

# Effect of environmental conditions on juvenile recruitment of alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*) in fresh water: a coastwide perspective

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**Abstract:** The abundance of alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*) has declined throughout their range, and there are increasing concerns about their conservation status. Because of their diadromous life history, variability in rates of survival in fresh water can affect overall recruitment. The objective of our study was to assess how river temperature and flow influence young of the year (YOY) river herring recruitment in the Northeast US. Observations of adult and juvenile fish in five rivers were used to construct spawner–YOY recruits models; these rivers were chosen because of the length of the time series (>15 years) and the paired observations of spawners and juveniles. An environmentally explicit stock–recruitment model explained a substantial fraction (41% to 80%) of the variance in YOY abundance, depending on river system. Our approach allowed for a preliminary discussion of potential mechanisms, which need to be further substantiated by focused field and laboratory studies. Early summer river flow and river temperature had the greatest influence, indicating the importance of conditions in nursery habitats. In certain systems, spring or fall conditions were also important determinants of survival, suggesting additional effects of the environment on spawning of adults and juvenile egress from freshwater nursery habitats.

**Résumé :** L'abondance des gaspareaux (*Alosa pseudoharengus*) et des aloses d'été (*Alosa aestivalis*) a diminué dans toute leur aire de répartition, et leur situation de conservation est l'objet d'inquiétudes croissantes. En raison du cycle biologique diadrome de ces poissons, la variabilité de leurs taux de survie en eau douce peut avoir une incidence sur leur recrutement global. L'objectif de l'étude consistait à évaluer l'influence de la température et du débit des rivières sur le recrutement d'alesos de l'année (YOY) dans le nord-est des États-Unis. Des observations sur des poissons adultes et juvéniles dans cinq rivières ont été utilisées pour bâtir des modèles géniteurs-jeunes de l'année YOY recrutés; ces rivières ont été choisies en raison de la disponibilité de longues séries chronologiques (>15 ans) et d'observations appariées de géniteurs et juvéniles. Un modèle stock–recrutement intégrant explicitement les conditions du milieu explique une fraction importante (de 41 % à 80 %, selon réseau hydrographique) de la variance de l'abondance des YOY. Notre approche permet une discussion préliminaire des mécanismes potentiels, qui devront être étoffés davantage par des études de terrain et de laboratoire ciblées. Les débits et la température des rivières au début de l'été exerçaient la plus grande influence, indiquant l'importance des conditions des habitats d'élevage. Dans certains réseaux, les conditions estivales ou automnales étaient également d'importants déterminants de la survie, donnant à penser que d'autres facteurs du milieu influencent le frai des adultes et le départ des juvéniles des habitats d'élevage en eau douce. [Traduit par la Rédaction]

## Introduction

Alewives (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), collectively known as “river herring”, are native to the east coast of North America. Alewives range from Labrador and Newfoundland to South Carolina (ASMFC 2012). Blueback herring are found from Nova Scotia to northern Florida (ASMFC 2012). Both are diadromous, with adults returning to their natal rivers every spring to spawn from ages 3, 4, or 5 onwards (Cianci 1969; Loesch and Lund 1977). Juvenile river herring spend their first summer in freshwater nursery habitats and migrate seaward in the summer and fall of their first year (Kosa and Mather 2001; Yako et al. 2002; Iafrate and Oliveira 2008; Gahagan et al. 2010).

Alewives and blueback herring, as forage fishes, constitute an important link between zooplankton and piscivores in estuarine and marine food webs (Fay et al. 1983; Ames and Lichter 2013).

They have also supported an active fishery since colonial times, and both have been overexploited (ASMFC 2012). Substantial losses in productivity occurred soon after the arrival of the first European settlers owing to dam construction, which reduced accessible habitat by more than 95% between 1600 and 1900 in Maine alone (Hall et al. 2011, 2012). More recently, overfishing, climate change, and declining freshwater habitat quality may all have contributed to the observed 93% decline in US commercial landings since the 1970s (Limburg and Waldman 2009; ASMFC 2012). This unprecedented decline led the Natural Resources Defense Council to petition the National Marine Fisheries Service (NMFS) in 2011 to list river herring as threatened under the Endangered Species Act in the USA. Severe harvest restrictions have been in place in all US eastern coastal states since January 2012. After a careful review of population trends, NMFS determined that blueback

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**Table 1.** Potential mechanisms affecting river herring survival and associated environmental variables tested in GAM models.

Return to spawning habitats	Quality of nursery habitats	Egress
Spring flow (mean March–April)	Summer flow (mean May–June)	Fall flow (mean July–September)
Spring temperature (mean March–April)	Summer temperature (mean May–June)	Fall temperature (mean July–September)
March flow	May flow	July flow
April flow	June flow	August flow
March temperature	May temperature	September flow
April temperature	June temperature	July temperature
Date of peak flow in spring		August temperature
		September temperature
		Date of peak flow in fall

Note: Variables for the Androscoggin River are delayed by a month as spawning starts 1 month later in this system.

herring and alewife were Species of Concern and developed a recovery plan to allow rebuilding of the populations (<http://www.nero.noaa.gov/Protected/riverherring/>). In Canada, harvest levels are in decline (NMFS 2013), but river herring have yet to be determined a Species at Risk.

Recovery of river herring will depend on decreased mortality and on maintenance of habitat suitability. Climate change can impact habitat suitability by influencing those environmental variables that define optimal habitat. Indeed, over the past 40 years, marine habitat suitability, as described by optimal temperature, has been reduced in the Northeast Atlantic shelf region (Friedland and Hare 2007; Nye et al. 2009; Friedland et al. 2013), and adult alewife and blueback herring have shifted their spring center of distribution northward (Nye et al. 2009; Lynch et al. 2015). An inverse productivity pattern in fishery-independent surveys, with stocks north of Long Island showing increasing or stable numbers in recent years and more southern populations continuing to decline, even under decreasing or stable exploitation rates (ASMFC 2012), suggests that the observed change in distribution may be related to an environmental-driven decline in recruitment of the latter. Because of their complex life history, environmental stressors in both freshwater and marine environments can affect recruitment. River herring marine distributions are projected to continue to move northward, with abundance on the northeast US shelf being projected to decrease for alewife and to increase for blueback herring (Lynch et al. 2015).

The impacts of climate variability on freshwater stages have, however, yet to be investigated. Year-class strength of many fish species is determined by mortality during their late larval stage (Shepherd and Cushing 1980; Smith 1985; Myers and Cadigan 1993), which for river herring is completed largely in fresh water. Year-class strength of another anadromous clupeid, American shad (*Alosa sapidissima*) has been shown to be dependent on freshwater survival (Crecco et al. 1983). However, the relative importance of rates of mortality in freshwater and marine environments on river herring recruitment is unknown. Thus, to assess the potential effect of climate variability on river herring population dynamics, the environmental factors affecting freshwater recruitment need to be understood. Most studies of juvenile river herring dynamics have, however, generally been conducted over a short time period in specific systems or have focused on triggers of juvenile migration timing rather than the effect of environmental variation on freshwater recruitment (e.g., Kosa and Mather 2001; Yako et al. 2002; Walsh et al. 2005; Gahagan et al. 2010; Overton et al. 2012). In contrast, we use long-term data series on the abundance of adult and young of the year (YOY) alewife and blueback herring to assess the influence of both density-dependent and environmental effects on alewife and blueback freshwater recruitment across much of their range.

Variation in river flow and temperature are the two main factors affecting the abundance of YOY river herring (Henderson and Brown 1985; Rulifson 1994; Kosa and Mather 2001; Walsh et al. 2005; Gahagan et al. 2010) and of other anadromous clupeids such as American shad (Crecco and Savoy 1984; Limburg 1996). Their

effect on YOY recruitment is complex, may be synergistic, and can act directly or indirectly through a myriad of pathways. Both variables can influence river herring year-class strength by acting during any of the three phases of their freshwater residence: spawning, growth in nursery habitat, or juvenile egress to sea.

There exist many mechanisms, often more complex than a single threshold, through which temperature affects juvenile river herring recruitment. For example, exposure to temperature extremes during development in nursery habitats may constrain juvenile growth and decrease performance (Pörtner and Farrell 2008; Kellogg 1982; Henderson and Brown 1985; Overton et al. 2012). Moreover, temperature can reduce the suitability of nursery areas by influencing predation rates (Fuiman 1991) or food availability (Crecco and Savoy 1984). Temperature also alters the timing of adult spawning (Kissil 1974; Collette and Klein-MacPhee 2002; Ellis and Vokoun, 2011) or juvenile emigration (Gahagan et al. 2010), generating the potential for mismatches between YOY and optimal conditions in nursery habitat or estuaries.

Similarly, river flow affects river herring year-class strength through a myriad of pathways. For example, variation in river flow during spawning influences the energy expenditure of migrating adults and spawning habitat availability (Haro et al. 2004; Walsh et al. 2005) and has been shown to have an effect on the timing of spawning in other anadromous fish (Hodgson et al. 2006). River discharge can also affect juvenile river herring in nursery grounds by altering feeding success (Crecco and Savoy 1984; Burbidge 1974), as well as the availability of nursery habitat (Kosa and Mather 2001; Gahagan et al. 2010). During egress, variation in flow alters emigration timing (Gahagan et al. 2010). In addition, river discharge affects stream navigability and energy expenses during egress (Walsh et al. 2005; Kosa and Mather 2001; Gahagan et al. 2010).

Here we explore the effect of variation in temperature and river discharge on recruitment of YOY river herring. To better understand the potential mechanisms for the observed empirical environment–recruitment relationship, we grouped potential month or seasonal environmental effects into one of the three river herring freshwater life-history phases (Table 1).

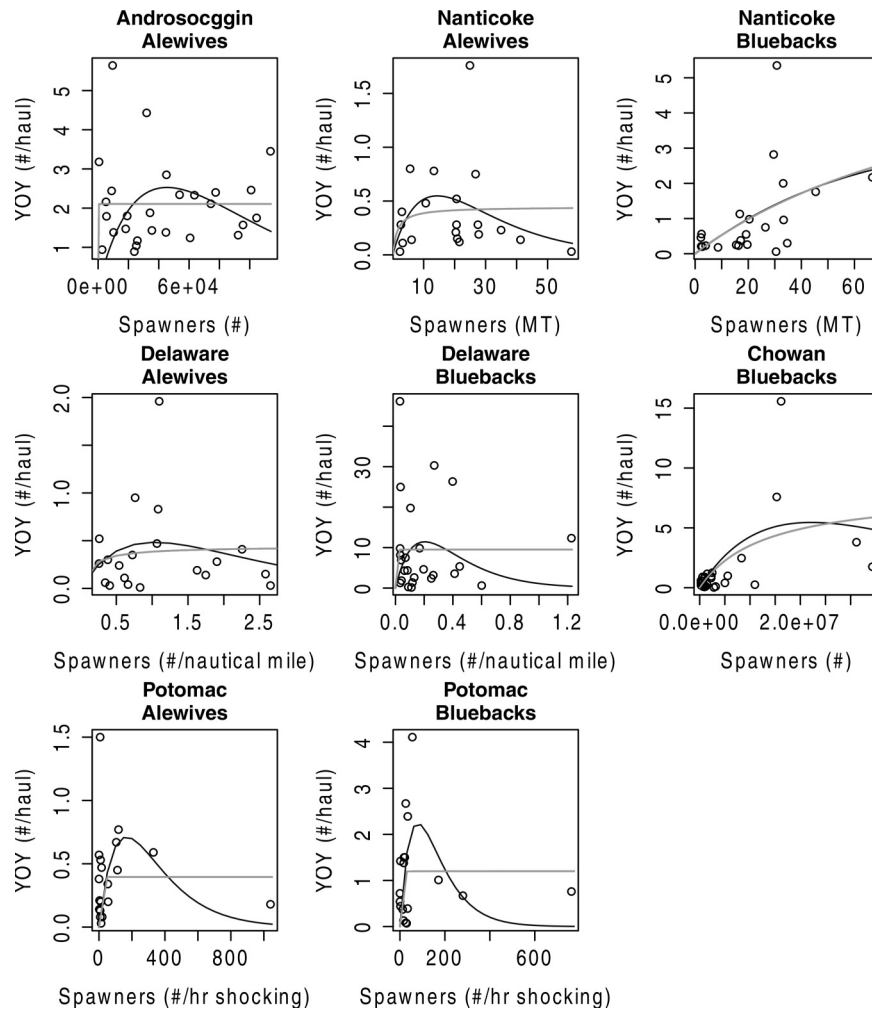
## Methods

The relationship between spawner abundance and recruitment is often described using the Ricker model (Walters and Martell 2004):

$$(1) \quad R_t = S_t e^{a - bS_t + C_t + \varepsilon_t}$$

where  $R$  is the number of recruits of year-class  $t$ ,  $S$  is the number of spawners of year-class  $t$ ,  $e^a$  is the maximum reproductive performance,  $b$  represents density-dependent effects,  $C$  represents environmental effects, and  $\varepsilon_t$  are lognormal errors. We selected the Ricker stock–recruitment model over the Beverton–Holt because, for most of the river herring populations under study, it provided a moderately better fit to the recruits–spawner data (Fig. 1). The same model can be written as a linear equation relating recruits

**Fig. 1.** Plots of juvenile recruits against spawners for all river herring populations used in the analysis. The black line represents the Ricker stock-recruitment model fit; the grey line represents the Beverton–Holt model fit. (Note: MT = metric tons; 1 nautical mile = 1.852 km.)



( $\log(R_t)$ ) to spawner abundance, density-dependent effects, and environmental effects:

$$(2) \quad \ln(R_t) = \ln(S_t) + a - bS_t + C_t + \varepsilon_t$$

Here recruits are the YOY that are just exiting the freshwater phases and entering the marine environment, and the above equation can be rewritten as

$$(3) \quad \ln(\text{YOY}_t) = \ln(S_t) + a - bS_t + C_t + \varepsilon_t$$

To assess the effect of spawner abundance and environmental variability on recruits, we selected rivers with data series longer than 15 years of YOY and spawner abundance. Five US river systems fit these criteria: the Androsocggin River (for alewives), the Delaware River (for alewives and blueback herring), the Potomac River (for alewives and blueback herring), the Nanticoke River (for alewives and blueback herring), and the Chowan River (for blueback herring) (Fig. 2). These rivers are highly variable in terms of habitat, covering a variety of sizes, hydrography, spawning environments, productivity, and predator guilds. As such, specific environmental effects are expected to influence river herring juvenile recruits in each system. Data were obtained from the Atlantic States Marine Fisheries Commission River Herring Benchmark Stock Assessment (ASMFC 2012).

Annual YOY indices for both alewives and blueback herring were derived from seine sampling conducted fortnightly from July to September in Merrymeeting Bay for the Androsocggin population (ASMFC 2012), monthly from June to November in the Delaware Estuary (ASMFC 2012), monthly from July to September in the lower Potomac River (ASMFC 2012; Durell and Weedon 2011), monthly from July to September in the lower Nanticoke River (ASMFC 2012; Durell and Weedon 2011), and monthly from June to October in the Albemarle Sound for the Chowan River (ASMFC 2012). Relative abundance estimates of spawning stock size were derived from fishway data for the Androsocggin River, a fishery-independent bottom trawl survey in the Delaware River, and statistical catch-at-age (SCA) models for the Nanticoke River and Chowan River. The Nanticoke River SCA model was based on proportion of catch-at-age, proportion of repeat spawners, total Maryland catch, and a fisher-dependent catch per unit effort (CPUE) from the Nanticoke River fyke net fishery (ASMFC 2012). The Chowan River SCA model was based on total in-river catches, age compositions, length compositions, and the YOY index for the Chowan River (ASMFC 2012).

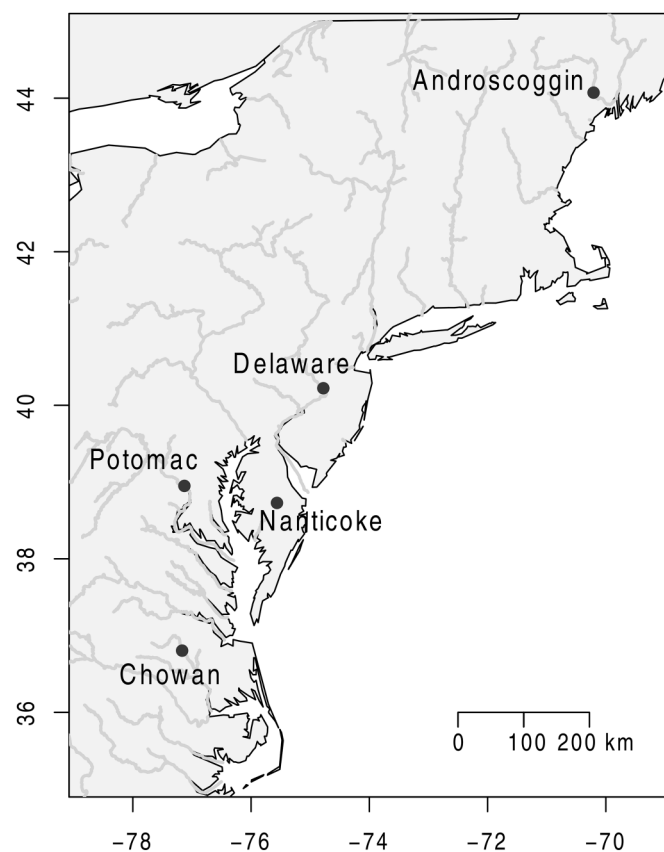
We restricted the analysis to 1980–2010, as all stocks had data covering the majority of this time period. We removed years that had missing data for spawners (Table 2) prior to analysis. In one instance, 1984 in the Delaware River, no adult blueback herring were counted, and this year was treated as missing (Table 2). Years

**Table 2.** River hydrographic characteristics and river herring time series information.

River	USGS gage No.	Basin size (km <sup>2</sup> )	Length (km)	Mean daily discharge (m <sup>3</sup> ·s <sup>-1</sup> )	Missing data, alewife spawners	Missing data, blueback spawners	Missing data, alewife YOY
Androscoggin	01059000	8 935	264	175	1980–1982		2010
Delaware	01463500	36 568	484	371	1982, 1985–1989	0 in 1984, 1985–1989	
Potomac	01646500	38 000	405	306	1980–1989	1980–1989, 1992, 1993, 2002	
Nanticoke	01487000	193	103.5	2.7	1980–1988	1980–1988	
Chowan	02047000	12 000	80	165		2010	

**Note:** Spawner data was collected for blueback herring in the Delaware River in 1984, but no fish were caught, so this year is specified as 0 rather than missing. No missing young-of-the-year (YOY) data were present for blueback herring.

**Fig. 2.** Map of the five rivers in which river herring were examined. Circles indicate USGS river flow gages for all the river herring populations used in the analysis.



with missing YOY were also removed, while years with zero YOY were retained. However, a zero YOY to spawners ratio resulted in a recruitment of  $\ln(0)$ . To log-transform data containing zeros, a small number must be added to the all data points, the value of which depends on the smallest nonzero value in the data set. We did so, following the procedure outlined in McCune and Grace (2002). Note that juvenile and adult numbers are based on relative abundance estimates of YOY and spawning stock size. As such, they were standardized to zero mean and a standard deviation of one for ease of comparison.

To assess which environmental variables drive variation in river herring juvenile recruitment, we selected river flow and river temperature, environmental variables for which physiological or ecological mechanisms affecting freshwater survival have been established. Daily river flow data were obtained from the USGS gages available from the USGS Surface-Water Daily Data at <http://>

[waterdata.usgs.gov/nwis/dv/?referred\\_module=sw](http://waterdata.usgs.gov/nwis/dv/?referred_module=sw) (see Table 2). No USGS gages were available on the Chowan River; thus, flow data from the Nottoway River (one of its main tributaries) were used. Except for the Delaware River, no USGS gage maintained long-term river temperature data. Rivers have a low thermal capacity, and linear regression models have successfully related water to air temperature at a daily scale (Pilgrim et al. 1998; Webb et al. 2003). Thus, while we recognize that the air–river temperature relationship will vary across different watersheds, we believe air temperature to be a good first approximation of river temperature anomalies. Comparison of 2 m air temperature data and river temperature for the Delaware River showed this to be a good approximation (see online supplementary data, Fig. S1<sup>1</sup>).

Daily mean air temperature was computed by averaging minimum and maximum 2 m air temperature obtained from the gridded, observation-based Livneh dataset at a 1/16th degree resolution. This gridded dataset was derived from daily temperature and precipitation observations from approximately 20 000 NOAA Cooperative Observer stations (Livneh et al. 2011). For each river, air temperature data from the grid cell closest to the USGS river gage location were selected.

Daily mean river flow and air temperature were averaged over each month of the river herring freshwater residence (March to September). As most juvenile sampling programs ended in September (ASMFC 2012), this was considered the last month of emigration. To better interpret the potential mechanisms associated with the emerging empirical environment–recruitment relationships, we grouped potential monthly environmental effects into one of the three river herring freshwater life-history phases (spawning, nursery rearing, and egress; Table 1). Environmental data were also averaged at seasonal (season = duration of each phase) scales to assess the importance of temporal granularity in the environment–recruitment relationship. The mean timing of each phase was assessed for each stock from a review of the literature. As the northernmost system, the Androscoggin River (Fig. 2) displays the latest alewife spawning period, peaking in May (ASMFC 2012). In the Delaware, Potomac, and Chowan river, spawning of both river herring species is centered in April (ASMFC 2012; Overton et al. 2012). No spawning phenology information was available for the Nanticoke River, and it was assumed that timing of spawning would be comparable to that of the nearby Potomac River. In summary, we considered the spawning season for the Androscoggin River to be April–May and March–April for the other systems (Table 1). For many regions, information is sparse on the timing of initiation of egress. Nevertheless, most studies have observed the main peak in emigration in July and a smaller, more variable emigration peak in the fall (Kosa and Mather 2001; Yako et al. 2002; Gahagan et al. 2010). Thus, the egress period for all stocks but that in the Androscoggin River was set to start in July (Table 1). Differences in emigration timing are associated with different hatch dates (Iafate and Oliveira 2008); thus, in the Androscoggin River the start of emigration was set to August (Table 1). The nursery phase was the period between spawning and egress: June–

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0259>.

July for the Androscoggin River and May–June for the other systems (Table 1). In addition, we included the date of spring peak flow for the spawning period and the date of fall peak flow for the egress period. Following Hodgkins et al. (2003), the spring flow season ranged from 1 January to 31 May and the fall flow season from 1 October to 31 December. These were also the two periods of highest flow for all the rivers under investigation (Fig. S2<sup>1</sup>).

Since most fish exhibit a critical thermal growth maximum, we hypothesized the freshwater survival–environment relationship to be nonlinear. Thus, we employed generalized additive models (GAMs) to establish the survival–environment relationship, as they are a particularly effective method when the relationship between response and explanatory variables is unknown and potentially nonlinear. The models were built in R using the mgcv package (Wood 2006). Given the relatively short length of the data series (18 to 30 years), the maximum number of smooth variables allowed in a model was set to two to avoid overparametrization. Furthermore, since we had less than 30 data points, the  $k$  parameter (number of knots) was set to a maximum of three (Keele 2008). The freshwater recruitment equation described above can be rewritten as a GAM model including two smooth, nonlinear environmental parameters,  $s(C_{1t})$  and  $s(C_{2t})$ , and two linear terms representing spawner abundance,  $\ln(S_t)$ , and density dependence,  $bS_t$ :

$$(4) \quad \ln(\text{YOY}_t) = \ln(S_t) + a - bS_t + s(C_{1t}) + s(C_{2t}) + \varepsilon_t$$

For each river and species, we built all possible models with two environmental effects and compared them using the Akaike information system metric corrected for small sample sizes,  $AIC_c$  (Burnham and Anderson 2002). The model with the lowest  $AIC_c$  was selected as the best model for each river system. Furthermore, we computed the probability that a variable would be selected just by random chance by adding a random variable to each dataset and repeating the model selection process 100 times. The random variable was selected 1 of 100 times on average (0–3 times range across systems), giving a 1% chance that a random variable would be picked, thus increasing our confidence in the robustness of the selected models. All environmental variables were standardized to zero mean and a standard deviation of one before analysis. To avoid collinearity, we identified and removed collinear variables using variance inflation factors (VIF). A higher VIF value indicates a higher collinearity (Zuur et al. 2007). There is no agreed-upon cut-off for VIF, but values higher than 5–10 are generally considered to indicate a highly collinear variable (Zuur et al. 2007; Montgomery and Peck 1992). Models whose predictor variables exhibited VIF greater than 5 were excluded. Residuals from the best models were examined to verify the assumptions of homogeneity and normality and for the absence of autocorrelation. Shapiro–Wilk normality test of the residuals from each model confirmed they were all normally distributed, plots of residuals versus fitted values showed no serious heterogeneity, and plots of the autocorrelation function of the residuals did not show significant autocorrelation.

## Results

### Stock–recruitment relationship

The stock–recruitment relationship alone did not explain much variance in juvenile blueback or alewife recruits (Table 3; Fig. 1). There was no significant density dependence and no relationship between adult and juvenile abundance in either species (Table 3; Fig. 1). For the Delaware and Nanticoke rivers alewife populations, adult abundance and density-dependent effects became significant after the inclusion of environmental covariates (Table 3), implying that the underlying stock–recruitment relationship may have been obscured by the high environmentally driven variability in recruitment.

**Table 3.** Comparison of models with density-dependent effect only and with density dependence and environmental covariates.

Stock	Effects	Deviance explained (%)	$AIC_c$
<b>Alewife</b>			
Androscoggin	lnS, S	5.04	41.4
	lnS, S, <b>t6, DPf</b>	44.5	35.9
Delaware	lnS, S	14.0	93.7
	<b>lnS, S, r3, fallt</b>	77.9	74.3
Potomac	lnS, S	3.22	59.3
	lnS, S, <b>t5</b>	41.0	52.9
Nanticoke	lnS, S	18.5	64.2
	<b>lnS, S, summert, summerr</b>	52.8	62.7
<b>Blueback herring</b>			
Delaware	lnS, S	4.89	93.4
	lnS, S, <b>r3, t4</b>	72.8	79.2
Potomac	lnS, S	0.46	66.1
	lnS, S, <b>r5, DPf</b>	77.0	53.7
Nanticoke	lnS, S	28.9	68.4
	lnS, S, <b>summert, springf</b>	79.6	54.8
Chowan	lnS, S	33.7	98.3
	lnS, S, <b>t5, t6</b>	58.9	92.2

**Note:** The letter t stands for temperature, r for river flow, and the number specifies the month of the significant effect. DPf is the date of peak flow in fall. S represents density-dependent effects, while lnS represents the proportional trend of increasing recruits with increasing spawners. Effects highlighted in bold are significant at  $\alpha = 0.05$ .

### Environmental drivers of recruitment

#### Alewife

Changes in river flow and temperature accounted for a large fraction of the unexplained variability in alewife recruitment (Tables 3 and 4). Most models selected individual months rather than seasonal means, highlighting the granularity of the environment–recruitment relationship. Recruitment in each system was determined by environmental variability during specific “critical” months. Recruitment of the Androscoggin River population was influenced by temperature in the nursery phase and by flow during egress. Numbers of juveniles increased with a later date of fall peak flow and with June temperature being highest at the maximum temperature of 20.5 °C during June (Table 4; Fig. 3). Recruitment of the Delaware River alewife stock was influenced by changes in temperature during egress and by flow during spawning (Table 4). Numbers of recruits were maximized at a flow of 672 m<sup>3</sup>·s<sup>−1</sup> during March and at a temperature of 22 °C during fall (Fig. 3). By contrast, recruitment in the Potomac River was solely affected by temperature during the nursery phase, being highest at the warmest temperature of 22.3 °C during May (Fig. 3; Table 4). We selected the model with one environmental covariate, because the  $AIC_c$  of the best one-variable model was lower than the best two-variable model. Recruitment of the Nanticoke River alewife population was also solely influenced by conditions during the nursery period. This was the only system where seasonal means explained more variability in recruits as compared with monthly means (Table 4). Juvenile abundance was highest at the highest summer (May–June) mean temperature of 21.8 °C and flow of 6 m<sup>3</sup>·s<sup>−1</sup> (Fig. 3).

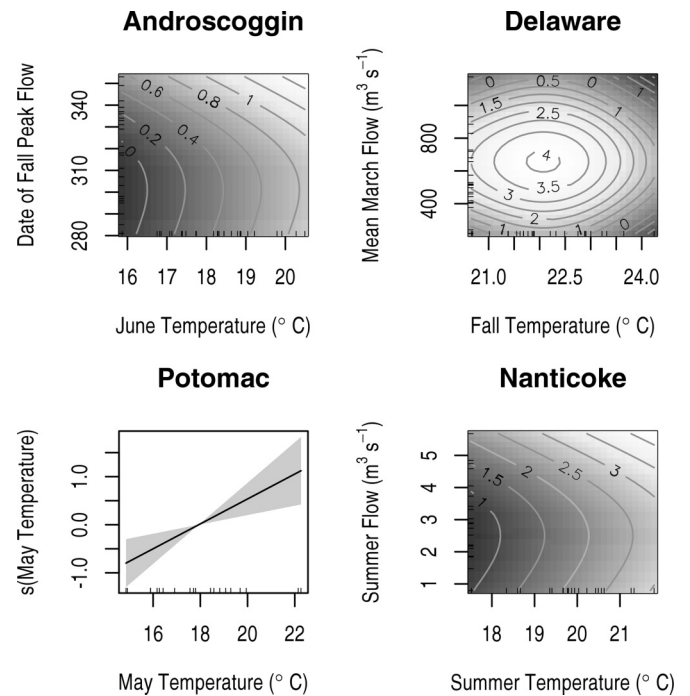
While the environmental covariates were specific to each river system, some commonalities in the effect of environmental conditions on recruitment of juvenile alewife were apparent across systems. First, juvenile abundance in three out of four alewife populations was associated with optimal nursery habitat temperature (Table 5). The “critical” period of the significant nursery temperature–recruitment relationship differed by river system,

**Table 4.** Best GAM models of freshwater survival for each species and river system.

	<i>p</i> value
<b>Alewife</b>	
<b>Androscoggin River</b>	
Spawners	0.147
ln(Spawners)	0.623
June temperature	0.007
Date of fall peak flow	0.041
Deviance explained = 44.5%	
N = 27	
<b>Potomac River</b>	
Spawners	0.209
ln(Spawners)	0.104
May temperature	0.005
Deviance explained = 41%	
N = 20	
<b>Delaware River</b>	
Spawners	0.004
ln(Spawners)	0.015
March flow	<0.001
Fall temperature	0.003
Deviance explained = 77.9%	
N = 25	
<b>Nanticoke River</b>	
Spawners	0.006
ln(Spawners)	0.017
Summer temperature	0.012
Summer flow	0.120
Deviance explained = 52.8%	
N = 22	
<b>Blueback herring</b>	
<b>Delaware River</b>	
Spawners	0.881
ln(Spawners)	0.879
March flow	<0.001
April temperature	0.040
Deviance explained = 72.8%	
N = 25	
<b>Nanticoke River</b>	
Spawners	0.113
ln(Spawners)	0.891
Summer temperature	<0.001
Spring flow	0.007
Deviance explained = 79.6%	
N = 22	
<b>Potomac River</b>	
Spawners	0.602
ln(Spawners)	0.490
Date of fall peak flow	0.005
May flow	<0.001
Deviance explained = 77%	
N = 18	
<b>Chowan River</b>	
Spawners	0.212
ln(Spawners)	0.340
May temperature	0.009
June temperature	0.011
Deviance explained = 58.9%	
N = 30	

with the Androscoggin River being influenced by June temperature, the Potomac River by May temperature, and the Nanticoke River by summer temperature (Fig. 3). The temperature range experienced during this critical period was similar across the different nursery habitats (Fig. 3). Indeed, June temperatures in the Androscoggin River, the northernmost system, are comparable to May temperatures in the Potomac River (Fig. S3<sup>1</sup>). Second, half of

**Fig. 3.** Effect of environmental conditions on each alewife stock. The variables depicted are those highlighted in the best GAM models for each stock (see Table 4). Darker shading represents the lowest freshwater survival anomalies, while lighter shading represents the highest, as specified by the contour lines. The little vertical lines along the *x* and *y* axes indicate the environmental covariate value of the observations. For the Potomac River, freshwater survival included only one environmental covariate. For this river, the *x* axis shows the values of the environmental covariate, and the *y* axis shows the contribution of that smoother to the fitted values. The solid line is the smoother, and the grey region the 95% confidence bands.



**Table 5.** Summary of the main mechanisms impacting river herring freshwater survival in each system.

	Return to spawning habitats	Quality of nursery habitats	Egress	Spawner abundance	Density dependence
<b>Alewife</b>					
Androscoggin		T	R	No	No
Delaware	R		T	Yes	Yes
Potomac		T		No	No
Nanticoke		T, R		Yes	Yes
<b>Blueback herring</b>					
Delaware	T, R			No	No
Potomac		R	R	No	No
Nanticoke	R	T		No	No
Chowan		T		No	No

**Note:** T stands for a temperature effect, R for a flow effect. “Yes” indicates a significant ( $\alpha = 0.05$ ) density-dependent effect.

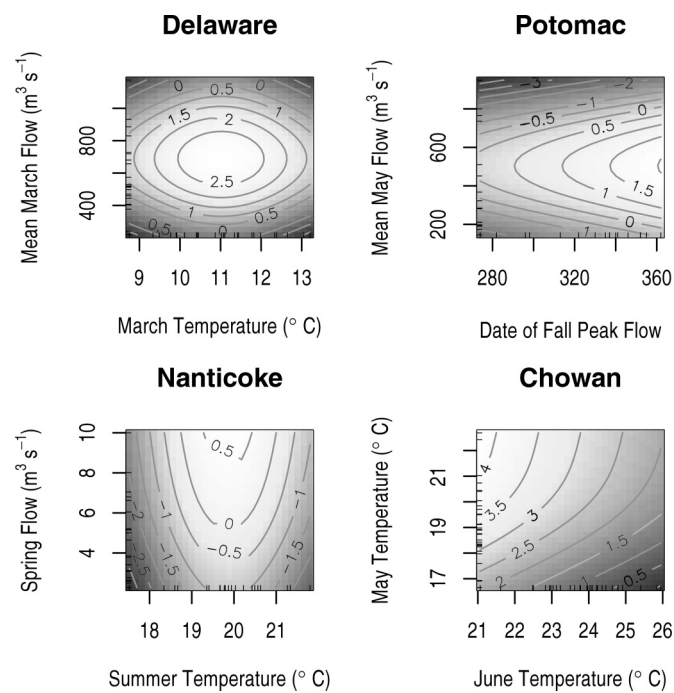
the alewife populations were affected by changes in egress conditions, with the date of peak flow in fall influencing the survival of the Androscoggin River stock and fall temperature the survival of the Delaware River population (Tables 4 and 5).

**Blueback herring**

Flow and temperature also explained a large fraction of the variation in blueback herring recruitment (Table 4). Most models chose individual months rather than seasonal means, highlighting the granularity of the environment–recruitment relationship. Recruitment in each system was determined by environmental

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**Fig. 4.** Effect of environmental conditions on each blueback herring stock. The variables depicted are those highlighted in the best GAM models for each stock listed in Table 4. Darker shading represents the lowest freshwater survival anomalies, while lighter shading represents the highest, as specified by the contour lines. The little vertical lines along the  $x$  and  $y$  axes indicate the environmental covariate value of the observations.



variability during specific critical months. In the Delaware River, blueback herring recruitment was influenced by variation in conditions during the spawning phase. Juvenile abundance was affected by March flow and was optimal at a flow of  $672 \text{ m}^3 \cdot \text{s}^{-1}$  (Table 4; Fig. 4). In addition, numbers of recruits were highest at an intermediate April temperature of  $11 \text{ }^\circ\text{C}$  (Fig. 4). Flow rate was also an important driver of recruitment in the Potomac River, with survival being highest if the date of peak flow in fall was latest, and at an optimal May flow of  $430 \text{ m}^3 \cdot \text{s}^{-1}$  (Fig. 4). Nanticoke River blueback herring recruitment was influenced by seasonal rather than monthly means. Juvenile abundance increased with spring flow and was optimal at a temperature of  $20 \text{ }^\circ\text{C}$  during summer (Fig. 4). Temperature during the nursery period was also an important determinant of recruitment in the Chowan River (Table 4). Numbers of juveniles were highest at the lowest June temperature of  $21 \text{ }^\circ\text{C}$  (Fig. 4). Survival was also influenced by May temperature (Table 4) and was highest at the maximum temperature of  $22.7 \text{ }^\circ\text{C}$  (Fig. 4).

Environmental covariates were specific to each river system, but some commonalities in the effect of environmental conditions on recruitment were apparent across systems. First, conditions during the nursery phase were an important determinant of recruitment for the Potomac, Nanticoke, and Chowan rivers stocks (Table 5). While the Potomac River juvenile abundance was affected by flow during the nursery phase, the Nanticoke and Chowan rivers recruits were influenced by temperature (Table 5). The optimal nursery rearing temperature was  $20\text{--}23 \text{ }^\circ\text{C}$  (Fig. 4). Thus, in the Chowan River, the southernmost system (where June temperatures were above  $21 \text{ }^\circ\text{C}$ ) temperature had the opposite effect on recruits than in the Nanticoke River or in the alewife populations, with juvenile abundance decreasing with increasing temperature (Fig. 4). Indeed, June temperature is higher in the Chowan River than in any other system (Fig. S3<sup>1</sup>). In addition to

temperature, fluctuations in flow during the spawning phase were also an important determinant of juvenile abundance for half of the blueback herring populations (Table 5). Freshwater survival in the Nanticoke River (the system with the lowest river flow) increased with spring flow, while in the Delaware River it was highest at an intermediate May flow (Fig. 4).

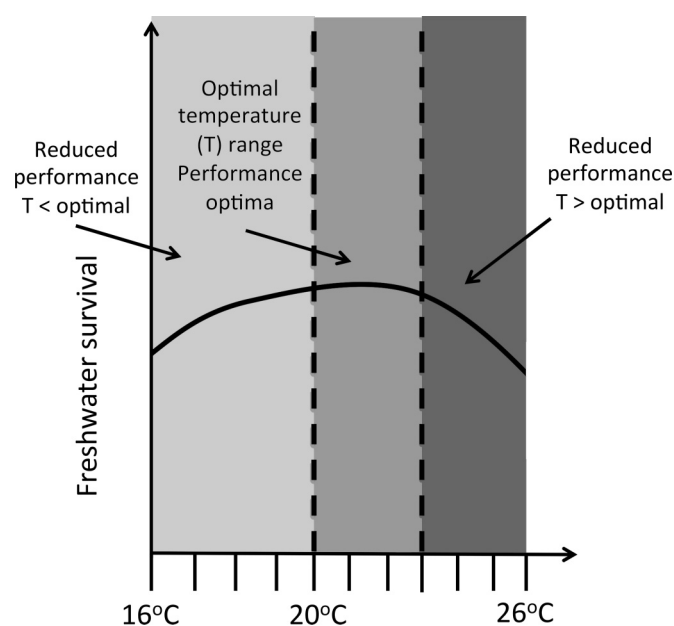
## Discussion

Our findings suggest that recruitment of YOY alewife and blueback herring is largely affected by environmental variability. There was no relationship between river herring spawners and juvenile recruits. Other studies have observed that year-class strength of alewives or of other anadromous clupeids such as American shad is largely regulated by environmental factors and independent of parent stock size (Crecco and Savoy 1984; Kosa and Mather 2001). We may not have been able to detect density-dependent effects as our spawner–recruits time series cover a period of largely declining or low stock sizes, compared with what was the historical river herring abundance. A significant stock–recruitment relationship may become apparent at a wider range of parent stock sizes (Walters and Martell 2004). We also expect density-dependent effects to be less explicit at lower stock sizes because recruitment variability tends to increase at lower population sizes (Myers 2001). In two alewife populations, a stock–recruitment relationship was evident after accounting for environmental variability, suggesting that the high environmentally driven variability in recruits may be obscuring an underlying stock–recruitment relationship.

The results of this analysis support the hypothesis that changes in temperature and river flow explain a large fraction of variability in river herring juvenile recruitment. While several common environmental dependencies emerged across systems and species, there were also considerable system- and species-specific variations and trends. The watersheds under study were highly variable in terms of habitat, covering a variety of sizes, hydrography, spawning environments, productivity, and predator guilds. As such, system-specific environmental effects on juvenile recruitment are expected. The granularity of the environment–recruitment relationship was also apparent temporally, with juvenile abundance in most populations being affected by a critical month rather than a critical season. Elucidating the mechanisms underlying common and system- or species-specific relationships is essential for robust prediction, and the remainder of this Discussion is devoted to underlying mechanisms. However, we stress that while our approach allowed for a preliminary discussion of potential mechanisms, they need to be further substantiated by focused field and laboratory studies.

Recruitment of YOY river herring across their US range was maximized at optimal nursery temperatures. All river herring stocks under investigation, except for the Delaware River stocks and the Potomac River blueback herring, were influenced by variation in nursery habitat temperature (Table 5). Physiological theory states that all organisms maximize their fitness over an optimal temperature range, with performance being reduced as temperature deviates from this optima (Pörtner and Farrell 2008). The optimal temperature for river herring juveniles during the nursery phase varied across systems and species, but ranged between  $20$  and  $22 \text{ }^\circ\text{C}$  (Fig. 5). Indeed, we observed that temperature had an opposite effect on juvenile abundance in the southernmost system as compared with the more northern populations. It was apparent that in the Chowan River (where juveniles may already experience June temperatures near their thermal optima) temperature increases in June result in reduced survival. Latitudinal differences in the effects of temperature on survival rates have also been observed for Pacific salmon (*Oncorhynchus* spp.) (Mueter et al. 2002).

Fig. 5. Conceptual diagram of the relationship between temperature during the nursery phase and river herring freshwater survival.



We suggest three potential mechanisms underlying the observed optimal thermal range during the nursery phase. But we stress that more field and laboratory studies are required to verify these hypotheses. Optimal thermal windows reflect both direct and indirect temperature effects (Pörtner and Farrell 2008). For example, temperature can directly affect survival through its effect on growth and indirectly through prey availability or predation pressure. First, temperatures could have influenced river herring survival by its direct effect on growth rates (Kellogg 1982). Indeed, the Chowan River was the only system in which June maximum air temperature reached values above both the temperature of maximum alewife larval growth rate (29.1 °C) and their upper thermal tolerance (31 °C) (Kellogg 1982). Instances of temperature-driven, growth-mediated survival have been observed for Atlantic salmon (*Salmo salar*) (Rikardsen and Dempson 2011). Growth to some minimum size may be important in reducing predation because of enhanced swimming ability, as well as escape from size-selective predators. Second, higher temperature may indirectly affect growth by producing more favorable food conditions. Higher temperatures in May and June were associated with (i) higher zooplankton densities, (ii) higher feeding incidence (more larvae with full stomachs), and (iii) higher abundance of juvenile American shadanother anadromous clupeid species) in the Connecticut River (Crecco and Savoy 1984). Third, a differential thermal threshold between prey and predators may have led to higher freshwater survival at higher temperatures. Interspecific differences in the capacity for thermal acclimation have been observed to modulate prey–predator interaction (Grigaltchik et al. 2012). Indeed, striped bass (*Morone saxatilis*), one of river herring’s main predators (Heimbuch 2008), has a lower thermal constraint (Cyterski and Ney 2005). Future research focused on river herring tolerance to low or high temperatures (or both) and on the thermal sensitivity of prey–predator interactions needs to be carried out to test these hypotheses and proposed mechanisms.

In addition to temperature variation, changes in flow during the nursery phase were an important driver of river herring freshwater survival. The effect of discharge appeared to be system-specific. Kosa and Mather (2001) also hypothesized the effect of river flow to be site-specific, as large systems rarely become de-

watered and thus juveniles may be less susceptible to stranding and increased predation during periods of low discharge. In the Nanticoke River, freshwater survival was highest when summer flow was largest, at 6 m<sup>3</sup>·s<sup>-1</sup>. The Nanticoke River was the smallest under study. Thus, juvenile river herring in this system may have been more susceptible to stranding and higher predation rates at low discharge (Yako et al. 2002). By contrast, highest recruitment of blueback herring in the Potomac River (one of the largest rivers in the system) was associated with intermediate May discharge levels of 430 m<sup>3</sup>·s<sup>-1</sup>. Recruitment decreased at both higher and lower discharge rates. Jessop (1990) observed that increasing discharge in May and June reduced year-class size of blueback herring and attributed the decrease in survival to reduced abundance of the plankton available at first feeding. Indeed, high discharge can decrease feeding efficiency of anadromous clupeids (Crecco and Savoy 1984; Limburg 1996). Similarly, Burbidge (1974) observed that a flooding event between August and September in the James River (Virginia) resulted in lower zooplankton availability and a lower blueback herring condition factor.

While quality of nursery habitat was highlighted as the most common mechanism driving variation in recruitment across the range of river herring, egress was a critical period for some alewife populations. The juvenile seaward emigration has been observed to be a critical stage for other anadromous fish. It is a transition period between two life-history stages, a time of physiological change, and movement into unknown habitats, with a potential to introduce high mortality (Thorstad et al. 2012). Alewife recruitment in the Delaware River was dependent on optimal egress temperature. The observed optimal thermal window may be due to the same mechanisms described above for the nursery phase. Furthermore, a drop in temperature can serve as a cue for emigration in blueback herring juveniles (Iafate and Oliveira 2008). Thus, temperature variation may also indirectly impact juvenile recruitment by altering the timing of migration, and this creates a potential for a match–mismatch between the emigrating juveniles and their estuarine food sources. For example, the timing of smolt migration is important for Atlantic salmon to achieve maximum immediate growth efficiency and survival through the optimization of their overlap with high abundance of estuarine prey (Juttila et al. 2009). Matches between spawning and development of peak food abundance have also been associated with higher recruitment of marine clupeids (Hjort 1914; Cushing 1990). For the Androscoggin River alewife and the Potomac River blueback populations, flow during egress was an important determinant of juvenile abundance. Juvenile recruits were more numerous when the date of peak flow in fall was latest. High flow events can serve as a prompt for migration (Gahagan et al. 2010). Thus, like temperature, flow can indirectly impact freshwater survival by altering the timing of migration and creating a potential for a match–mismatch between the emigrating juveniles and their estuarine food sources. Changes in stream navigability and energy expenses during egress (Kosa and Mather 2001; Walsh et al. 2005; Gahagan et al. 2010) may be other pathways whereby juvenile recruitment is affected by flow during egress.

Finally, our data imply that spawning conditions may also indirectly affect recruitment. In the Delaware River, recruitment of both alewives and blueback herring juveniles was influenced by river flow at the start of the spawning season, being optimal at an intermediate March discharge of 672 m<sup>3</sup>·s<sup>-1</sup>. By contrast, in the Nanticoke River, juvenile recruits were most numerous at the highest spring discharge of 10 m<sup>3</sup>·s<sup>-1</sup>. Indeed, Walsh et al. (2005) showed that increased river flow during spawning is beneficial to both alewives and blueback herring because of increased spawning and nursery habitat. However, they only examined a 141–425 m<sup>3</sup>·s<sup>-1</sup> range in discharge (Walsh et al. 2005). Data from the Delaware River show that too high flows may also be detrimental to juvenile recruitment. High flow increases water velocity and may create high velocity barriers that reduce the swimming per-



formance of anadromous fish (Haro et al. 2004). Thus, at higher discharge rates, adults may reach spawning areas in a poorer condition or spawn in less suitable habitat. Both likely reduce the survival of their offspring. In the Delaware River, freshwater survival of blueback herring was also dependent on spawning temperature. Alewives begin spawning at temperatures of 10.5 °C (Cianci 1969). Our results demonstrate that the spawning temperature that maximized juvenile blueback herring abundance in the Delaware River was 11 °C, suggesting that the timing of spawning may affect survival by enhancing a match with optimal feeding conditions in nursery habitats.

The empirical environment–recruitment relationships here highlighted may be used to assess potential effects of future climate variability on recruitment of river herring juveniles. Temperature all along their range is projected to rise in the next century following climate change (Hayhoe et al. 2007; Hare et al. 2010, 2012). Our findings suggest that abundance of river herring juveniles in the southernmost part of their range may decline as a result. However, if temperature during the nursery phase remains on average below the river herring thermal threshold, northern populations may actually see an increase in juvenile numbers. Furthermore, we have demonstrated that a variety of stressors act on river herring recruitment, even in the same system. Thus, the response of river herring to climate variability may be quite complex, as climate may affect different environmental stressors, and thus freshwater survival, in opposite ways. Additional sources of uncertainty in how river herring will respond to climate variability and change include potential for variation in interspecific interactions and climate conditions that fall outside the current experienced range. Clearly, to be able to project future changes in river herring freshwater survival, further research will be needed to both assess the extent of future temperature increases along the entire river herring range and to refine our understanding of the mechanisms that underlie the emergent environmental dependencies.

### Caveats

Our index of recruitment depends on the abundance of YOY sampled by the yearly beach seine surveys. We assumed that the numbers of YOY are sampled accurately and that catchability remains comparable between years. More specifically, we assumed that the environmental variables highlighted here reflect changes in YOY abundance due to changes in survival rather than catchability. This is hard to assess as no studies have examined the catchability of river herring YOY under different environmental conditions. However, the fact that the controlling variables differed between systems suggests that these environmental variables did not reflect changes in catchability. Moreover, different stocks had inverse relationships with the same variable, while the YOY sampling method (i.e., seining) remained the same across systems. Furthermore, many models highlighted spawning or nursery period variables (e.g., May discharge), collected prior to the start of YOY sampling, which could not have affected catchability.

Another caveat for the interpretation of our results was to have considered the freshwater phases and months within phases as constant across years. River herring phenology, however, is likely to vary between years. For example, spawning is temperature-dependent (Kissil 1974; Collette and Klein-MacPhee 2002; Ellis and Vokoun 2011), and while generally peaking in March, it may start in February during a warm year. Thus, a more biologically sensible temperature averaging window may be based on the environmental conditions affecting river herring migration timing rather than by calendar month. However, we do not yet understand all of the triggers of river herring phenology well enough to make predictive relationships of freshwater phase timing. This critical

knowledge gap should be addressed in future research efforts. In light of this, while recognizing the limitations of static characteristic phases, our results represent a clear advance relative to previous work on this topic and are the logical first step in assessing environmental dependencies across the broad scope of systems analyzed.

In conclusion, this paper demonstrates that an environmentally explicit stock–recruitment model accounts for a substantial fraction (63% on average across rivers and species) of the observed variability in river herring recruitment. Although much work has been done on factors that control juvenile survival and egress at small spatial and temporal scales (Kosa and Mather 2001; Yako et al. 2002; Walsh et al. 2005; Gahagan et al. 2010; Overton et al. 2012), this is the first paper that compares river herring freshwater recruitment from systems throughout its range, and it is the first to highlight common environmental dependencies of river herring juvenile recruitment. Variation in the quality of nursery habitat affected juvenile abundance across the US range of river herring. However, system-specific environmental dependencies were also apparent, stressing the granularity of the environment–freshwater survival relationship both temporally and spatially. Our model is empirical, and as such it cannot mechanistically assess the importance of environmental factors. Despite the observed strong relationships between recruitment and the environmental conditions highlighted here, we can only speculate on the potential mechanisms impacting recruitment, which could include reduced growth, prey availability, and vulnerability to predation. These factors could be system-specific. We stress that more local field and physiological studies are needed to uncover the actual environment–recruitment links.

River herring have declined through much of their range (ASMFC 2012), and at low population sizes their recruitment may now be more sensitive to environmental-induced variation in survival. The empirical relationships established here can guide the development of effective freshwater restoration actions and form an essential first step in the evaluation of how river herring stocks will respond to directional climate change. As marine survival is also an important determinant of recruitment, the work presented here could be coupled with similar work on marine stages (Lynch et al. 2015) to begin to develop a full life-history understanding of river herring dynamics and the effect of climate variability and change.

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