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Modeling larval American Shad recruitment in a large river

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Running head: American Shad larval recruitment

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 (1 April - 31 August) to understand how spawning date and location drive larval recruitment differentially across years and decades (1993-2002, 2007-2016). For both temperature and flow, inter-annual 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. Greatest potential recruitment occurred in 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 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 upstream of Vernon Dam in the Connecticut River, especially as conditions shift with climate change.

While 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 east coast of the United States, like much of the continent, is predicted to see warm temperatures begin earlier in the spring and precipitation to become patchier, 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. Timing of important anadromous life cycle events, such as upstream migration (Quinn and Adams 1996; Peer and Miller 2012; Hinrichsen et al. 2013), 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), and thus a shift in patterns in these environmental variables may lead to a shift in migration timing, as well as have implications for success at each of these life cycle transitions (McNamara et al. 2011). Despite the fact that timing of appropriate flow and temperatures for migration and spawning differ greatly from year to year within a river, and 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 as to 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 U.S. As part of their anadromous life cycle, adult American Shad in the 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 the river has been described (, e.g., Beasely 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 drives the timing, location, and environmental conditions experienced by the larvae. While a number of research programs have focused on relating production of juveniles not only to stock size, but also to river conditions during the larval and juvenile stage (Crecco and Savoy 1984; Leggett 1977), little is known about how the decision of where and when to spawn affects the ultimate probability of success of larvae and juveniles (but see Limburg 1996a; O'Donnell & 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 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 not historically considered to be relevant.

Year-class strength of American Shad has been shown to be strongly correlated with environmental factors affecting pre-juvenile 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; Savoy and Crecco 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), while 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-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 United States. 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 United States, 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, it is critical that models capable of forecasting the effects of climate change on egg and larval survivorship be developed to understand 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 model 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 five-month period. We have intentionally removed spawning time and site choice from the model. We began by asking, 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 inter-annual 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 ask 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.

<A>Methods

While this study is intended to address questions about the interaction between larval shad 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. The Connecticut River is the largest river in the New England part of the United States, with a watershed area of 29,100 km^2. Its flow is interrupted by a number of dams along the course of the mainstem of the river. Detailed descriptions of the river are numerous, including two examples containing information relevant to this study, Gephard and McMenemy (2004) and Marschall et al. (2011). We modeled a 142-km section of the river, from immediately above the Holyoke Dam (RKM 138; RKM is the distance in km from the mouth of the river 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 Holyoke Dam and Bellows Falls (see map in Figure 1 in Castro-Santos and Letcher 2010).

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-km sections of the river on each day from 1 April to 31 August. Rather than predict where (in which 1-km section) and when (what 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 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 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, or probability of recruitment. 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 vary with respect to the mortality rate experienced. Given that mortality rate decreased with developmental stage, a shorter duration in each stage would lead to higher expected probability of recruitment. Temperature and current velocity experienced by modeled offspring through their development was determined for each river section from a spatially coarse model 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 at each location along the river), a fish model (probability of survival through each early life stage; parameters in Table 1), and a particle-tracking model (links 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 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 were functions 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 were dependent on growth rate, which was modeled with a bioenergetics model (Limburg 1996b). Details are provided in *Fish model: late-larval development and survival* below.

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 outmigration as juveniles (Limburg 1996a; O'Donnell and Letcher 2008), but their movement in relation to flow is not well understood. We believe reality falls somewhere between the two extremes represented in our model scenarios and used these extremes to bound the possible outcomes. In the presence of dams, we assumed 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 (Stier and Crance 1975; Auld and Schubel 1978; 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 (online Supplementary File S1) for three major areas of the reach of the river we were modeling: Holyoke, MA (RKM 137-139); Turners Falls, MA (RKM 195-203); and Vernon, VT (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 (less than seven days), 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 16 July during the first 10 years were missing and had to be interpolated from sites with season-specific correlated temperatures. For the remaining dataset, over 90% of the temperatures came from original data.

We used mean daily river discharge data from the United States Geological Survey (USGS) National Water Information 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 to 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 RKM 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 river-kilometer 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 zero 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 (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 dataset because it is the most comprehensive published set of zooplankton density data with relevance to American Shad larvae for the Connecticut River. We matched historical daily mean water temperatures and discharge to the zooplankton sample dates. The spatial and temporal heterogeneity in zooplankton density (ZP; #/m^3) was then modeled as a function of temperature (τ, °C) and river discharge (D, 1000 m^3/s):

$$\mathrm{ZP} = e^{1.7915t - 0.04966\tau^2 - 0.3306\log(D) + 0.008482\log(D^2) - 6.5986} \qquad \text{adjusted } R^2 = 0.33$$

On dates and locations in which discharge was zero, discharge of 1000 m^3/s (the smallest unit of discharge) was used to estimate zooplankton density.

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; days) to temperature (τ, °C) by incorporating additional values from the literature: $T_e = 5356.84\tau^{-2.379}$ ($R^2 = 0.887$). 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., one day 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. 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). 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. Yet, little information is available on yolk-sac larvae due to sampling difficulties (Marcy 2004). Development time ranges between 3.5 and 7 days 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 is similar to its influence on eggs; thus, we assumed lower and upper lethal temperatures of 11 °C and 27 °C. The egg development function provided reasonable estimates for duration of time spent as yolk-sac larvae (T_y). As with eggs, we assumed that development and yolk-sac absorption was complete when the cumulative proportion of daily development ($1/T_y$) was at least 1. 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 total length, as opposed to age as done in some 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:

$$\frac{dW}{dt} = \frac{pk_1W^{k_2}f(\tau) - k_3W^{k_4}e^{k_5t}}{k_6}$$

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) came from Limburg (1996b), corrected for changes in time step duration.

We estimated larval American shad proportion of maximum consumption p as a function of zooplankton density 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/week) 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 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/m^3). We then scaled p by 0.25, following Limburg's observation that this scaling provided fits to observed larval shad growth data (Limburg 1996b). 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): small larvae = 20.8%, medium larvae = 9.4%, large larvae = 5.2%. We acknowledge that predation can be a major source of mortality at these early life stages, yet assume that probability of predation is drawn from the same distribution across space and is therefore included in a spatially homogenous natural mortality parameter. While we recognize that 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, eggs and larvae within 1 km upstream of the dam were imposed a 100% mortality, 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 km).

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: a stationary model, in which offspring development occurs in the same place that spawning occurred, and a passive drift model, which represents the farthest the offspring could travel as a massless particle 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 is passive such that the location of offspring on any given day is dependent on its location the previous day and the current velocity experienced. Specifically, river kilometer- and time-specific estimates of current velocity (km/day) were used to determine the duration of time spent within a given river km (days/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 stay and forage 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 river kilometers) and potential spawning date (1 May through 31 August) 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 days. We chose 60 days because this is the maximum time required for successful metamorphosis in a hatchery setting in which growth rate is often poor (Howly 1985). If individual offspring did not complete transition to the juvenile stage by 31 August, 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 RKM over all dates for each year; we also calculated location-specific potential recruitment, an index of recruitment potential of each individual RKM by summing over all modeled spawning dates in a given year for each RKM separately.

Analysis.–We chose the two ten-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 date 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, inter-annual 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 through 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), mid (June), 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 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-by-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 to compare season-specific effects of environmental characteristics on larval shad survival. The characterizations of specific years and seasons are given in the Supplementary File S1.

We were interested in understanding how temperature and flow affect success of larval American Shad across seasons and across locations in the river. We used Classification and Regression Tree (CART) analysis to explore variables most responsible for heterogeneity in annual potential recruitment. Variables considered included RKM (continuous scale) as well as temperature (categorical) and flow (categorical) during early (May), mid (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; a 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 is not intended to be predictive of recruitment of American Shad 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 five-month period, uniformly distributed across sites and days. We have intentionally removed spawning time and site choice from the model. The Connecticut Department of Energy and Environmental Protection (CTDEEP) annually samples Connecticut River sites from below the Holyoke Dam (i.e. below our modeled reach) downstream to Essex, CT, from July to October to produce a juvenile abundance index (JAI), calculated as the geometric mean of catch per unit effort from their samples. We tested whether the JAI (U.S. Fish and Wildlife Service 2017) was correlated with our modeled annual recruitment potential from the downstream end (RKM 138-153) of our modeled reach.

<A>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 in Supplementary Files S2, S3, and S4; example of a "typical" year, 1994, in Figure 2). A typical year has April (DOY 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 (DOY approximately 170-210 in Figure 2, middle right panel). Because, in a typical year, discharge and temperature are strongly negatively correlated through 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 were 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.

<B>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). Highest mean annual potential recruitment was associated with warmer than average June 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.—In model scenario 2, in which eggs and early larvae drifted passively with the current, the effect of spawning location was greatly reduced in comparison to 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 middle panel to lower 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 and temperatures and July-August temperatures (Table 2), though 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, survival was low. July-August temperature also was an important explanatory variable (Table 2). When we consider spawning locations upstream of the pool of the most-upstream 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).

<B>Comparison with empirical data

Empirical estimates of juvenile abundance were available only from the portion of the river downstream from and not overlapping our modeled reach. Using the results from modeled spawning occurring closest to the juvenile collection sites (i.e. using mode results from the 15 furthest downstream kilometers of the modeled reach), modeled annual potential recruitment was positively correlated with the empirically based juvenile abundance index 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.

<A> DISCUSSION

Our modeling of larval shad recruitment, 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 known spawning habitats and peak spawning dates, our model simulates American Shad spawning across all days of a five-month period, across the entire longitude of a 142-kilometer 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 in 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 movement of eggs and larvae with the current reduced variability in shad recruitment, but this reduction occurred by homogenizing experiences across spawning locations and thus eliminating 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 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 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 size and growth of young fish through the bioenergetic combination of food and temperature (Eaton et al.

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 shad. Thus, through direct effects, interactive effects with other variables, and by influencing the length of time that shad are in the vulnerable larval stage, temperature affected growth and survival. Elsewhere, variation in thermal regime has been explored (Caissie 2006). Given the surprising and diverse variation within and across years in temperature patterns explored in this study, looking at 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, though 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 were possibly because of 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 has a negative effect on larvae through advection to unfavorable locations (Savoy and Crecco 1988). The silty substrates in these pools behind dams are not conducive to survival of eggs and young larvae, though 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 conditions that lead to growth and survival, either at that site or at 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 in 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, but 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 and 26 °C (reviewed in Beasley and Hightower 2000). The 20-year mean temperatures in our data for the Connecticut River were in this range in May and June and at the upper end of the range in 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 to the lower portion of the reach. Our models show 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; U.S. Fish and Wildlife Service 2017), 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 occurring 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) have 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 spawning rivers (Leggett and Carscadden 1978; Hasselman et al. 2013). Because of this, we expect that our individual-based model of larval shad growth and survival, when applied to a river model representative of a southern river, would yield very different baseline results as well as different responses to extreme patterns in temperature and flow consistent with climate change. The southeastern coast of the United States 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 to 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 models.

While we refer to our modeled recruitment as "potential recruitment", in fact, by removing spawner choice of spawning sites and dates and removing larval habitat choice, we have removed the potential of the spawning population to spawn in greater abundance in certain areas on certain dates and receive either the benefit (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 what combination of variables drives recruitment success. The fact that potential recruitment in 19 of our 20 modeled years was strongly correlated with the juvenile abundance index (JAI) measured downstream of our modeled reach (U.S. Fish and Wildlife Service 2017) suggests that our model captured the main elements driving recruitment. To be able to apply these results to predictions of how effects of climate change 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 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.

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<A>SUPPLEMENTARY INFORMATION

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

Table 1. Table of model parameters, values, and sources.

Parameter/Function	**Value/Form**	**Source**
Egg development time (T_e; days) as a function of temperature (τ, °C)	$T_e = 5356.84\tau^{-2.379}$	Limburg 1996a, Rice 1887, Ryder 1887, Leim 1924, Watson 1970
Minimum viable egg temperature	11° C	Ryder 1887, Leim 1924
Maximum viable egg temperature	27° C	Ryder 1887, Leim 1924
Background egg and yolk-sac larval mortality rate. d^{-1}	0.30	Savoy and Crecco 1988
Minimum viable yolk-sac larva temperature	11° C	Assumed, from Ryder 1887, Leim 1924 for eggs
Maximum viable yolk-sac larva temperature	27° C	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 1966b
Larval daily growth in mass (W, g)	$\frac{dW}{dt} = \frac{pk_1W^{k_2}f(\tau) - k_3W^{k_4}e^{k_5t}}{k_6}$	Limburg 1996b
k_1,k_2,k_3,k_4,k_5	0.220, 0.2, 0.036, 0.776, 0.02	Limburg 1996b

k_6, larval energy density (Kcal/g)	1	From range reported in Limburg 1994, Appendix C, assuming a dry weight-to-wet weight ratio of 0.2 (Limburg 1996b)
Natural mortality rate, d^{-1}		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

Table 2. Importance (%) of each variable in explaining variation in annual potential recruitment from classification and regression tree analysis for model scenarios 1, 2, and 3. Location (RKM), 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

Figure headings

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. Duration of each of the larval stages 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.

Figure 2. Spatiotemporal visualizations of temperature (°C; upper left), discharge (100 m^3/s, upper right), zooplankton density (1000/m^2, 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, model 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 every year.

Figure 3. Combinations of discharge and temperature that occurred in a specific reach of the river (RKM 228) between 1 April and 31 August. 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 1 April at the far left of the figure. Top panel: 1994, a "typical" year, with high and variable discharge and cold temperatures early in the season and low discharge with high temperatures late in the season. High recruitment is limited to spawning dates late in the season. Middle panel: 2012, spawning during low discharge, when it occurs at

low temperatures, does not result in high recruitment. Bottom panel: 2013, spawning at moderately high discharge, when it is associated with high temperatures, can result in high recruitment, though not as high as the combination of high temperatures and low discharge.

Figure 4. Nodes and branches of the classification and regression tree describing effect of environmental variables on modeled annual potential recruitment for scenario 1.

Figure 5. Annual potential recruitment from spawning at each RKM along the river. Left panel: scenario 1. Years with warmer than average June (black lines) and cooler than average June (gray lines). Right panel: scenario 3. Years with warmer than average July-August (black lines) and cooler than average July-August (gray lines).

Figure 6. Spatiotemporal visualizations of modeled recruitment for eggs spawned at each combination of day of year (*x*-axis) and river kilometer (*y*-axis). Top panel: model scenario 1, cool June temperatures (2000). Middle panel: model scenario 1, warm June temperatures (1999). Lower panel: model scenario 2, warm July-August and low May flow (1999).

Figure 7. Modeled annual potential recruitment from spawning occurring in the downstream end of the modeled reach (RKM 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 (U.S. Fish and Wildlife Service 2017). Scenario 1: stationary, no dams; scenario 2: maximum drift, no dams; scenario 3: stationary, with dams. *R*-squared values are based on the first 19 years of data (1993-2002 and 2007-2015). One outlier, 2016, is plotted separately.