, 1314 Kinnear Road, Columbus, Ohio 43212, USA; and Illinois Department of Natural Resources, 11731 State Highway 37, Benton, Illinois 62812, USA

Martha E. Mather (iD)

U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, Kansas 66506, USA

Donna L. Parrish* (iD)

U.S. Geological Survey, Vermont Cooperative Fish and Wildlife Research Unit, Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, Vermont 05405, USA

Abstract

Climate change is altering the spatial and temporal patterns of temperature and discharge in rivers, which is expected to have implications for the life stages of anadromous fish using those rivers. We developed an individual-based model to track American Shad *Alosa sapidissima* offspring within a coarse template of spatially and temporally variable habitat conditions defined by a combination of temperature, river velocity, and prey availability models. We simulated spawning at each river kilometer along a 142-km reach of the Connecticut River on each day (April 1–August 31) to understand how spawning date and location drive larval recruitment differentially across years and decades (1993–2002 and 2007–2016). For both temperature and flow, interannual variation was large in comparison to interdecadal differences. Variation in simulated recruitment was best explained by a combination of season-specific spawning temperature and location along the course of the river. The greatest potential recruitment occurred during years in which June temperatures were relatively high. In years when June and July were warmer than average, maximum recruitment resulted from spawning taking place at the upstream portion of the modeled reach. Model scenarios (stationary or passive-drift larvae; and dams or no dams) had predictable effects. We assumed that the pools above dams had negative impacts on eggs and yolk-sac larvae that may have been deposited there. Allowing eggs and larvae to drift passively with the current reduced spatial differences in recruitment success among spawning sites relative to stationary eggs and larvae. Our results demonstrate the importance of spatiotemporal environmental heterogeneity for producing positive recruitment over the long term. In addition, our results suggest the importance of successful passage of spawners to historical spawning sites in the Connecticut River upstream of Vernon Dam, especially as conditions shift with climate change.

Although anadromous fish using large rivers have evolved to be successful in the face of high levels of environmental variation, their success may be challenged in a new climate regime as it affects river conditions (Crozier et al. 2008). The U.S. East Coast, like much of the continent of North America, is predicted to have warm

---

temperatures beginning earlier in the spring and to experience patchier precipitation, with rain being concentrated in heavy precipitation events (Karl et al. 2009; Berton et al. 2016), leading to changes in the patterns of river discharge. The timing of important anadromous life cycle events, such as upstream migration (Quinn and Adams 1996; Hinrichsen et al. 2013; Peer and Miller 2014), spawning (Nack et al. 2019), and downstream migration (Aldvén et al. 2015), are cued by temperature and flow in many populations (Northcote 1984; Bauer et al. 2011); thus, a shift in patterns of these environmental variables may lead to a shift in migration timing and may have implications for success at each of these life cycle transitions (McNamara et al. 2011). Despite the fact that (1) the timing of appropriate flow and temperatures for migration and spawning differs greatly from year to year within a river and (2) the plasticity in timing of migration is assumed to have evolved to deal with annual variation in potential environmental cues (Winkler et al. 2014), there is uncertainty about whether plasticity in timing of spawning and migration will be sufficient to allow populations to persist under a new regime of river conditions (McNamara et al. 2011; Crozier and Hutchings 2014).

The American Shad *Alosa sapidissima* is a widespread anadromous fish species that is native to the East Coast of North America and has been introduced into rivers in the western USA. As part of their anadromous life cycle, adult American Shad enter northeastern coastal rivers in the spring and summer to migrate upstream to spawn, their eggs are spawned in the moving current, and their larvae develop in the river and transform into juveniles, which migrate downstream before winter. The question of how the timing of American Shad upstream migration may be cued by temperature and flow has been studied across the broad native latitudinal and introduced range of this species (e.g., Walburg 1960; Leggett and Whitney 1972; Quinn and Adams 1996; Greene et al. 2009; Hinrichsen et al. 2013). The timing and location of spawning within rivers have been described (e.g., Beasley and Hightower 2000; Greene et al. 2009) and modeled (Castro-Santos and Letcher 2010) across the range of this species as well. The timing and location of spawning drive the timing, location, and environmental conditions experienced by the larvae. A number of research programs has focused on relating production of juveniles not only to stock size but also to river conditions during the larval and juvenile stage (Leggett 1977; Crecco and Savoy 1984); however, little is known about how the decision of where and when to spawn affects the ultimate probability of success for larvae and juveniles (but see Limburg 1996a; O'Donnell and Letcher 2008). To understand how the potential of a river to produce American Shad juveniles may shift as the underlying patterns in temperature and flow change over time, we first need an understanding of how spawning time and location—and the larval and juvenile environmental conditions that follow—drive juvenile success, including considering spawning times and locations that were not historically considered to be relevant.

Year-class strength of American Shad has been shown to be strongly correlated with environmental factors affecting prejuvenile life stages, with recruitment believed to be set at the transition to the juvenile stage in the Connecticut River (Crecco and Savoy 1985; Crecco et al. 1986; Savoy and Crecco 1988, 2004). Water temperature and flow conditions during early development may be particularly important. For instance, water temperatures below 11°C can cause deformities and mortality in eggs (Ryder 1887; Leim 1924), and larvae may stop foraging when water temperatures drop below 9°C (Backman and Ross 1990). Even cool water temperatures (~16°C) may increase mortality in these critical life stages by prolonging egg and larval development (Marcy 1972, 2004). High flows are also correlated with poor egg survival, potentially due to increased physical damage or advection into unfavorable habitats (Savoy and Crecco 1988) and decreased foraging efficiency of larvae (Crecco and Savoy 1984).

The timing of water temperature and flow conditions in relation to egg and larval development may be particularly important for determining year-class strength. For instance, high flows and cool water temperatures in the Connecticut River during June increase the likelihood of a poor year-class (Leggett 1977; Crecco et al. 1983; Crecco and Savoy 1984; Marcy 2004). In contrast, high precipitation during May (and presumably higher flows) can have a positive effect on recruitment (Crecco et al. 1983). Thus, ideal conditions for a strong year-class may include high precipitation (and flows) in May but low flows and high water temperatures during June. Changes in the timing of high flows and temperatures may therefore alter the survival of American Shad eggs and larvae. Successful survival through the egg, larva, and juvenile stages requires that a series of life-stage-specific physical and biotic conditions be met sequentially. Poor recruitment or low year-class strength may be attributed to both unsuitable stage-specific physical conditions and a disconnect between the temperature, velocity, food, and habitat needed for subsequent life stages. Climate change is expected to exacerbate this mismatch.

Climate change is expected to increase air temperatures over the coming decades in the northeastern USA. This may benefit American Shad by increasing egg and larval development rates. However, climate change is also expected to alter the timing and intensity of precipitation—and, thus, high flows—in this region. Specifically, in the northeastern USA, high flows are expected to occur earlier in the spring, partly as a result of more winter precipitation arriving as rain rather than snow, and warm

temperatures are expected to occur earlier in the spring (Karl et al. 2009; Berton et al. 2016). This may affect American Shad if the severity and timing of these high flows alter egg and larval survival. Given these uncertainties, the development of models that are capable of forecasting the effects of climate change on egg and larval survivorship is critical to achieve an understanding of how climate change may affect American Shad populations.

Our main objective was to characterize how the recruitment potential for American Shad in a large river responds to temporal and spatial patterns in temperature and flow. Rather than modeling how spawners select spawning dates and sites in response to altered temperatures and flow, we developed a model to compare offspring success across a broad range of possible spawning dates and sites. Our model estimates the potential annual recruitment under the condition that spawners use all sites along the length of the modeled reach and spawn on all days of a 5-month period. We intentionally removed spawning time and site choice from the model. We began by asking the following: "How do the best locations and best timing for spawning and recruitment shift, if at all, from the early period, 1993–2002, to the more recent period, 2007–2016?" We discovered that interannual variation in seasonal patterns of temperature and flow were so great that they masked any potential differences between the time periods. Thus, we then used the variation among all 20 years to examine how seasonal dynamics of temperature and flow drive patterns in the timing and location of successful spawning and recruitment. We took advantage of years with extremes in season-specific temperature and flow to understand how recruitment may respond to new patterns in these environmental conditions.

METHODS

Although this study was intended to address questions about the interaction between American Shad larval success and river conditions (temperature and flow) in a general large-river system, we parameterized our model with information from a specific system: the Connecticut River. With a watershed area of $29,100 \text{ km}^2$, the Connecticut River is the largest river in the New England region. The flow of the river is interrupted by a number of dams along the course of the main stem. Detailed descriptions of the river are numerous, including two examples containing information relevant to this study (i.e., Gephard and McMenemy 2004; Marschall et al. 2011). We modeled a 142-km section of the river from immediately above the Holyoke Dam (river kilometer [RKM] 138; where RKM 0 = the Connecticut River mouth at Long Island Sound) to immediately below Bellows Falls (RKM 280), the historical upstream extent of American Shad spawning (Connecticut River Atlantic Salmon Commission 2017). There

are two additional dams located between the Holyoke Dam and Bellows Falls (see Castro-Santos and Letcher 2010: their Figure 1 map).

Model structure.— We used an individual-based modeling approach to track offspring within a template of spatial and temporal habitat conditions defined by a combination of abiotic conditions and prey availability models. We modeled American Shad spawning in each of the 142 1-linear-kilometer sections of the river on each day from April 1 to August 31. Rather than predict where (i.e., in which 1-km section) and when (i.e., on which date) American Shad actually spawn in a given year, we modeled the total potential of the river to produce recruits if all areas were available for spawning and if spawners were present on all dates. Our interest was in how the recruitment potential of the river varied across years and time periods rather than the related question of how spawners respond to environmental cues to move through the river and spawn (e.g., Castro-Santos and Letcher 2010). Given that the year-class strength of American Shad is believed to be set by the juvenile stage in the Connecticut River (Crecco et al. 1983), we modeled the probability of an individual offspring successfully transitioning from the egg stage to juvenile metamorphosis (~25 mm TL; Ryder 1887; Leim 1924; Crecco et al. 1983) as an index of recruitment success (hereafter, "probability of recruitment"). The probability of recruitment was conditional on the location and time of spawning and the subsequent habitat conditions experienced by individual offspring. Particularly important was the duration of time spent in each of five distinct developmental stages that varied with respect to the mortality rate experienced. Given that the mortality rate decreased with developmental stage, a shorter duration in each stage would lead to a higher expected probability of recruitment. Temperature and current velocity experienced by modeled offspring through their development were determined for each river section from a spatially coarse model, which was parameterized using available historical data from the Connecticut River. Prey availability within each river section was modeled as a function of temperature and discharge. Below, we describe in further detail each model compartment and associated assumptions.

The entire model itself consisted of three pieces: a river model (daily temperature, flow rate, and zooplankton density [ZP] at each location along the river), a fish model (probability of survival through each early life stage; parameters defined in Table 1), and a particle-tracking model (linking individual fish to locations in the river). The time-dependent survival portion of the model (Figure 1) used stage-specific instantaneous mortality estimates and the duration of time spent within each stage to determine the probability of survival through each of four early life stages: egg, yolk-sac larva, first-feeding larva, and advanced larva. The model endpoint was the juvenile
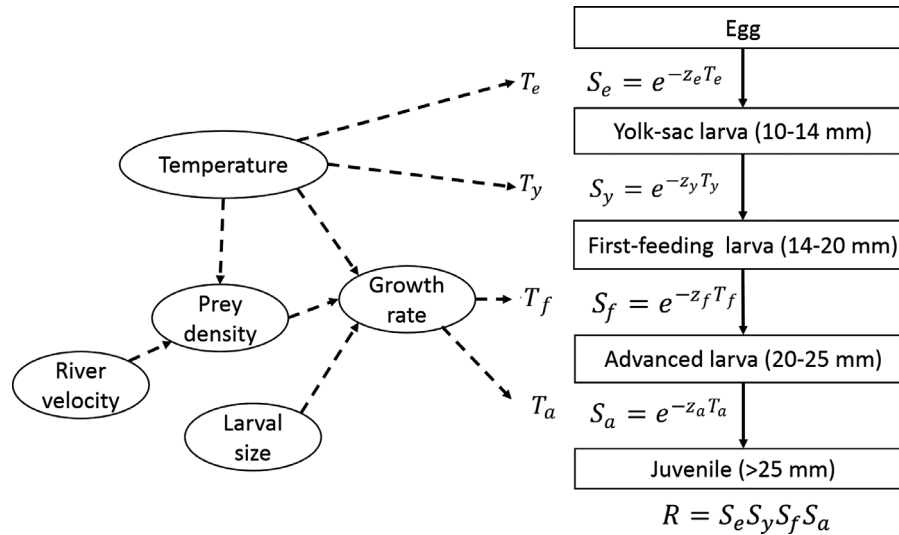
FIGURE 1. Diagram of the processes in the fish model leading to potential recruitment (R). Parameter values are given in Table 1. Survival S_x ($x = e$, y, f, a) through each egg and larval stage is determined by a stage-specific mortality rate (z_x) and the duration of time (T_x) spent in that stage. Egg development time (i.e., the duration of the egg stage) and yolk-sac stage durations are a function of temperature. The duration of each larval stage is determined by larval growth rate, which is a bioenergetic function of larval size, temperature, and prey density. Prey density is determined from the river model as a function of temperature and velocity.

stage, and the probability of recruitment was the product of survival through the four early life stages to the final juvenile stage. The time spent in the egg and yolk-sac larval stages was a function of water temperature, which influenced egg development rate and yolk-sac absorption rate. The duration of time spent in the first-feeding and advanced larval stages was dependent on growth rate, which was modeled with a bioenergetics model (Limburg 1996b). Details are provided below (see *Fish model: late-larval development and survival*).

Model scenarios.— We modeled four scenarios, including each combination of two larval movement (stationary or passive drift) and two dam (absent or present) scenarios. The stationary scenario kept the eggs and larvae at the site of spawning, not allowing them to move downstream with the current. The passive-drift scenario allowed the eggs and early larvae to drift with the current as passive, massless particles. There is evidence that American Shad move downstream during the larval period before beginning out-migration as juveniles (Limburg 1996a; O'Donnell and Letcher 2008), but their movement in relation to flow is not well understood. We believe that the reality falls somewhere between the two extremes represented in our model scenarios, and we used these extremes to bound the possible outcomes. In the presence of dams, we assumed that current velocity approached zero near the dams (due to the lack of unidirectional flow resulting from currents being reflected by the dam; Ellis 1942; Baxter 1977) and that siltation and suspended sediment in the pools above the dam had a negative effect on egg and

larval survival (Auld and Schubel 1978; Stier and Crance 1985; Hightower et al. 2012). Eggs and larvae that were spawned in the pools above dams or that encountered dams during their movement downstream experienced an increased mortality rate that progressively intensified with proximity to the dam (see *Fish model: late-larval development and survival*).

River model.— We used mean daily temperature data from multiple sources (Supplementary File S1 available in the online version of this article) for three major areas of the river reach we were modeling: Holyoke, Massachusetts (RKM 137–139); Turners Falls, Massachusetts (RKM 195–203); and Vernon, Vermont (RKM 229–237). For each major area, we had several sources of nearby data. Not all years were represented in all data sets. Data sets for some sites were missing certain days and, in some cases, weeks. If the gaps in data within a year were short (<7 d), we interpolated between values from surrounding days. For longer data gaps, which tended to occur very early and very late in the season, we took advantage of the fact that daily temperatures at a given site were correlated with temperatures at other sites during individual seasons. At one reach (RKM 137–139), the majority of the temperatures for the month of April and after July 16 during the first 10 years were missing and had to be interpolated from sites with season-specific correlated temperatures. For the remaining portion of the data set, over 90% of the temperatures came from original data.

We used mean daily river discharge data from the U.S. Geological Survey (USGS) National Water Information

TABLE 1. American Shad recruitment model parameters, values, and sources.

Parameter/function	Value/form	Source
Egg development time (T_e; d) as a function of temperature (τ; °C)	$T_e = 5{,}356.84\tau^{-2.379}$	Rice 1878; Ryder 1887; Leim 1924; Watson 1970; Limburg 1996a
Minimum viable egg temperature (°C)	11	Ryder 1887; Leim 1924
Maximum viable egg temperature (°C)	27	Ryder 1887; Leim 1924
Background egg and yolk-sac larval mortality rate (d)	0.30	Savoy and Crecco 1988
Minimum viable yolk-sac larva temperature (°C)	11	Assumed (from Ryder 1887; Leim 1924 for eggs)
Maximum viable yolk-sac larva temperature (°C)	27	Assumed (from Ryder 1887; Leim 1924 for eggs)
Larval length (TL; mm) to mass (W; g) function	$W = 0.00000646 \cdot \mathrm{TL}^{3.023}$	Limburg 1996b
Larval daily growth in mass (W; g)	$\frac{dW}{dt} = \frac{pk_1 W^{k_2} f(\tau) - k_3 W^{k_4} e^{k_5 t}}{k_6}$	Limburg 1996b
k_1, k_2, k_3, k_4, k_5	0.220, 0.20, 0.036, 0.776, 0.02	Limburg 1996b
k_6, larval energy density (kcal/g)	1.0	From range reported in Limburg 1994 (their Appendix C) assuming a dry weight : wet weight ratio of 0.20 (Limburg 1996b)
Natural mortality rate (d)		Savoy and Crecco 1988
Small larvae	0.208	
Medium larvae	0.094	
Large larvae	0.052	
Minimum water temperature for feeding (°C)	9	Backman and Ross 1990

System (http://waterdata.usgs.gov/nwis). Although some discharge data existed for many sites, we were limited to using those sites that had sufficient data over the spring–summer period (April–August) for each of the years 1993–2002 and 2007–2016. Because current velocity (linear distance per time) is more relevant for larval shad movement than is discharge (volume per time), we converted discharge data to current velocity by dividing by the cross-sectional area of the river near each discharge monitoring site. We used linear interpolation over RKMs to coarsely represent spatial patterns in current velocity along the course of the river—ignoring dams—between monitoring sites. Our model considered only coarse-scale, longitudinal changes in temperature and velocity along the course of the river rather than fine-scale habitat differences within and among RKM sections. We assumed that the dam influenced velocity for a total of 5 km upstream. This assumption was somewhat arbitrary, informed by satellite images of the rivers above and below dams. First, we assumed that velocity was 0 km/d in the first 1 km upstream of the dam. For the next 4 km upstream, we linearly interpolated between 0-km/d velocity and the estimates of unimpacted velocity for the section 6 km upstream of the dam.

To determine prey available to American Shad offspring, we estimated the influence of river discharge and temperature on zooplankton (the primary prey of larval American Shad; Crecco and Blake 1983; Limburg 1996a) availability from empirical data collected within a 145-km stretch of the Connecticut River in Massachusetts between 1980 and 1982 (Crecco et al. 1983). We chose this data set because it is the most comprehensive published set of ZP data with relevance for American Shad larvae in the Connecticut River. We matched historical daily mean water temperatures and discharge to the zooplankton sample dates. The spatial and temporal heterogeneity in ZP (number/m³) was then modeled as a function of temperature (τ; °C) and river discharge (D; 1,000 m³/s):

$$ZP = e^{1.7915t - 0.04966\tau^2 - 0.3306\log_e(D) + 0.008482\log_e(D^2) - 6.5986}.$$

The adjusted R^2 was 0.33. For dates and locations at which discharge was zero, discharge of 1,000 m³/s (the smallest unit of discharge) was used to estimate ZP.

Fish model: egg development and survival.— The duration of egg development was modeled as a function of temperature. We updated an existing function from Limburg (1996a) relating egg development time (T_e; d) to temperature (τ; °C) by incorporating additional values from the literature: $T_e = 5{,}356.84\tau^{-2.379}$ ($R^2 = 0.887$). To

account for different temperatures experienced by eggs over time, we used the average temperature for each day and calculated the proportion of development gained per day as $1/T_e$ (i.e., 1 d of development gained out of the total time required at the temperature experienced). Eggs hatched into yolk-sac larvae when the cumulative proportion of egg development summed to 1.0. Eggs were assumed to die at temperatures below 11°C and above 27°C (Ryder 1887; Leim 1924). We used a background mortality rate of 30% per day for eggs (Savoy and Crecco 1988). An increased egg stage duration in cooler periods therefore equated to higher total background mortality and a lower probability of recruitment than during warmer periods.

Fish model: yolk-sac larval development and survival.— Of particular concern for our model was to incorporate factors that influence yolk-sac larval development rate, background daily mortality rates typically experienced, and any other factors that induce mortality. However, little information is available on yolk-sac larvae due to sampling difficulties (Marcy 2004). Development time ranges between 3.5 and 7.0 d and is influenced by temperature (Ryder 1887; Leim 1924; Howly 1985; Wiggins et al. 1985; Marcy 2004). Rather than using a fixed duration for the yolk-sac larval stage, which has been assumed in previous models, we assumed that the influence of temperature on yolk-sac larvae was similar to its influence on eggs; thus, we assumed lower and upper lethal temperatures of 11°C and 27°C, respectively. The egg development function provided reasonable estimates for the duration of time spent as yolk-sac larvae (T_y). As with eggs, we assumed that development and yolk-sac absorption were complete when the cumulative proportion of daily development ($1/T_y$) was at least 1.0. We assumed a background mortality rate of 30% per day (Savoy and Crecco 1988).

Fish model: late-larval development and survival.—We modeled three distinct stages of late-larval (i.e., post-yolk-sac) fish that varied with respect to their development and mortality rates (Savoy and Crecco 1988). We chose to differentiate these stages by TL as opposed to age (done in some previous models: e.g., Limburg 1996a; Harris and Hightower 2012) to ensure that total mortality was a reflection of both development (or growth rates) and age. Post-yolk-sac larval stages included (1) first-feeding larvae lacking developed pelvic fins (10–13 mm TL; Wiggins et al. 1985), (2) larvae possessing developed pelvic fins (14–19 mm TL; Lippson and Moran 1974), and (3) advanced larvae approaching metamorphosis, characterized by invagination of the gut (20–24 mm TL; Maxfield 1953). Larval growth was estimated using a bioenergetics model parameterized specifically for larval and juvenile American Shad (Limburg 1996b), which we modified for daily rather than weekly growth estimates:

$$\frac{dW}{dt} = \frac{pk_1 W^{k_2} f(\tau) - k_3 W^{k_4} e^{k_5 t}}{k_6},$$

where W is larval mass, τ is temperature, p is the proportion of maximum consumption rate, and $f(\tau)$ is the effect of temperature on feeding rate. Larval mass was estimated from TL using a relationship between TL and mass (Limburg 1996b). We used the same relationship between TL and mass to convert the new mass from the bioenergetics model to estimate growth in length. In cases of weight loss, we assumed that TL did not change. Starvation mortality was imposed when loss in mass exceeded 10% (Trebitz 1991). Values for all parameters k_i ($i = 1, 2...6$) were obtained from Limburg (1996b), corrected for changes in time step duration.

We estimated the proportion of maximum consumption p for larval American Shad as a function of ZP by using a modified version of a Holling type II functional response (Holling 1966) generalized for riverine species (Limburg 1996b). Estimates of predator (larval shad) consumption (G; g·g^{-1}·week^{-1}) in its original functional form was $G = \frac{W^{b_0} b_1 q}{1 + b_2 q}$, where W is fish mass and q is prey density (mg/m^3), with parameters b_0, b_1, and b_2 taking the respective values of −0.183, 1.661/7 (to convert it from weekly to daily consumption), and 0.00148 (Limburg 1996b). Proportion of maximum consumption was calculated as a ratio of G (calculated for a day- and location-specific prey density) and G_{max} (calculated from maximum observed prey density over all dates and sites: 10,000 individuals/m^3). We then scaled p by 0.25, in accordance with Limburg's (1996b) observation that this scaling provided fits to observed larval shad growth data. Lastly, we assumed that foraging would cease at water temperatures below 9°C (Backman and Ross 1990).

To estimate background natural mortality rates, we used length-specific daily mortality rates from Savoy and Crecco (1988): 20.8% for small larvae, 9.4% for medium larvae, and 5.2% for large larvae. We acknowledge that predation can be a major source of mortality at these early life stages, yet we assumed that the probability of predation was drawn from the same distribution across space and was therefore included in a spatially homogeneous natural mortality parameter. Although we recognize that the probability of predation in nature is patchy in space and time, we do not have the data to support a more complex representation of it.

We imposed additional mortality costs in scenarios in which a negative dam effect was included. Specifically, 100% mortality was imposed on eggs and larvae within 1 km upstream of the dam based on the fact that at these life stages, American Shad reside near the substrate, which is strongly characterized by silt, cold temperatures, and low

oxygen behind dams (Ellis 1942; Baxter 1977). Additional dam-induced mortality rates were reduced linearly with distance from the dam down to no additional mortality at 6 km above the dam (i.e., 20% change per kilometer).

Fish movement (particle-tracking) model.— Little is known about the fine-scale substrate and the fluvial conditions along the course of the Connecticut River that typically affect downstream advection at the different life stages. At one extreme, we might expect the offspring to stay very close to the location at which spawning occurred. For example, after the negatively buoyant, non-adhesive eggs of American Shad have been broadcast into the water column, they sink and often become lodged in the substrate within a few meters (Carlson 1968). However, eggs that do not settle have been shown to drift as far as 6 km downstream (Marcy 1972). Therefore, we used two approaches that represented the extremes in possible movement: (1) a stationary model, in which offspring development occurred in the same place that spawning occurred; and (2) a passive-drift model, which represented the farthest the offspring could travel as massless particles passively drifting at the same speed as current velocity. Below, we describe in more detail the passive-drift model.

We assumed that during the egg and early larval stages (<17 mm TL), movement was passive such that the location of offspring on any given day was dependent on (1) its location the previous day and (2) the current velocity experienced. Specifically, RKM- and time-specific estimates of current velocity (km/d) were used to determine the duration of time spent within a given RKM (d/km). The offspring drifted at the same rate as the current velocity until larvae reached 17 mm TL. This is a size at which swimming ability has been found to greatly improve, possibly due to increased development of fins (Lippson and Moran 1974). We assumed that larvae stayed and foraged at that river location for the duration of development.

Simulations.— We tracked growth and survival of modeled offspring from each potential spawning location (each of the 142 modeled RKMs) and potential spawning date (May 1–August 31) over 20 years (1993–2002 and 2007–2016). Growth and survival were simulated until larvae reached 25 mm TL or until death but never exceeded 60 d. We chose 60 d because this is the maximum time required for successful metamorphosis in a hatchery setting, where the growth rate is often poor (Howly 1985). If individual offspring did not complete transition to the juvenile stage by August 31, the probability of recruitment was recorded as zero. This creates an artificial end date on the window for successful recruitment. The scarcity of historical daily autumn temperature data limited our ability to make predictions beyond this date. Thus, the model does not include the risk of late-spawned offspring not growing into juveniles in time to leave the river before the water temperature falls too low.

We used the term "annual potential recruitment" to refer to the summed probability of recruitment from all modeled spawning dates in a given year. We calculated this for the entire modeled river reach, summing over all RKMs over all dates for each year; we also calculated location-specific potential recruitment, an index of recruitment potential in each individual RKM, by summing over all modeled spawning dates in a given year for each RKM separately.

Analysis.— We chose the two 10-year time periods (1993–2002 and 2007–2016) based on availability of data and an attempt to represent early and more recent environmental conditions, with the intent of comparing between decades. We found, however, that river flow and water temperature during any given period in spring and summer were quite variable across years. Seasonal periods with consistently low flow, consistently high flow, or highly variable flow occurred with fairly equal frequency between the early years (1993–2002) and the more recent years (2007–2016). Temperature showed only subtle, specific trends between the decades. In April, the later years had more instances of extremely high temperatures than were seen in the earlier years. During May, the early years had more instances of extremely low temperatures than were seen in recent years. Overall, though, interannual variability within a decade was large in comparison to differences between decades. Thus, we used the entire set of variability represented in the 20 years of data to test hypotheses on the effects of environmental conditions on recruitment.

We divided the total modeled time period (April–August) into four seasons in relation to the timing of American Shad spawning and early development in the Connecticut River: very early (April), early (May), middle (June), and late (July–August). We included dates earlier than the typical spawning season (1) to understand what drives limits to the season and (2) to allow for potential changes in weather patterns that could influence the timing of successful larvae. We characterized temperature and river velocity for each season within each year as being above average, below average, or neither (either approximately average or too variable to characterize as above or below average). We characterized as low or high temperature or low or high flow those season × year combinations that had temperatures or flow consistently below or above the mean. With this method, we took advantage of the variability in environmental conditions among years to create subsets of data for comparing season-specific effects of environmental characteristics on larval American Shad survival. The characterizations of specific years and seasons are given in Supplementary File S1.

We were interested in understanding how temperature and flow affect the success of larval American Shad across seasons and across locations in the river. We used classification and regression tree (CART) analysis to explore variables that were most responsible for heterogeneity in annual potential recruitment. The variables considered included RKM (continuous scale) as well as temperature (categorical) and flow (categorical) during early (May), middle (June), and late (July–August) time periods; only low and high classifications were used for these analyses. Variable importance—a value representing the relative importance of a variable in terms of explaining heterogeneity among annual potential recruitment in both primary and surrogate splits—was determined from a fully parameterized tree. The most parsimonious tree was then determined using a modified 1-SE rule approach (Breiman et al. 1984). Specifically, we used a forward selection approach in which additional splits were not accepted if the reduction in relative error (±1 SE) overlapped with that of a tree with fewer splits; tenfold cross-validation was used to determine SE. Separate CART analyses were performed on each of the four scenarios representing presence or absence of dams and movement. The RPART package (Therneau and Atkinson 2018) was used to conduct CART analyses in R version 3.5.1 (R Core Team 2018).

Finally, although our use of this model was not intended to be predictive of American Shad recruitment in the Connecticut River, we compared a spatial subset of our results with an empirically derived index of juvenile recruitment. Note that our model estimates the potential annual recruitment under the condition that spawners use all sites along the length of the modeled reach and spawn on all days of a 5-month period, with spawning uniformly distributed across sites and days. We intentionally removed spawning time and site choice from the model. The Connecticut Department of Energy and Environmental Protection annually samples Connecticut River sites from below the Holyoke Dam (i.e., below our modeled reach) downstream to Essex, Connecticut, from July to October to produce a juvenile abundance index (JAI), calculated as the geometric mean of CPUE from their samples. We tested whether the JAI (USFWS 2017) was correlated with our modeled annual recruitment potential from the downstream end (RKM 138–153) of our modeled reach.

RESULTS

For each year, we created spatiotemporal visualizations of temperature, discharge, prey density, and the resulting modeled recruitment for offspring spawned at any combination of date and site for each model scenario (all results are given in Supplementary Files S2, S3, and S4 available

in the online version of this article; an example of a "typical" year [1994] is depicted in Figure 2). A typical year has April (day of year = 91–120) characterized by high and variable discharge with low temperatures; as the season progresses, temperature increases and discharge decreases and becomes less variable (Figure 2). These "typical" environmental patterns result in recruitment success increasing with spawning date throughout the summer, with periods of lower recruitment at downstream sites during the hottest part of summer (day of year ~170–210 in Figure 2, middle right panel). Because in a typical year discharge and temperature have a strong negative correlation in late spring through mid-summer (Figure 3, top panel), high temperature and low discharge are confounded as possible drivers of strong recruitment. We observed several years, however, that had different environmental patterns, with low discharge and moderate temperatures occurring together early in the season (2012; Figure 3, middle panel) or high discharge and high temperatures occurring late in the season (2013; Figure 3, bottom panel). Results of these simulations suggested that regardless of the temporal patterns in discharge, the high recruitment associated with late-summer spawning dates was driven mostly by high temperatures, although the very highest recruitment still occurred at combinations of low discharge and high temperature (Figure 3).

Choice of model scenario (stationary or passive-drift larvae; and dams or no dams) had predictable effects. When dams were present, but offspring were stationary (scenario 3), the area directly above the dams resulted in poor recruitment due to the habitat being inappropriate for eggs (Figure 2, lower right panel). When offspring exhibited passive movement (with the flow of the river), they traveled far downstream. When larvae moved downstream but their movement was not limited by dams (scenario 2), it tended to reduce the spatial differences in expected recruitment relative to spawning sites (Figure 2, compare middle right panel to lower left panel). If dams were present (scenario 4), eggs and larvae frequently ended their movement at the dams, suffering high mortality, with little variation in recruitment among spawning locations, dates, or years. Thus, below, we address the results from only the first three model scenarios.

Environmental Correlates of Recruitment

Each model scenario produced a different set of environmental correlates of annual potential recruitment (i.e., the relative recruitment that resulted from adults spawning in all possible sites on all possible days).

Scenario 1: no larval drift, no dams.— Under model scenario 1, location within the river and June temperature contributed the greatest amount of explanatory importance in the CART model of annual potential recruitment (Table 2). The highest mean annual potential recruitment was associated with warmer-than-average June
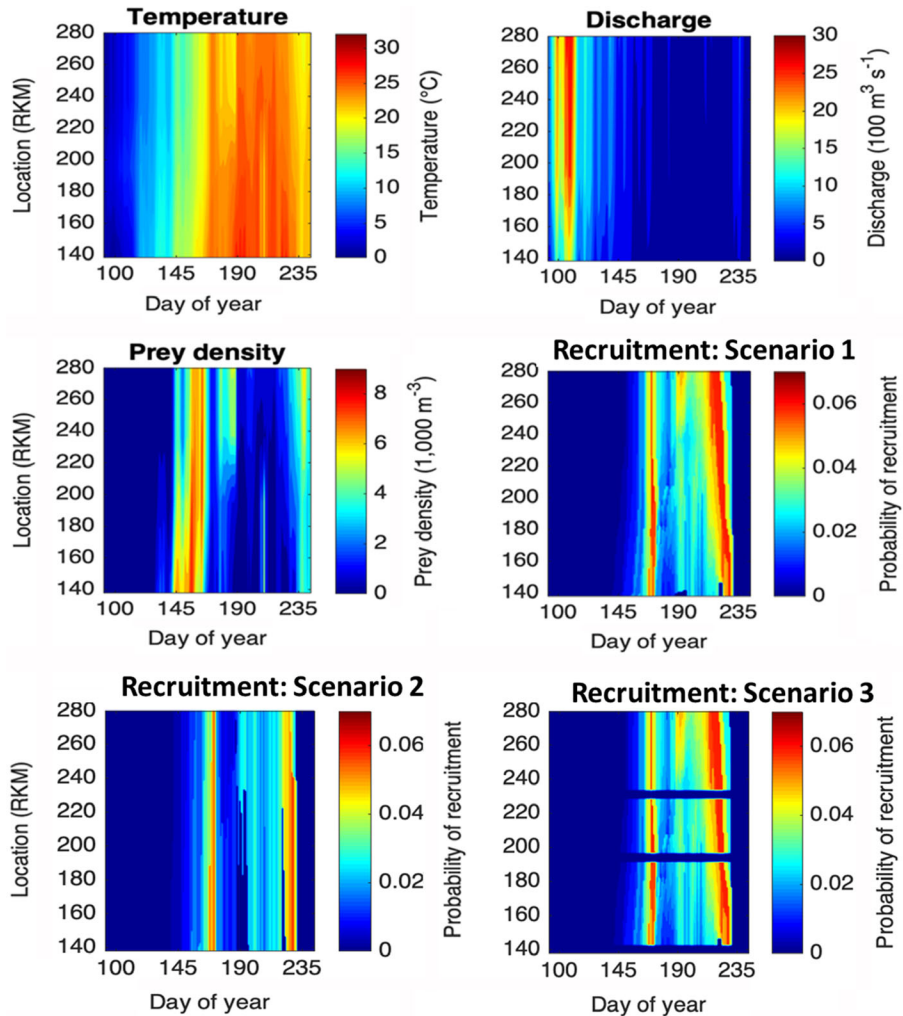
FIGURE 2. Spatiotemporal visualizations of temperature (°C; upper left), discharge (100 m³/s; upper right), zooplankton density (1,000 m⁻³; middle left), and resulting modeled recruitment for eggs spawned at each combination of day of year (*x*-axis) and river kilometer (*y*-axis). This example represents modeled potential recruitment for 1994 with model scenario 1 (middle right), in which offspring remain at the spawning site (stationary) and there are no effects of dams; scenario 2 (lower left), in which offspring move with the flow of the river (maximum drift) and there are no effects of dams; and scenario 3 (lower right), with stationary offspring and effects of dams included. Results from scenario 4 (maxumum drift, effects of dams included) are not shown because modeled potential recruitment was at or near zero during every year.

temperatures (Figure 4); in these years, spawning in June yielded positive recruitment. In years characterized by cool June temperatures, recruitment either was poor over the entire year or was positive only from later spawnings. Much of the difference in mean recruitment potential between years with warm and cool Junes was due to recruitment potential from spawning that occurred in the upstream half of the modeled reach (Figure 5, left panel; Figure 6, top and middle panels).

Scenario 2: passive drift, no dams.— For model scenario 2, in which eggs and early larvae drifted passively with the current, the effect of spawning location was greatly reduced in comparison with model scenario 1 (Table 2). In general, potential recruitment was much more homogeneous across

spawning locations in scenario 2 than in scenario 1 (Figure 6, compare the middle panel to the bottom panel), and scenario 2 had less variation among years in location-specific potential recruitment. The most important variables for explaining differences in annual recruitment potential among years in scenario 2 were May discharge, May temperatures, and July–August temperatures (Table 2); however, the range of values of mean annual recruitment at the terminal nodes of the regression tree was small and not necessarily ecologically meaningful.

Scenario 3: no larval drift, dams present.— Variation in annual location-specific potential recruitment in model scenario 3 was mostly due to spawning location (Table 2); when eggs were spawned in the pool upstream of a dam,
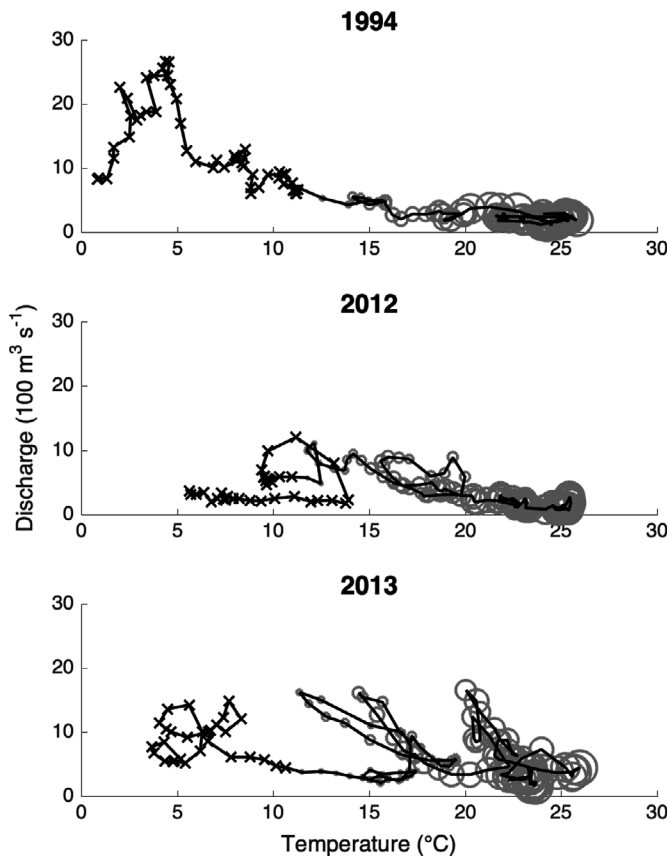
FIGURE 3. Combinations of discharge and temperature that occurred in a specific reach of the river (river kilometer [RKM] 228) between April 1 and August 31. The black ✕-symbols indicate spawning dates with no successful recruitment. Gray circles indicate spawning dates resulting in positive recruitment, with recruitment strength represented by circle area. The black line connecting points indicates sequential dates, beginning on April 1 at the far left of the figure. The year 1994 (top panel) was "typical," with high and variable discharge and cold temperatures early in the season and low discharge with high temperatures late in the season. High recruitment was limited to spawning dates late in the season. The year 2012 (middle panel) represents spawning during low discharge; when such spawning also occurs at low temperatures, it does not result in high recruitment. The year 2013 (bottom panel) represents spawning at moderately high discharge; when such spawning also is associated with high temperatures, it can result in high recruitment, although not as high as the combination of high temperatures and low discharge.

survival was low. July–August temperature also was an important explanatory variable (Table 2). When we consider spawning locations upstream of the pool at the upstream-most dam, high July–August temperatures resulted in high annual potential recruitment. Warm late-season temperatures allowed good recruitment from late, far-upstream spawners (Figure 5, right panel).

Comparison with Empirical Data

Empirical estimates of juvenile abundance were available only from the portion of the river downstream

TABLE 2. Importance (%) of each variable in explaining variation in annual potential recruitment of American Shad from classification and regression tree analysis for model scenarios 1, 2, and 3. Location (river kilometers), temperature, and flow refer to the conditions at the spawning site.

Variable	Time period	Scenario 1	Scenario 2	Scenario 3
Location		68	2	70
Temperature	Early	9	36	1
	Middle	14	<1	2
	Late	5	38	15
Flow	Early	4	20	5
	Middle	<1	5	5
	Late	<1	<1	1

from and not overlapping with our modeled reach. Using the results from modeled spawning occurring closest to the juvenile collection sites (i.e., using model results from the furthest-downstream 15 km of the modeled reach), modeled annual potential recruitment was positively correlated with the empirically based JAI for 19 of the 20 modeled years (scenario 1: Pearson $r = 0.57$, $P = 0.011$; scenario 2: Pearson $r = 0.52$, $P = 0.22$; scenario 3: Pearson $r = 0.58$, $P = 0.009$; Figure 7). The final modeled year, 2016, was an outlier, with extremely high juvenile abundance and fairly low modeled potential recruitment.
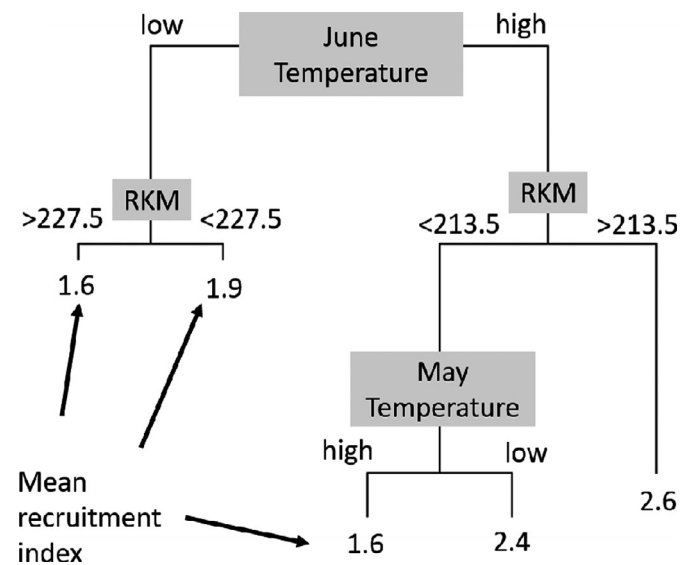

FIGURE 4. Nodes and branches of the classification and regression tree describing the effect of environmental variables on modeled annual potential recruitment of American Shad for scenario 1 (RKM = river kilometer).
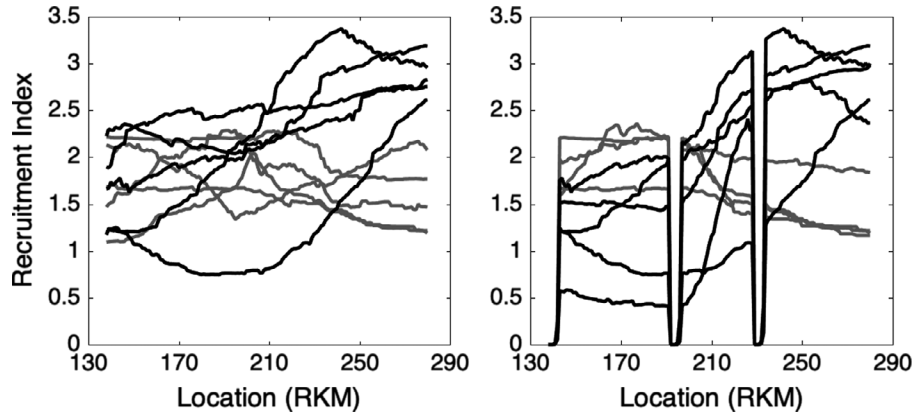
FIGURE 5. Annual potential recruitment from American Shad spawning at each river kilometer (RKM) along the river for scenario 1 (left panel; black lines = years with warmer-than-average June temperatures; gray lines = years with cooler-than-average June temperatures) and scenario 3 (right panel; black lines = years with warmer-than-average July–August temperatures; gray lines = years with cooler-than-average July–August temperatures).
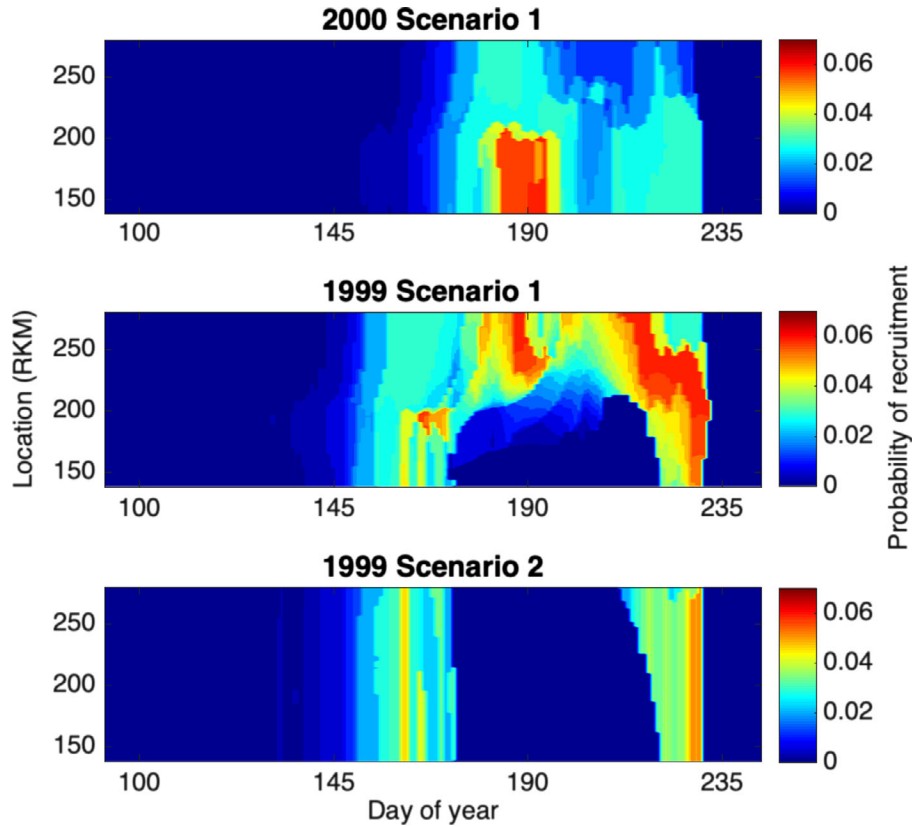

FIGURE 6. Spatiotemporal visualizations of modeled recruitment for American Shad eggs spawned at each combination of day of year (*x*-axis) and river kilometer (RKM; *y*-axis) for model scenario 1 and cool June temperatures (2000; top panel); model scenario 1 and warm June temperatures (1999; middle panel); and model scenario 2, warm July–August temperatures, and low May flow (1999; bottom panel).

DISCUSSION

Our modeling of larval shad recruitment by using multiple decades of empirical temperature and discharge data revealed interestingly complex but highly variable patterns of potential recruitment across locations, seasons, and years. A lack of understanding of this variability hampers current fisheries management and impedes future studies of the effects of climate change. Rather than focusing on
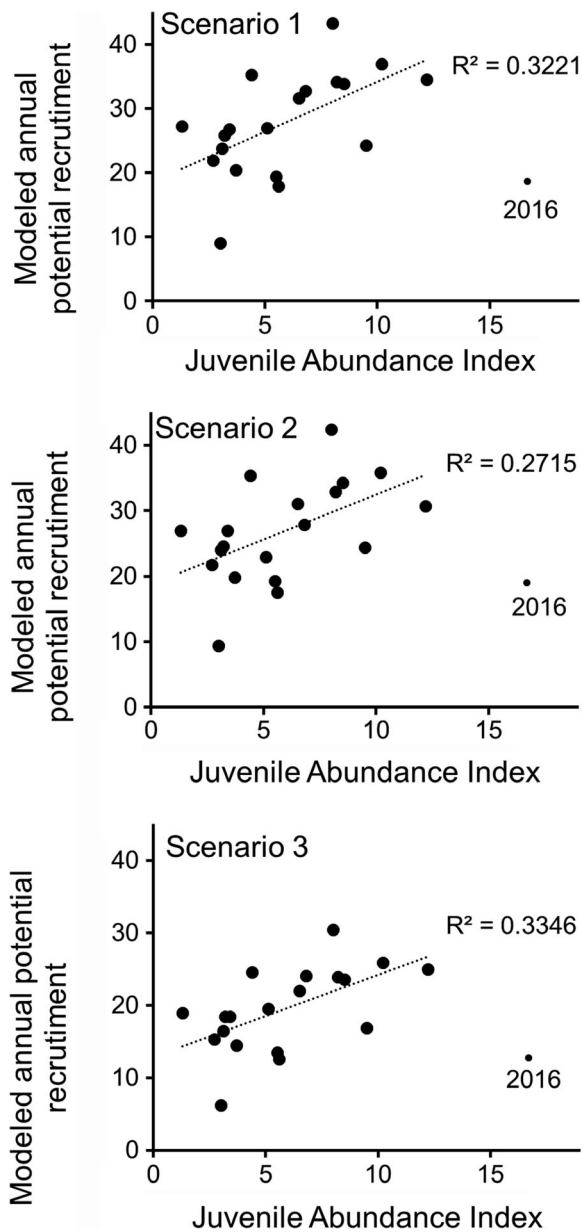
FIGURE 7. Modeled annual potential recruitment from American Shad spawning occurring in the downstream end of the modeled reach (river kilometers 138–153) plotted against the juvenile abundance index estimated from sampling juveniles in the Connecticut River at sites extending from immediately below the modeled reach downstream almost to the mouth (USFWS 2017). Scenario 1 depicts stationary larvae in the absence of dams; scenario 2 depicts maximum passive drift of larvae in the absence of dams; and scenario 3 depicts stationary larvae in the presence of dams. The R^2 values are based on the first 19 years of data (1993–2002 and 2007–2015). One outlier (2016) is plotted separately.

known spawning habitats and peak spawning dates, our model simulates American Shad spawning across all days of a 5-month period and across the entire longitude of a 142-km reach of the river. In this way, we can assess the potential of the river to produce American Shad juveniles

separately from the actual behavior of the spawners, even as environmental conditions vary from year to year and possibly shift with climate change. Quantitative insights that explain patterns of spatial and temporal heterogeneity and the drivers of those patterns can be extremely useful, especially for times, places, and correlates of very good and very poor recruitment. High variability in spatial and temporal patterns of recruitment often is viewed as undesirable, and reduction in variation is often a goal. However, in a heterogeneous system pockets or hotspots of high recruitment can be embedded in patterns of high variation and can carry a strong year-class. In this case, heterogeneity is a positive attribute that is desirable to maintain.

In our modeled systems, spatial (upstream to downstream within the river and near dams) and temporal (within and across years) patterns in temperature, discharge, prey, and recruitment provided useful insights about heterogeneity. As one example, our modeling scenario that allowed the movement of eggs and larvae with the current reduced the variability in American Shad recruitment, but this reduction occurred by homogenizing experiences across spawning locations, thus eliminating the sometimes-rare conditions for the highest recruitment. As a second example, higher temperatures in the late period (July) were associated with high recruitment in the upper river, but the temperatures were too high for larval shad during that same period in the lower river. Thus, documenting where and when the high and low variability occurs and the predictability and consequences of variability is critically important. Several current frameworks seek to understand complex patterns of spatial heterogeneity by quantifying spatial mosaics of conditions within a system (Hitchman et al. 2017) or linking individual systems into an integrated portfolio (Schindler et al. 2010; DuFour et al. 2015). Viewed in this way, variable riverine fish recruitment can be examined as a temporally flickering spatial mosaic (Brennan et al. 2019). This approach has great potential to guide fish recruitment research across spatially complex, temporally variable large-river systems.

Complexity exists in the direct and indirect effects of water temperature on larval American Shad. Temperature affects fish survival at extreme temperatures; influences size, growth, and the rate of development at a wide range of temperatures; and can alter the size and growth of young fish through the bioenergetic combination of food and temperature (Eaton and Scheller 1996; Beitinger et al. 2000). River temperatures did not affect larval shad recruitment equally across the early (May), middle (June), and late (July) time periods. Without dams, high temperatures in the middle time period (June) yielded the highest recruitment upstream and cool temperatures during this period yielded low recruitment everywhere (upstream and

downstream). Adding to this temporal complexity, the temperatures that affected larval shad recruitment spanned multiple time periods (recent and previous years). For example, without dams or movement, high temperatures during June yielded moderately high recruitment downstream, especially when early (May) temperatures were low. Furthermore, the impact of temperature on shad recruitment interacted with other variables (e.g., dams, river position, and discharge). With dams, the highest recruitment occurred at upstream sites when July temperatures were above average in low-flow years, likely because reduced flow made the lower river too warm for larval American Shad. Thus, temperature influenced growth and survival through direct effects, through interactive effects with other variables, and by influencing the length of time for which shad were in the vulnerable larval stage. Elsewhere, variation in thermal regime has been explored (Caissie 2006). Given the surprising and diverse variation within and across years in the temperature patterns explored in this study, an examination of detailed, real data records over a multi-year time period is important for examining past, present, and future climate change effects.

Discharge affected larval recruitment in our model, as has been reported in previous studies, although its effect was not as strong as that of temperature. Temperature within a period is correlated with discharge, such that the lack of direct effects of discharge on survival and growth in our results was possibly due to predictable correlations between discharge and temperature. Discharge also was indirectly important in our model results by moving eggs and larvae to new places. When eggs and larvae were simulated as drifting with the current, they often were transported to the pools above dams. Previous empirical research has shown that high discharge exerts a negative effect on larvae through advection to unfavorable locations (Savoy and Crecco 1988). The silty substrates in pools behind dams are not conducive to the survival of eggs and young larvae, although older larvae may find the potentially high zooplankton density advantageous for growth.

Upstream portions of the river may experience appropriate spawning conditions (i.e., temperature and discharge patterns that result in offspring experiencing the conditions leading to growth and survival, either at that site or the site to which they are transported) later in the season than lower portions of the river. Studies report optimal current velocities for spawning as about 25–75 km/d (reviewed by Beasley and Hightower 2000). In our data for the Connecticut River, the 20-year mean current velocities were above this range during April, within this range during May and June, and at the lower limit of this range during July–August in the lower portion of the modeled reach, whereas mean current velocities in the

upper portion of the modeled reach did not fall within this range until July–August. Similarly, spawning temperatures have been reported most commonly as between about 11°C and 26°C (reviewed by Beasley and Hightower 2000). The 20-year mean temperatures in our data for the Connecticut River were in this range during May and June and at the upper end of the range during July–August in the lower portion of the modeled reach; mean temperatures in the upper portion of the modeled reach were slightly delayed in comparison with the lower portion. Our models showed that in a subset of years, conditions were right for a pulse of potential recruitment resulting from late-season, far-upstream spawning. Recent success in upstream passage of potential spawners at the Vernon Dam (Vermont; USFWS 2017), situated at the upstream end of our modeled reach, has coincided with high production of juveniles above the dam (Normandeau Associates 2015). These upstream spawning grounds may become increasingly important as river conditions change in the future. Our model showed that in years when mid- to late summer was warmer than usual, as we might expect to happen in the future, spawning that occurred upstream made major contributions to total potential recruitment.

The strong dependence of modeled potential recruitment on environmental factors that are likely to shift with climate change (e.g., temporal patterns in temperature and flow rate; Karl et al. 2009; Berton et al. 2016) has implications for American Shad beyond the populations in the Connecticut River. The native spawning range of this species extends from Florida into Canada (Greene et al. 2009). Spawning phenology differs greatly across this latitudinal range, with spawning commencing as early as December in Florida rivers and as late as August in northern rivers (Greene et al. 2009). In addition, latitudinal patterns in life history traits, such as degree of iteroparity and mass-specific fecundity, are believed to have evolved in response to variability in environmental differences in the spawning rivers (Leggett and Carscadden 1978; Hasselman et al. 2013). Because of this, we expect that when applied to a river model representative of a southern river, our individual-based model of larval American Shad growth and survival would yield very different baseline results as well as different responses to extreme patterns in temperature and flow consistent with climate change. The southeastern U.S. coast has seen a mean increase in winter temperatures of 1.5°C from 1970 to 2008 and considerable increases in the number of days above 32°C annually (Karl et al. 2009). During the same period, there was a 9–29% reduction in winter/spring precipitation in this region (Karl et al. 2009). Given the historical cultural and ecological importance of American Shad along the eastern coast of North America, understanding the complex interactions among latitude,

phenology, river conditions, and climate change is an important area in need of modeling.

Although we refer to our modeled recruitment as "potential recruitment," by removing spawner choice of spawning sites and dates and removing larval habitat choice we in fact have removed the potential of the spawning population to spawn in greater abundance within certain areas on certain dates and to receive either the benefits (from choice of valuable habitat) or costs (exceeding carrying capacity; Leggett 1977) of having many offspring in the same place, which may be above or below average in quality and may exceed carrying capacity in some cases. In structuring our model to assess the total potential of the river and the season to produce recruits, even on days and in locations where spawning may not typically occur, we were able to better test for the combination of variables that drives recruitment success. The fact that potential recruitment in 19 of our 20 modeled years was strongly correlated with the JAI measured downstream of our modeled reach (USFWS 2017) suggests that our model captured the main elements driving recruitment. To be able to apply these results to predictions of how climate change effects may lead to shifts in timing and location of the most successful spawning, we need detailed models of climate change, downscaled to local landscapes, including how anticipated shifts in air temperature and precipitation patterns translate into water temperature and discharge.

Climate change is one of the most pressing environmental issues that fisheries professionals will face in upcoming decades (Barange et al. 2018). At present, no single best approach exists to understand, predict, and mitigate the adverse effects of this multi-faceted phenomenon relative to fish populations. The specifics of how climate change will alter aquatic environments will differ from place to place, across years, and with fish life stage and species. However, two uncontested predictions of climate change are increasing and increasingly variable air temperatures intertwined with changes in the magnitude, timing, and form of precipitation. These patterns will translate to shifts in water temperature and river discharge, which has particularly important implications for anadromous fish (Lassalle and Rochard 2009; Ward et al. 2015). As such, our approach, which allows researchers and managers to ask "What if…?" questions about the fate of cohorts as they encounter novel spatial and temporal patterns of food, temperature, and discharge, will be a useful addition to the variety of approaches necessary to make progress in understanding the impacts of climate change.

ORCID

Elizabeth A. Marschall https://orcid.org/0000-0002-8026-4203
David C. Glover https://orcid.org/0000-0001-6532-1815
Martha E. Mather https://orcid.org/0000-0003-3027-0215
Donna L. Parrish https://orcid.org/0000-0001-9693-6329

REFERENCES

Aldvén, D., R. Hedger, F. Okland, P. Rivinoja, and J. Hojesjo. 2015. Migration speed, routes, and mortality rates of anadromous Brown Trout *Salmo trutta* during outward migration through a complex coastal habitat. Marine Ecology Progress Series 541:151–163.

Auld, A. H., and J. R. Schubel. 1978. Effects of suspended sediment on fish eggs and larvae: a laboratory assessment. Estuarine and Coastal Marine Science 6:153–164.

Backman, T. W., and R. M. Ross. 1990. Comparison of three techniques for the capture and transport of impounded subyearling American Shad. Progressive Fish-Culturist 52:246–252.

Barange, M., T. Bahri, M. C. Beveridge, K. L. Cochrane, S. Funge-Smith, and F. Poulain. 2018. Impacts of climate change on fisheries and aquaculture: synthesis of current knowledge, adaptation and mitigation options. Food and Agriculture Organization of the United Nations, Rome.

Bauer, S., B. A. Nolet, J. Giske, J. W. Chapman, S. Åkesson, A. Hedenström, and J. M. Fryxell. 2011. Cues and decision rules in animal migration. Pages 68–87 *in* E. J. Milner-Gulland, J. M. Fryxell, and A. R. Sinclair, editors. Animal migration: a synthesis. Oxford University Press, New York.

Baxter, R. M. 1977. Environmental effects of dams and impoundments. Annual Review of Ecology and Systematics 8:255–283.

Beasley, C. A., and J. E. Hightower. 2000. Effects of a low-head dam on the distribution and characteristics of spawning habitat used by Striped Bass and American Shad. Transactions of the American Fisheries Society 129:1316–1330.

Beitinger, T. L., W. A. Bennett, and R. W. McCauley. 2000. Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. Environmental Biology of Fishes 58:237–275.

Berton, R., C. T. Driscoll, and D. G. Chandler. 2016. Changing climate increases discharge and attenuates its seasonal distribution in the northeastern United States. Journal of Hydrology: Regional Studies 5:164–178.

Breiman, L., J. H. Friedman, R. A. Olshen, and C. G. Stone. 1984. Classification and regression trees. Wadsworth International Group, Belmont, California.

Brennan, S. R., D. E. Schindler, T. J. Cline, T. E. Walsworth, G. Buck, and D. P. Fernandez. 2019. Shifting habitat mosaics and fish production across river basins. Science 364:783–786.

Caissie, D. 2006. The thermal regime of rivers: a review. Freshwater Biology 51:1389–1406.

Carlson, F. T. 1968. Suitability of the Susquehanna River for restoration of shad. U.S. Department of Interior, Washington, D.C.

Castro-Santos, T., and B. H. Letcher. 2010. Modeling migratory bioenergetics of Connecticut River American Shad (*Alosa sapidissima*): implications for the conservation of an iteroparous anadromous fish. Canadian Journal of Fisheries and Aquatic Sciences 67:806–830.

Connecticut River Atlantic Salmon Commission. 2017. Connecticut River American Shad management plan. Connecticut River Atlantic Salmon Commission, Sunderland, Massachusetts.

Crecco, V. A., and M. M. Blake. 1983. Feeding ecology of coexisting larvae of American Shad and Blueback Herring in the Connecticut River. Transactions of the American Fisheries Society 112:498–507.

Crecco, V. A., and T. F. Savoy. 1984. Effects of fluctuations in hydrographic conditions on year-class strength of American Shad (*Alosa sapidissima*) in the Connecticut River. Canadian Journal of Fisheries and Aquatic Sciences 43:457–463.

Crecco, V., and T. Savoy. 1985. Effects of biotic and abiotic factors on growth and relative survival of young American Shad in the Connecticut River. Canadian Journal of Fisheries and Aquatic Sciences 42:1640–1648.

Crecco, V. A., T. F. Savoy, and L. Gunn. 1983. Daily mortality rates of larval and juvenile American Shad (*Alosa sapidissima*) in the Connecticut River with changes in year-class strength. Canadian Journal of Fisheries and Aquatic Sciences 40:1719–1728.

Crecco, V. A., T. F. Savoy, and W. Whitworth. 1986. Effects of density-dependent and climatic factors on American Shad, *Alosa sapidissima*, recruitment: a predictive approach. Canadian Journal of Fisheries and Aquatic Sciences 43:457–463.

Crozier, L. G., A. P. Hendry, P. W. Lawson, T. P. Quinn, N. J. Mantua, J. Battin, R. G. Shaw, and R. B. Huey. 2008. Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. Evolutionary Applications 1:252–270.

Crozier, L. G., and J. A. Hutchings. 2014. Plastic and evolutionary responses to climate change in fish. Evolutionary Applications 7:68–87.

DuFour, M. R., C. J. May, E. F. Roseman, S. A. Ludsin, C. S. Vandergoot, J. J. Pritt, M. E. Fraker, J. J. Davis, J. T. Tyson, J. G. Miner, E. A. Marschall, and C. M. Mayer. 2015. Portfolio theory as a management tool to guide conservation and restoration of multi-stock fish populations. Ecosphere [online serial] 6:296.

Eaton, J. G., and R. M. Scheller. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. Limnology and Oceanography 41:1109–1115.

Ellis, M. M. 1942. Fresh-water impoundments. Transactions of the American Fisheries Society 71:80–93.

Gephard, S., and J. McMenemy. 2004. An overview of the program to restore Atlantic Salmon and other diadromous fishes to the Connecticut River, with notes on the current status of these species in the river. Pages 287–317 *in* P. M. Jacobson, D. A. Dixon, W. C. Leggett, B. C. Marcy, and R. R. Massengill, editors. The Connecticut River ecological study (1965–1973) revisited: ecology of the lower Connecticut River, 1973–2003. American Fisheries Society, Monograph 9, Bethesda, Maryland.

Greene, K. E., J. L. Zimmerman, R. W. Laney, and J. C. Thomas-Blate. 2009. Atlantic coast diadromous fish habitat: a review of utilization, threats, recommendations for conservation, and research needs. Atlantic States Marine Fisheries Commission, Habitat Management Series 9, Washington, D.C.

Harris, J. E., and J. E. Hightower. 2012. Demographic population model for American Shad: will access to additional habitat upstream of dams increase population sizes? Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 4:262–283.

Hasselman, D. J., D. Ricard, and P. Bentzen. 2013. Genetic diversity and differentiation in a wide ranging anadromous fish, American Shad (*Alosa sapidissima*), is correlated with latitude. Molecular Ecology 22:1558–1573.

Hightower, J. E., J. E. Harris, J. K. Raabe, P. Brownell, and C. A. Drew. 2012. A Bayesian spawning habitat suitability model for American Shad in southeastern United States rivers. Journal of Fish and Wildlife Management 3:184–198.

Hinrichsen, R. A., D. J. Hasselman, C. C. Ebbesmeyer, and B. A. Shields. 2013. The role of impoundments, temperature, and discharge on colonization of the Columbia River basin, USA, by nonindigenous American Shad. Transactions of the American Fisheries Society 142:887–900.

Hitchman, S. M., M. E. Mather, J. M. Smith, and J. Fencl. 2017. Identifying keystone habitats with a mosaic approach can improve biodiversity conservation in disturbed ecosystems. Global Change Biology 24:308–321.

Holling, C. S. 1966. The functional response of predators to prey density and its role in mimicry and population regulation. Memoirs of the Entomological Society of Canada 1966:5–60.

Howly, R. G. 1985. Intensive culture of juvenile American Shad. Progressive Fish-Culturist 47:203–212.

Karl, T. R., J. M. Melillo, T. C. Peterson, and S. J. Hassol. 2009. Global climate change impacts in the United States. Cambridge University Press, New York.

Lassalle, G., and E. Rochard. 2009. Impact of twenty-first century climate change on diadromous fish spread over Europe, North Africa and the Middle East. Global Change Biology 15:1072–1089.

Leggett, W. C. 1977. Density dependence, density independence, and recruitment in the American Shad (*Alosa sapidissima*) population of the Connecticut River. Pages 3–17 *in* W. Van Winkle, editor. Proceedings of the conference on assessing the effects of power-plant induced mortality on fish populations. Pergamon Press, New York.

Leggett, W. C., and J. E. Carscadden. 1978. Latitudinal variation in reproductive characteristics of American Shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. Journal of the Fisheries Research Board of Canada 35:1469–1478.

Leggett, W., and R. Whitney. 1972. Water temperature and the migrations of American Shad. U.S. Fish and Wildlife Service Fishery Bulletin 70:659–670.

Leim, A. H. 1924. The life history of the shad (*Alosa sapidissima* (Wilson)) with special reference to the factors limiting its abundance. Contributions to Canadian Biology, New Series II:161–284.

Limburg, K. E. 1994. Ecological constraints on growth and migration of juvenile American Shad (*Alosa sapidissima* Wilson) in the Hudson River estuary, New York. Doctoral dissertation. Cornell University, Ithaca, New York.

Limburg, K. E. 1996a. Growth and migration of 0-year American Shad (*Alosa sapidissima*) in the Hudson River estuary: otolith

microstructural analysis. Canadian Journal of Fisheries and Aquatic Sciences 53:220–238.

Limburg, K. E. 1996b. Modelling the ecological constraints on growth and movement of juvenile American Shad (*Alosa sapidissima*) in the Hudson River estuary. Estuaries 19:794–813.

Lippson, A. J., and R. L. Moran. 1974. Manual for the identification of early developmental stages of fishes of the Potomac River estuary. Maryland Department of Natural Resources, Power Plant Siting Program, Report PPSP-MP-13, Solomons.

Marcy, B. C. Jr. 1972. Spawning of the American Shad, *Alosa sapidissima*, in the lower Connecticut River. Chesapeake Science 13:116–119.

Marcy, B. C. Jr 2004. Early life history studies of American Shad in the lower Connecticut River and the effects of the Connecticut Yankee plant. Pages 155–180 in P. M. Jacobson, D. A. Dixon, W. C. Leggett, B. C. Marcy, and R. R. Massengill, editors. The Connecticut River ecological study (1965–1973) revisited: ecology of the lower Connecticut River 1973–2003. American Fisheries Society, Monograph 9, Bethesda, Maryland.

Marschall, E. A., M. E. Mather, D. L. Parrish, G. W. Allison, and J. R. McMenemy. 2011. Migration delays caused by anthropogenic barriers: modeling dams, temperature, and success of migrating salmon smolts. Ecological Applications 21:3014–3031.

Maxfield, G. H. 1953. The food habits of hatchery-produced pond-cultured shad *Alosa sapidissima*, reared to a length of two inches. Chesapeake Biological Laboratory, Publication Number 98, Solomons, Maryland.

McNamara, J. M., Z. Barta, M. Klaassen, and S. Bauer. 2011. Cues and the optimal timing of activities under environmental changes. Ecology Letters 14:1183–1190.

Nack, C. C., D. P. Swaney, and K. E. Limburg. 2019. Historical and projected changes in spawning phenologies of American Shad and Striped Bass in the Hudson River estuary. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 11:271–284.

Normandeau Associates. 2015. Abundance of juvenile American Shad in lower Vernon pool during 2014. Prepared for Entergy Nuclear Vermont Yankee, Vermont Yankee/Connecticut River System, Analytical Bulletin 95, Bedford, New Hampshire.

Northcote, T. G. 1984. Mechanisms of fish migration in rivers. Pages 487–508 in J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill, editors. Mechanisms of migration in fishes. Springer, Boston.

O'Donnell, M. J., and B. H. Letcher. 2008. Size and age distributions of juvenile Connecticut River American Shad above Hadley Falls: influence on outmigration representation and timing. River Research and Applications 24:929–940.

Peer, A. C., and T. J. Miller. 2014. Climate change, migration phenology, and fisheries management interact with unanticipated consequences. North American Journal of Fisheries Management 34:94–110.

Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American Shad and Sockeye Salmon. Ecology 77:1151–1162.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rice, H. J. 1878. Notes upon the development of the shad, *Alosa sapidissima*. Report of the Commissioners of Fisheries of Maryland, Annapolis.

Ryder, J. A. 1887. On the development of osseous fishes, including marine and freshwater forms. U.S. Government Printing Office, U.S. Commercial Fisheries Report 13 (1885), Washington, D.C.

Savoy, T. F., and V. A. Crecco. 1988. The timing and significance of density-dependent and density-independent mortality of American Shad, *Alosa sapidissima*. U.S. National Marine Fisheries Service Fishery Bulletin 86:467–482.

Savoy, T. F., and V. A. Crecco. 2004. Factors affecting the recent decline of Blueback Herring and American Shad in the Connecticut River. Pages 361–377 in P. M. Jacobson, D. A. Dixon, W. C. Leggett, B. C. Marcy, and R. R. Massengill, editors. The Connecticut River ecological study (1965–1973) revisited: ecology of the lower Connecticut River 1973–2003. American Fisheries Society, Monograph 9, Bethesda, Maryland.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609–613.

Stier, D. J., and J. H. Crance. 1985. Habitat suitability index models and instream flow suitability curves: American Shad. U.S. Fish and Wildlife Service Biological Report 82(10.88).

Therneau, T. M., and E. J. Atkinson. 2018. An introduction to recursive partitioning using the RPART routines. Mayo Foundation, Rochester, Minnesota.

Trebitz, A. S. 1991. Timing of spawning in Largemouth Bass: implications of an individual-based model. Ecological Modelling 59:203–227.

USFWS (U.S. Fish and Wildlife Service). 2017. Connecticut River basin anadromous fish restoration: coordination and technical assistance. USFWS, Federal Aid in Sport Fish Restoration, Project F-100-R-34, Annual Progress Report, Sunderland, Massachusetts.

Walburg, C. H. 1960. Abundance and life history of the shad, St. Johns River, Florida. U.S. Fish and Wildlife Service Fishery Bulletin 60:487–501.

Ward, E. J., J. H. Anderson, T. J. Beechie, G. R. Pess, and M. J. Ford. 2015. Increasing hydrologic variability threatens depleted anadromous fish populations. Global Change Biology 21:2500–2509.

Watson, J. F. 1970. Distribution and population dynamics of American Shad, Alosa sapidissima (Wilson), in the Connecticut River above Holyoke Dam, Massachusetts. Doctoral dissertation. University of Massachusetts, Amherst.

Wiggins, T. A., T. R. Bender Jr., V. A. Mudrak, and J. A. Coll. 1985. The development, feeding, growth, and survival of cultured American Shad larvae through the transition from endogenous to exogenous nutrition. Progressive Fish-Culturist 47:87–93.

Winkler, D. W., C. Jørgensen, C. Both, A. I. Houston, J. M. McNamara, D. J. Levey, J. Partecke, A. Fudickar, A. Kacelnik, D. Roshier, and T. Piersma. 2014. Cues, strategies, and outcomes: how migrating vertebrates track environmental change. Movement Ecology 2:10.

SUPPORTING INFORMATION

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