NRC Research Press
ARTICLE

# Evidence for temperature-dependent shifts in spawning times of anadromous alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*)

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**Abstract:** We analyzed four decades of presence–absence data from a fishery-independent survey to characterize the long-term phenology of river herring (alewife, *Alosa pseudoharengus*; and blueback herring, *Alosa aestivalis*) spawning migrations in their southern distribution. We used logistic generalized additive models to characterize the average ingress, peak, and egress timing of spawning. In the 2010s, alewife arrived to spawning habitat 16 days earlier and egressed 27 days earlier (peak 12 days earlier) relative to the 1970s. Blueback herring arrived 5 days earlier and egressed 23 days earlier (peak 13 days earlier) in the 2010s relative to the 1980s. The changes in ingress and egress timing have shortened the occurrence in spawning systems by 11 days for alewife over four decades and 18 days for blueback herring over three decades. We found that the rate of vernal warming was faster during 2001–2016 relative to 1973–1988 and is the most parsimonious explanation for changes in spawning phenology. The influence of a shortened spawning season on river herring population dynamics warrants further investigation.

**Résumé :** Nous avons analysé quatre décennies de données de présence–absence tirées d'une évaluation indépendante de la pêche, dans le but de caractériser la phénologie à long terme des migrations de frai d'aloses (gaspareau *Alosa pseudoharengus* et alose d'été *Alosa aestivalis*) dans leur aire de répartition méridionale. Nous avons utilisé des modèles logistiques additifs généralisés pour caractériser les moments de l'entrée dans les lieux de frai, du pic du frai et de la sortie de ces lieux. Dans les années 2010, les gaspareaux arrivaient dans les habitats de frai 16 jours plus tôt et en ressortaient 27 jours plus tôt (le pic étant 12 jours plus tôt) que dans les années 1970. Les aloses d'été arrivaient 5 jours plus tôt et ressortaient 23 jours plus tôt (le pic se produisant 13 jours plus tôt) dans les années 2010 que dans les années 1980. Ces changements du moment de l'entrée et de la sortie ont raccourci la présence dans les réseaux de frai de 11 jours sur quatre décennies pour les gaspareaux et de 18 jours sur trois décennies pour les aloses d'été. Nous avons constaté que le taux de réchauffement hivernal était plus rapide durant l'intervalle de 2001 à 2016 que durant celui de 1973 à 1988, et ce facteur constitue l'explication la plus parcimonieuse des modifications de la phénologie du frai. L'influence d'une saison de frai plus courte sur la dynamique des populations d'aloses mérite des études plus poussées. [Traduit par la Rédaction]

## Introduction

Globally, average temperatures have increased steadily from 1880 to 2012, with the three most recent decades having been successively warmer than any preceding decade since 1850 (IPCC 2014). A meta-analysis by Chen et al. (2011) linked range shifts and warming climate for 23 terrestrial species groups to higher latitudinal distributions and higher elevations. Poleward shifts in distribution have also been observed in marine species across taxa (Murawski 1993; Perry et al. 2005; Nye et al. 2009). Marine species whose life histories are solely dependent upon marine or estuarine environments are often capable of modifying their spatial distributions to stay within optimal thermal ranges for their various life stages (Perry et al. 2005; Poloczanska et al. 2013). However, diadromous species that exhibit some degree of natal homing may not be able to spatially adapt to environmental changes and are at greater risk of experiencing negative effects due to climate change (Hare et al. 2016), but could temporally adapt their behavior to maintain accessibility to preferred temperatures in response to changes in thermal regime.

Phenology is the study of seasonal or cyclical biological processes and how they are influenced by climate, environment, and species interactions. Plants and animals alike rely upon external stimuli to optimize the timing of migrations, blooms, molts, and reproduction (Newton 1966; White et al. 1997; Sherry et al. 2007; Miller-Rushing et al. 2008). Climate change has disrupted the natural timing of such biological processes for many species through intensified rates of warming, prolonged seasons of precipitation or drought, amplification of weather events, and cascading effects through trophic interactions (Cushing 1990; Zhang et al. 2005; Ciannelli et al. 2007; Prieto et al. 2008; Richardson et al. 2013; Asch 2015). For diadromous fishes, changes in thermal regime have already been shown to impact the phenology of spawning migrations (Kovach et al. 2013; Otero et al. 2014; Peer and Miller 2014).

River herring, the collective name for alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), are anadromous fishes that

Received 22 April 2019. Accepted 28 October 2019.

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Can. J. Fish. Aquat. Sci. **00**: 1–11 (0000) dx.doi.org/10.1139/cjfas-2019-0140

are at historically low levels of abundance (Hightower et al. 1996; ASMFC 2012, 2017). River herring once supported large fisheries along the North American Atlantic coast from Nova Scotia down to the St. Johns River, Florida (Jackson 1944; Schmidt et al. 2003; Watts 2003). Declines in river herring stocks have been attributed to overfishing (Hightower et al. 1996), offshore bycatch (ASMFC 2012; Bethoney et al. 2013; Cournane et al. 2013), and loss of spawning habitat due to obstructions and degradation (Collier and Odom 1989; Hall et al. 2011). Attempts to ameliorate the population decline include moratoria, offshore bycatch caps, offshore spatial–temporal closures in the Atlantic herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) fisheries, and dam removal, all of which have been ineffective at recovering stocks (ASMFC 2012; Bethoney et al. 2013; Cournane et al. 2013).

While the decline of river herring was likely caused by a combination of fishing pressures and habitat loss, the continued depression of population levels may result from other ecological mechanisms, including climatological phenomena. For example, Lynch et al. (2015) provide evidence that river herring are vulnerable to ocean warming off the northeast US shelf, reducing the amount of suitable habitat, and that the population may be more sensitive to climate effects at low levels of abundance. Furthermore, a vulnerability assessment of 82 Northeast Atlantic marine fish and invertebrate species by Hare et al. (2016) identified both alewife and blueback herring as species of the highest concern for negative effects of climate change, citing water temperature and the limited periodicity and spatial constraints of their anadromous spawning strategy as the most critical environmental and biological factors, respectively. A tagging study by Jessop (1994) in the Saint John River system shows that river herring exhibit high interannual spawning site fidelity (63%–97% return rate), a process likely driven by olfactory natal homing (Thunberg 1971). In freshwater systems utilized by river herring as spawning and nursery habitat, river flow conditions and water temperature are the dominant influencers of stock recruitment (Tommasi et al. 2015). Early studies in New England at fish weirs and dams have shown the timing and behavior of pre- and postspawning migration river herring to be tightly coupled with stream temperatures and insolation (Collins 1952; Saila et al. 1972; Beltz 1975). Ellis and Vokoun (2009) provided the first suggestion that alewife spawning migrations may be occurring earlier due to higher water temperatures in recent time periods. However, they did not have historical and modern fish count data in the same watershed. Both Lynch et al. (2016) and Tommasi et al. (2015) suggest further examination of the climatological effects on river herring in freshwater systems, and specifically on adult spawning migrations. Despite colloquial and managerial grouping of alewife and blueback herring, the two sympatric species display different behaviors, with alewife spawning migrations happening earlier than blueback herring. Whether migrating blueback herring display the same response to climatological changes as alewife, as suggested by Ellis and Vokoun (2009), has yet to be examined.

Here, we test the hypothesis that the phenology of adult alewife and blueback herring has independently changed by examining river herring catch data during the spawning migration from 1973 to 2016 in the Albemarle Sound watershed (hereinafter referred to as ASW). After describing the temporal variation in spawning migrations, we also evaluate potential mechanisms responsible for the changes, including age structure, abundance, and water temperature. Our work aims to further characterize the response of river herring to shifting climate norms in their southern distribution and to provide life history information to better inform management decisions as the environment continues to change.

## Methods

### Study location and monitoring

The North Carolina Division of Marine Fisheries (NCDMF) has conducted a river herring spawning habitat survey since spring of 1973. The goal of the survey is to identify the annual extent of stream habitats used by both alewife and blueback herring for spawning in nine river systems and their associated tributaries that feed into the Albemarle Sound. Sampling for river herring was intermittent in years between 1973 and 2001 but has been annual since 2007 (see online Supplementary material, Table S1 for sampling summary[1]; Fig. 1 for sampling stations). Although only 24 of the possible 43 years were sampled, sampling occurred in at least 4 years per decade in all decades with the exception of the 1990s (only 1 year of sampling). Prior to 2007, sampling was conducted at randomly selected stations throughout the ASW with varied spatial and temporal extents (see Fig. S1[1]). Beginning with 2008, the methods were standardized to sample the entirety of the river herring spawning run within the Chowan River and Edenton Bay watershed plus at least one of 12 additional ASW river systems on a rotating basis. Additional systems were sampled if travel time to and from sampling stations was not limiting. In 2007, the sampling design changed from random sampling to sampling that tracked the migration progress of river herring through the watershed. Beginning in 2012, sample stations located at the nearest road crossing to the mouths of five Chowan River tributaries became fixed sampling stations that are sampled each week throughout the entire river herring spawning season.

The presence of river herring was monitored with staked or floating gillnets. Gillnet dimensions have varied over the time series, with bar meshes ranging from 1.13 to 1.88 inches (1 inch = 2.5 cm) and lengths ranging from 3 to 30 yards (1 yard = 0.9144 m). Since 2007, the protocol has been standardized, providing more consistent use of bar mesh sizes of 1.38 inches during the alewife run and 1.25 inches during the blueback herring run. Net lengths were also restricted to 5, 8, and 10 yards for staked gillnets; 5, 8, 10, 20, and 30 yards for floating gillnets; and fished at a maximum depth of 2.1 m where possible. Staked gillnets were stretched across the channel width on the effluent side of the furthest downstream bridge or culvert and moved upstream to the next road crossing when running ripe females were encountered. Navigable waterways were sampled with gillnet lengths that left watercraft passage uninterrupted. Gillnets were set on Mondays, checked every 24 h, and removed over weekends and holidays due to logistical constraints. Water surface temperature, air temperature, pH, salinity, conductivity, and dissolved oxygen (DO) were taken at each sampling station upon net inspection.

Prior to 2007, sampling was random in start date, end date, and location and mostly focused on monitoring the blueback herring spawning migration. Starting dates ranged from 4 February to 2 April, with a median start date of 8 March (Fig. S1[1]). Sampling end dates ranged from 21 April to 8 May, with a median end date of 29 April. From 2007 onward, sampling for alewife commenced when alewife were caught in the NCDMF striped bass (*Morone saxatilis*) fisheries-independent gillnet survey, which is conducted within the ASW at the mouths of the river systems. Starting dates ranged from 12 January to 29 February, with a median start date of 6 February. The sampling protocol for 2007 onward began sampling at the most downstream stations and only moved to upstream locations after a running ripe alewife was caught, with the exception of the five fixed nets (2012–present). Nets were reset to their original starting positions when the first blueback herring was caught in any of the alewife survey nets and then moved upstream again as running ripe blueback herring were caught.

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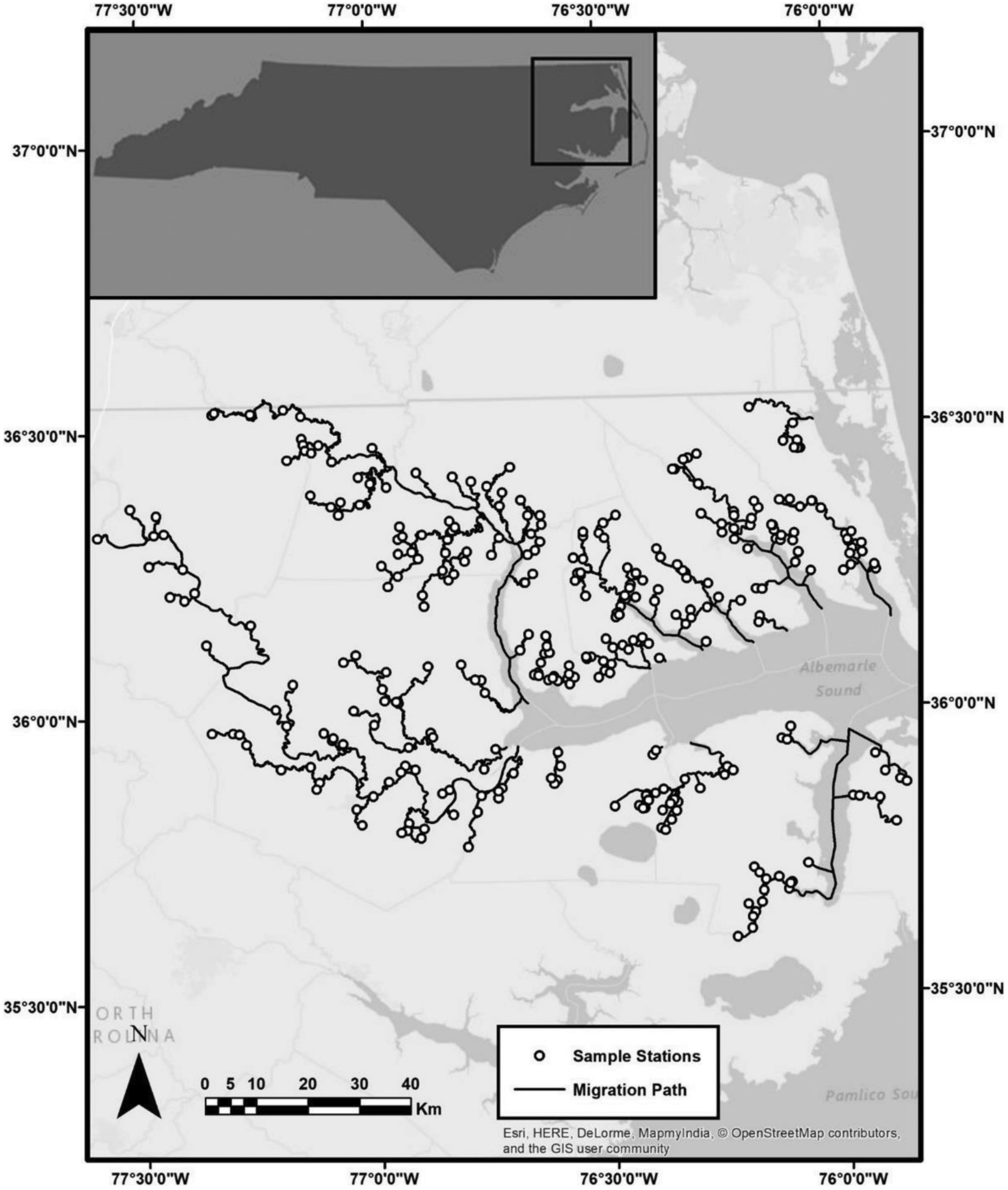
[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0140.

**Fig. 1.** The North Carolina Division of Marine Fisheries river herring spawning habitat survey has been conducted along their migration path (dark line) from 1973 to 2016. During this time period, 325 locations (circles) have been sampled throughout the Albemarle Sound, North Carolina watershed.



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Sampling ceased when catches of blueback herring in the NCDMF Chowan River pound-net survey, conducted in the main stem of the Chowan River, became sporadic (<10 fish per week). The end dates ranged from 29 April to 30 May, with a median end date of 9 May.

## Phenology

Studies on anadromous fish migrations characterize the phenology of the migration by identifying the initiation, peak, and completion (Quinn and Adams 1996; Juanes et al. 2004; Ellis and Vokoun 2009; Kennedy and Crozier 2010). Migration progress is typically delineated by identifying the day of the year that 25%, 50%, and 75% of yearly abundance is observed as reference points for the initiation, peak, and completion of the migration, respectively (Antonsson and Gudjonsson 2002; Kennedy and Crozier 2010; Otero et al. 2014). However, 5% of the run abundance has been used to identify the initiation of alewife spawning migrations in New England (Ellis and Vokoun 2009) and the Chesapeake Bay (Ogburn et al. 2017). Owing to the variability in gillnet sizes and amount of stream width covered by gillnets at sampling locations across years, presence–absence data were used instead of abundance data to characterize the phenology of river herring spawning.

We used generalized additive models (GAMs) with a logit link and a binomial distribution to examine the effects of several variables on river herring presence and absence data. GAMs are useful in modeling nonparametric relationships typical of ecological data (Hastie and Tibshirani 1990) and have been shown to be a more accurate representation of phenology than first appearance dates or alternative measures (Moussus et al. 2010). Penalized thin plate and tensor product splines with shrinkage parameters were used as smoothers. The inclusion of shrinkage parameters allows for completely smoothed predictors to be selected out of the model by reducing the splined term to zero (Wood 2006). Environmental (surface temperature, DO, pH, conductivity, upstream distance) and temporal (ordinal day and decade) variables were screened for correlation and brought into the models a priori based upon knowledge of the environmental cues that river herring use to initiate migratory behavior and inspection of plots of river herring presence probability and potential variables. Because of correlation with ordinal day, we dropped water quality parameters and retained ordinal day.

Owing to the sampling procedures and efforts varying across the 43-year time series, some special considerations needed to be made when constructing and making inferences from the models. Upon inspection of the data, we determined that sampling was too sparse to model the phenological trends at a yearly resolution. Modeling at a broader scale, using decade, allowed for a wider range of days for the model to be fitted to and more precise measures of fish presence within the system. It is important to note that similar changes in phenology (described below) were observed when using year instead of decade. Decadal differences in the first and last dates of sampling resulted in GAM predictions occurring outside of the dates where sampling occurred. Extrapolation is not recommended without ecological justification and results should be evaluated critically (Merow et al. 2014). Thuiller et al. (2004) showed that extrapolating from a restricted range of data (i.e., not capturing leading and trailing absences) can result in disruption of smoothed relationships and more conservative or liberal predictions depending on the information available to inform the model. Owing to river herring being anadromous, temporal extrapolation trending towards egress from the system (5% presence probability) can be ecologically and statistically justified as long as predictions are not extrapolated beyond the temporal bounds of sampling for the entire time series (i.e., the first and last ordinal days sampled). For instances where predictions are extrapolated, a second estimate of ingress can be made as the first detection of presence and egress as the last detection of presence. These latter estimates based on observations are biased late for ingress and biased earlier for egress given that sampling during these periods was limited.

Additionally, the changes in experimental design in 2007 could lead to changes in spatial coverage of the survey in recent years. Because the presence of river herring can change with distance upstream, we accounted for variability in the distance upstream that samples were taken. Distances from the mouth of the river systems to the sample stations were measured using ArcMap 10.3.1 (ESRI, Redlands, California) and the USGS National Hydrography Dataset (NHD; US Geological Survey 2013). Upstream distances ranged from 101 to 188 478 m. Spatial variation was accounted for by creating a proportion: the distance between the tributary mouth and each sample station to the maximum distance a river herring was observed in the tributary (hereinafter referred to as distance proportion).

Although we used distance proportion as a variable to correct for any changes in sampling design over the decades, the variability in sampling locations during the spawning run (i.e., from changing sampling protocol in 2007) was a source of uncertainty in modeling phenology with the complete dataset. The trends in presence at a subset of sample stations that were less impacted by spatial variability in sampling were examined to ensure our results using all data were not biased by changes in sampling protocol. Criteria for the subset selection was that sampling should span the spawning migrations of both alewife and blueback herring as best as possible and that at least 10 unique days were sampled. To obtain sufficient sampling resolution, we binned decades into an “early” set (1970s and 1980s) and a “late” set (2000s and 2010s). The reduction in degrees of freedom caused by binning decades prevented the creation of spline-fitted models similar to those created with the full dataset. The criteria used resulted in a subset of 36 sample stations.

Trends in daily presence (present = 1 or absent = 0) at the sampling event level for the 1970s (1973 to 1979), 1980s (1980, 1982, 1983, 1987, 1988), 2000s (2001 and 2007 to 2009), and 2010s (2010 to 2016) were modeled separately for alewife and blueback herring. The variables included in the models were distance proportion, ordinal day, decade, and the ordinal day and decade interaction.

Final variable selection and model fitting using restricted maximum likelihood (REML) was done within the R package MGCV (Wood 2011). Models were constructed with variables having associated smoothers, no smoothers (linear predictor), and tensor product interaction smooths with the interaction and main effects. Interactions were constructed with tensor product interaction smooths, which are more stable and interpretable than using full tensor product smooths that remove the main effects (Wood 2017). The basis dimensions (*k*), which control the number of basis functions and sets the maximum degrees of freedom for smooth terms in the model, were evaluated using the gam.check() function from the R package MGCV. The basis dimensions were adjusted to balance computational efficiency and reduce overfitting. Akaike’s information criterion (AIC) was used to select the model with the best fit and fewest degrees of freedom (Burnham and Anderson 2002). Percent deviance explained was calculated by subtracting the model deviance from the null deviance, then dividing by the null deviance and multiplying the result by 100 (Stoner et al. 2001).

Model prediction success was evaluated using receiver operating characteristics (ROC) plots generated in the R packages ROCR and pROC (Sing et al. 2005; Robin et al. 2011). The ROC uses a series of misclassification matrices computed for a range of presence probability cutoffs from 0 to 1, then plots the true positive fraction against the false positive fraction (Fielding and Bell 1997; Pearce and Ferrier 2000; Brotons et al. 2004). The area under the curve (AUC) is a measure of model performance, where an AUC = 0.5 yields the same predictive capacity as chance, and increases above 0.5 represent increases in predictive capacity (Hosmer and Lemeshow 2000; Mandrekar 2010).

Model predictions were used to estimate three spawning migration reference points. These were (*i*) ingress at 5% presence probability, (*ii*) peak presence probability, and (*iii*) egress at 5% presence probability. Where no single, clearly defined peak existed (i.e., a plateau or bimodal curve), the mean day along the plateau or between the peaks was designated as the peak (i.e., central measure) spawning day for that decade. There were instances where the beginning or end of the spawning migration was not sampled and predictions from the model would have to be extrapolated >1 day to reach 5% presence probabilities; in these cases, estimates of ingress and egress were made using the first and last date of observed detections. Confidence intervals (CIs) were established for ingress, peak (unimodal), and egress using the presence probability CIs for the preceding and following ordinal days.

## Drivers of phenology changes

Temperature can be a particularly strong driver in movement of anadromous fishes (Antonsson and Gudjonsson 2002; Ellis and Vokoun 2009; Kennedy and Crozier 2010). We used associated water temperature data to determine temperatures that triggered migrations and whether those were consistent across decades. The 36-station subset used to evaluate the phenology models was also used in a two-way ANOVA to examine the effect of the interaction between ordinal day and time period on temperature. The annual data were binned into early (1970s–1980s) and late decades (2000s–2010s) to provide sufficient data for regression. Water temperature data in the early decades were sparse, particularly in the early spring, relative to later decades; thus, we limited our temperature and migration analysis to egress only for alewife. We

**Table 1.** Logistic generalized additive model (GAM)-derived migration metrics for alewife and blueback herring spawning in the Albemarle Sound, North Carolina watershed.

(*a*) Alewife

| Decade | Ingress | Egress | Peak | Season length |
|---|---|---|---|---|
| 1970 | 43 (37–48) | 129 (124–138) | 82 | 86 |
| 1980 | 48 [≤ 55]* | 122 (113–127) | 81 | 74 [≥ 67] |
| 2000 | 24 [≤ 34]* | 107 (104–110) | 70 (67–73) | 83 [≥ 73] |
| 2010 | 27 (22–31) | 102 (100–104) | 70 (67–73) | 75 |
|  | Ingress diff. | Egress diff. | Peak diff. | Season diff. |
| 1970s vs 2010s | –16 | –27 | –12 | –11 |
| Per decade | –4 | –6.75 | –3 | –2.75 |

(*b*) Blueback herring

| Decade | Ingress | Egress | Peak | Season length |
|---|---|---|---|---|
| 1970 | 76 (73–79) | >150 [≥ 128]* | 117 (105–145) | >74 [≥ 52] |
| 1980 | 79 (76–82) | 138 [≥ 126]* | 108 (99–118) | 59 [≥ 47] |
| 2000 | 71 (70–73) | 117 (116–119) | 95 (88–102) | 46 |
| 2010 | 74 (73–75) | 115 (114–116) | 95 (90–101) | 41 |
|  | Ingress diff. | Egress diff. | Peak diff. | Season diff. |
| 1980s vs 2010s | –5 | –23 [≤ –9] | –13 | –18 [≤ –6] |
| Per decade | –1.66 | –7.66 [≤ –3] | –4.33 | –6 [≤ –2] |

**Note:** Metrics are ordinal date of ingress (5% probability of presence on left-hand side of the distribution), egress (5% probability on right-hand side), peak (maximum presence probability in a unimodal curve or mean day of maximum presence probabilities in bimodal–plateaued curve), and season length estimations (difference between ordinal dates of ingress and egress). The 95% confidence intervals for ingress, egress, and peak are given in parentheses. Some estimates of ingress and egress are extrapolated predictions and are denoted with an asterisk (*). For migration metrics estimated by extrapolation, we also provide estimates of ingress and egress based upon first presence and last presence in square brackets.

estimated the water temperature on the days when ingress (blueback herring only) and egress occurred in the early decades (alewife: 1970s; blueback herring: 1980s) using the early decades temperature fit. We then estimated the ordinal day when that temperature occurred in the late decades temperature fit and compared it with the ingress and egress days predicted by the later decade phenology models. To ensure our results were not biased by nonoverlapping periods, we also ran the regression only using data from the same ordinal day range.

Although we detected decadal shifts in ingress and egress timing (see Results below), we were interested in whether we could link annual variability in river herring migrations to annual variability in mean water temperature or rate of temperature change. This analysis was limited to 2008 to 2016 because of limitations with water temperature data for earlier years. Furthermore, estimates of ingress for alewife were not possible for all of these years, so we limited our analysis to egress timing only for blueback herring and alewife. A subset of Chowan River and Edenton Bay catch data from 2008 to 2016 were used to create both alewife and blueback herring GAM models with the same structure and interpretation of egress as the full dataset phenology models. Rates of water temperature change for each year between 2008 and 2016 were estimated by creating linear regression models over the range of days that egress was predicted for 2008–2016. Mean water temperature for each year from 2008 to 2016 was calculated as the mean water temperature over the range of days that egress was predicted for each species (alewife: 4–18 April, and blueback herring: 15–30 April; see Results below). Correlation between days of egress and the two water temperature metrics was assessed by Pearson's *r*.

### Comparison of presence–absence with abundance data

We used presence–absence data at multiple stations to examine for changes in phenology, while others have used percent-of-run abundance percentiles at stationary locations (see Antonsson and Gudjonsson 2002; Ellis and Vokoun 2009). We tested whether presence–absence data are a good proxy for abundance by comparing the ASW 2010s decade phenology metrics with phenology metrics calculated using 2016 river herring spawning run abundance data from the nearby (~140 km to the north) Chickahominy River, Virginia. The Virginia Institute of Marine Science (VIMS) operates a fishery-independent alosine monitoring program for this river (Hilton et al. 2017). We compared ingress (ingress 5% presence probability versus 5% run abundance), peak (peak presence probability versus 50% run abundance), and egress (egress 5% presence probability versus 95% run abundance).

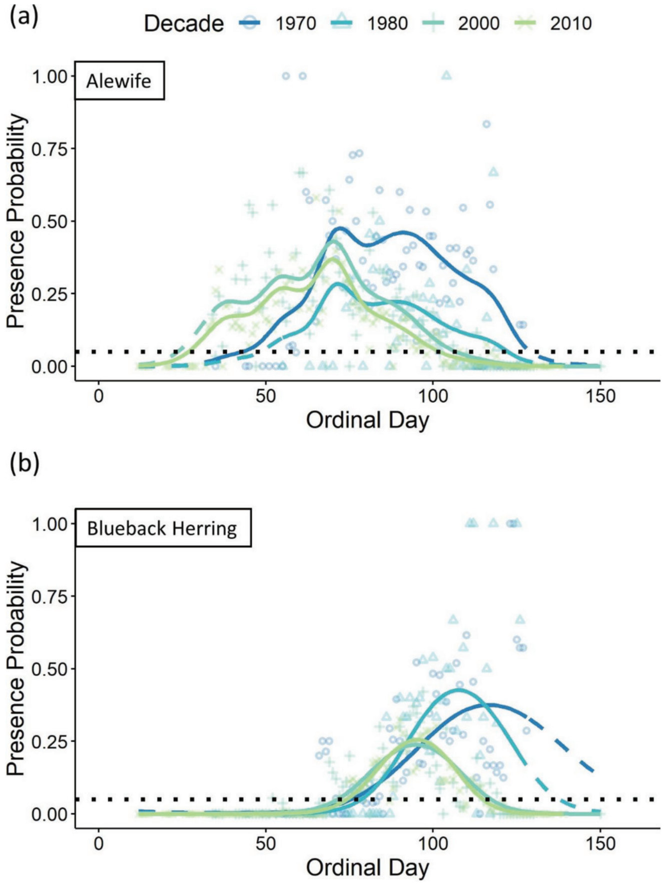
## Results

Over the 43-year time period (1973–2016), there were 12 839 sampling events made at 325 sample stations (see Fig. 1 for stations). A total of 8970 alewife were caught (40.4% female, 58.1% male) in 2241 net sets (17.5% catch rate), and 8609 blueback herring were caught (51.2% female, 47.8% male) in 1295 net sets (10.1% catch rate).

### Alewife phenology

AIC selection strongly favored the full model, which included distance proportion, day, decade, and the interaction between day and decade (Table S2[1]). The decadal change in timing on the spawning grounds is dramatic, with a clear shift in ingress, peak, and egress and a resulting shortening of time on spawning grounds (Table 1; Fig. 2*a*). The changes are evident even with estimations based upon the first and last presences. In the 1970s, estimated alewife ingress (5% presence probability) was 12 February, peaked at 23 March, and completed their time on spawning ground by 9 May (egress estimate extrapolated 1 day). In the 2010s, these three dates were 27 January, 11 March, and 12 April, respectively. The mean change in migration ingress and egress was –4 days per decade and –6.75 days per decade, with net changes of –16 and –27 days, respectively. The imbalanced shift in ingress and egress has reduced the time that the alewife population spent on

**Fig. 2.** Logistic generalized additive model (GAM)-derived predictions of (*a*) alewife and (*b*) blueback herring presence probability. Probabilities were modeled using ordinal day, decade, distance proportion, and ordinal day × decade interaction for samples collected in the North Carolina Division of Marine Fisheries river herring spawning habitat survey throughout the Albemarle Sound, North Carolina watershed. Solid curves are model predictions over dates sampled, while broken lines are extrapolated predictions; points represent the raw presence proportions for all nets set on each day of the decade. Predicted presence probabilities are shown as a function of ordinal day while holding other covariates at mean values. Black dotted horizontal line at 0.05 indicates estimates of ingress and egress. [Colour online.]



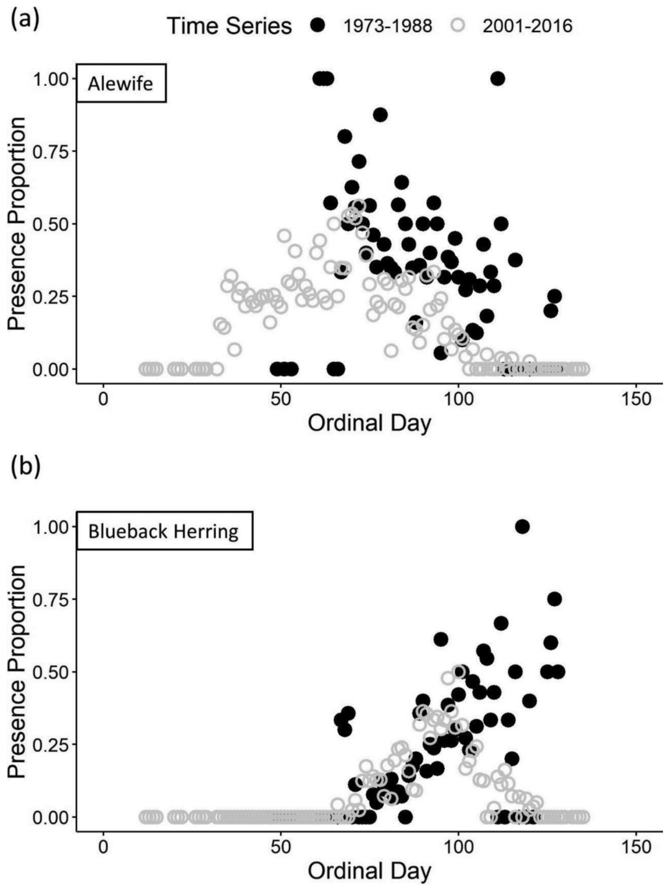
the spawning grounds by 11 days. The date of peak catch probability occurred 12 days earlier over the four-decade time period.

The proportion of alewife presence detections at a subset of 36 sample stations that were consistently sampled in the early decades (1970s and 1980s) and late decades (2000s and 2010s) corroborate the modeled phenological changes (Fig. 3*a*). During ingress time periods in the early decades (around day 43), presence proportions were much greater in the later decades. During the egress time periods in the early decades (around day 129), presence proportions were zero or near-zero in the later decades and substantially lower than the presence proportions in the early decades. Thus, changes in sampling design between the early and late decades does not explain the changes in phenology of alewife spawning.

## Blueback herring phenology

AIC selection strongly favored the full model, which included distance proportion, day, decade, and the interaction between day and decade (Table S2[1]). Blueback herring showed the same phenological shifts as alewife, but with a smaller change in the date of ingress and a larger shift in egress (Table 1; Fig. 2*b*). Decadal comparisons were not made with the 1970s because sampling or model extrapolation could not be done for the egress period. However, egress was captured by extrapolation in the 1980s, and decadal comparisons can be made for all 1980s migration metrics. In the 1980s, blueback herring arrived at 20 March, peaked at 18 April, and completed their spawning migration by 18 May. In the 2010s, these three dates were 15 March, 5 April, and 25 April, respectively. The mean change in migration ingress and egress was –1.67 days per decade and ~ –7.67 days per decade, respectively. The date of peak catch probability occurred 13 days earlier over the three-decade time period.

**Fig. 3.** Presence proportions for (*a*) alewife and (*b*) blueback herring at 36 sampling locations regularly sampled across four decades of North Carolina Division of Marine Fisheries river herring sampling. Proportions are calculated from samples taken on any given day within the early (1973–1988) or late (2001–2016) time periods.

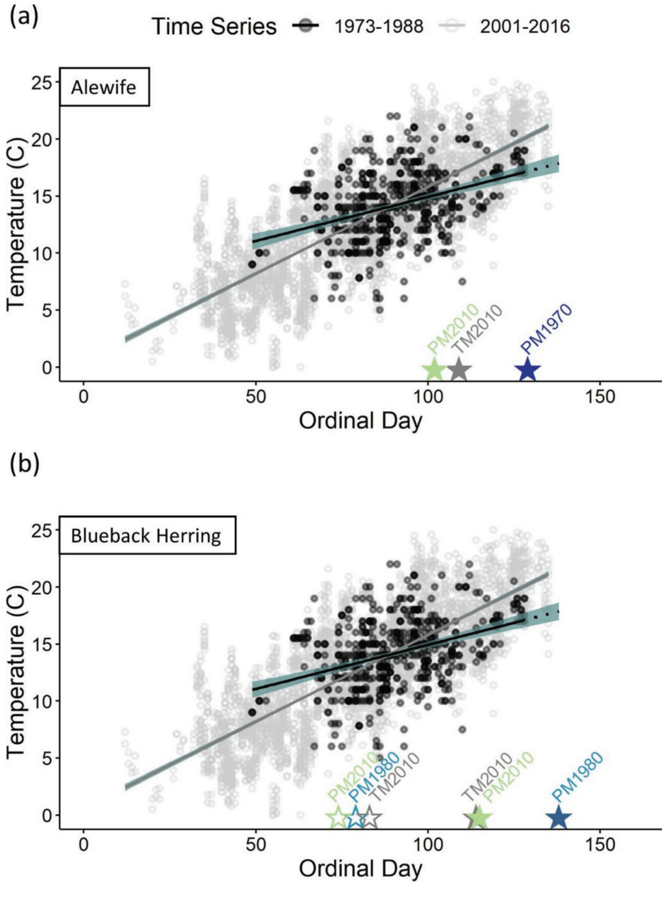


As with alewife, the proportion of blueback herring presence detections at the subset of 36 stations were examined and also corroborate the phenology model (Fig. 3*b*). During ingress time periods in the early decades (around day 79), presence proportions were marginally greater in the later decades. During the egress time periods in the early decades (around day 138), presence proportions were much lower or zero in the later decades compared with the higher and nonzero presence proportions in the early decades. Thus, changes in sampling design between the early and late decades do not explain the changes in phenology of blueback herring spawning.

## Effects of vernal warming rate on phenological shifts

Water temperatures recorded at the 36-station subset for both the early decades (1973–1988) and the late decades (2001–2016) provide the best data coverage to describe late spring warming

**Fig. 4.** Estimates of ingress and egress from the phenology models (PM) can be compared with temperature predicted (TM) ingress and egress dates. We input early decade PM predicted dates of ingress (open stars) and egress (solid stars) into the 1973–1988 water temperature and ordinal day models (lines) to identify associated temperatures. Those early decade-predicted temperatures of ingress and egress are then input into the 2001–2016 temperature and ordinal day regression to predict a date of ingress and egress for the late decade period (TM2010) that can be compared with the late decade PM predicted ingress and egress dates (PM2010). Water temperatures associated with early decade egress for alewife and blueback herring were 17.2 and 17.9 °C, respectively; TM2010 egress dates (solid stars) for these two species were estimated at days 109 and 114 and were similar to the PM2010 egress dates (solid stars) of days 102 and 115. Blueback herring ingress was also examined using the same approach. The PM1980 associated ingress temperature was 13.3 °C; the estimated date of ingress based on temperature (open star; TM2010) was day 83, which was slightly later than the estimated date of ingress (day 74; PM2010) from the phenology model. The blue shading represents the 95% CI. [Colour online.]



trends during the egress times of alewife and blueback herring. The rate of vernal warming during 2001 to 2016 (0.152 $°C·day^{-1}$; 95% CI 0.119–0.191 $°C·day^{-1}$) was significantly higher than warming rate (0.077 $°C·day^{-1}$; 95% CI 0.060–0.095 $°C·day^{-1}$) during springs of 1973–1988 (ordinal day × time period; $F_{[3,3665]} = 65.23$; $p < 0.001$; Fig. 4). A second comparison of warming rate between the two time periods but limited to the same range of ordinal days maintains this trend ($F_{[3,3140]} = 72.92$; $p < 0.001$; Fig. S2[1]). The increased rate of warming results in higher predicted temperatures from day 88 (29 March, at 14.0 °C) onward. Elevated temperatures, or faster warming, from 29 March onward may be responsible for expediting the egress of both alewife and blueback herring. The alewife phenology model predicted a 1970s egress date of 9 May (day 129). The egress associated water temperature estimated on this date for 1973–1988 was 17.2 °C, which occurred on 19 April (day 109) in 2001–2016 (estimates from temperature versus ordinal day regressions). The alewife phenology model predicts a 2010s egress date of 12 April (day 102) that is only 7 days earlier than the estimate based on temperature. The blueback herring phenology model predicted a 1980s egress date of 18 May (day 138). The egress associated water temperature estimated on this date for 1973–1988 was 17.9 °C, which occurred on 24 April (day 114) in 2001–2016. The blueback herring phenology model predicts a 2010s egress date of 25 April (day 115) that is only 1 day later than the estimation using egress temperature. The blueback herring phenology model predicted a 1980s ingress date of 20 March (day 79). The ingress associated water temperature estimated on this date in 1973–1988 was 13.3 °C, which occurred on 24 March (day 83) in 2001–2016. The blueback herring phenology model predicts a 2010s ingress date of 15 March (day 74). Although this represents a difference of 9 days, it is important to point out the similarities in dates for 13.3 °C water in the two time periods (20 March for 1973–1988 and 24 March for 2001–2016) and the similarities in dates for ingress predictions (20 March in the 1980s versus 15 March in the 2010s).

We examined the relationship between annual timing of river herring egress and annual water temperature metrics from 2008 to 2016. AIC model selection strongly favored the full model structure (Table S3[1]). Within the Chowan River and Edenton Bay systems, alewife were predicted to egress between 4 and 18 April (Table S4; Fig. S3[1]). Mean water temperatures over these days ranged from 13.8 to 17.9 °C, and the rate of temperature change ranged from −0.32 to 0.52 $°C·day^{-1}$. The relationships between alewife egress date and both water temperature metrics were slightly negative (Fig. S4[1]), but neither correlation was significant (temperature: $r = -0.09$, df = 7, $p = 0.82$; rate: $r = -0.04$, df = 7, $p = 0.92$). Blueback herring were predicted to egress between 15 April and 1 May. Mean water temperatures over these days ranged from 15.4 to 19.8 °C, and the rate of temperature change ranged from −0.63 to 0.56 $°C·day^{-1}$. The relationships between blueback herring egress and both temperature metrics were also not significant (temperature: $r = -0.46$, df = 7, $p = 0.22$; rate: $r = 0.27$, df = 7, $p = 0.48$; Fig. S4[1]). Thus, we did not find evidence of temperature metrics influencing egress dates for alewife and blueback herring during the 2008 to 2016 period.

### Comparing presence–absence and abundance data for spawning phenology metrics

For the most recent decade (2010s), our presence probability derived phenology metrics for river herring in the ASW match closely with the percent-of-run abundance phenology metrics (5%, 50%, and 95%) calculated for the 2016 river herring spawning run in the Chickahominy River. For alewife in the Chickahominy River, percent-of-run abundance yields 3 February, 9 March, and 6 April as the dates of ingress, peak, and egress, respectively, while our estimates are 27 January, 11 March, and 12 April, respectively. The three percentiles for blueback herring in the Chickahominy River occur on 16 March, 31 March, and 27 April, and our estimates are 15 March, 5 April, and 25 April. Thus, our migration metric predictions using presence–absence data were within ±7 days (mean ±3.5 days) of those using abundance data in a nearby system.

## Discussion

### Changes in river herring spawn phenologies and potential causes

We provide evidence that the spawning migrations of alewife and blueback herring have shifted to earlier dates in recent decades within the ASW, with substantial truncation of blueback herring spawning season length. Our results are consistent with trends observed in other anadromous populations: southern New England alewife (Ellis and Vokoun 2009), Atlantic salmon (*Salmo salar*) (Juanes et al. 2004), Pacific salmonids (*Oncorhynchus* spp.) (Kovach et al. 2015), and Chesapeake Bay striped bass (Peer and Miller 2014). Ellis and Vokoun (2009) found that changes in spring temperatures across approximately four decades was associated with alewife migrations that occurred ~12 days earlier. Peer and Miller (2014) observed earlier shifts in spring-spawning migration metrics (ingress, peak, and egress) of 800–899 mm female Chesapeake Bay striped bass. From 1991 to 2010, the striped bass arrived, peaked, and left 5, 6, and 14 days earlier, respectively. Shifts in the timing of anadromous spawning events can have cascading negative effects, such as reduced population resiliency through decreases in phenotypic variation (Sgrò et al. 2011), trophic mismatches that have substantial impacts on the survival of offspring (Cushing 1990; Durant et al. 2007; Fortier and Gagné 2011), nutrient influx (Walters et al. 2009), and especially food web dynamics in the case of forage fish (Yako et al. 2000). Management strategies, such as seasonal harvest closures, can also become less effective due to shifts in migration timing (Peer and Miller 2014).

Changes in the phenologies of migration and spawning across animal groups have been attributed to changes in age structure (Lambert 1987; Hutchings and Myers 1993; Trippel and Morgan 1994), changes in species abundance (Miller-Rushing et al. 2008), and shifts in environmental cues due to climate change (Quinn and Adams 1996; Ellis and Vokoun 2009). We examined the possibility for each of these for alewife and blueback herring in the ASW.

The relationship between the timing of spawning runs and age structure has not been addressed in the literature for river herring. Lambert (1987) detailed this relationship with another clupeid species, Atlantic herring, in both the Atlantic and Pacific stocks. Lambert (1987) concluded that larger, older fish arrived on the spawning grounds earlier than their smaller, younger conspecifics. It is reasonable to believe that the relationship between age–length and the timing of arrival upon the spawning grounds found in this confamilial applies to both alewife and blueback herring as well. The phenomenon has also been found in another anadromous species, striped bass (Peer and Miller 2014). Thus, any shift towards an older age structure should manifest itself in earlier spawning migration times. However, no change in alewife age structure was observed, and blueback herring age structure trended towards a younger age structure in recent decades, which is opposite of the pattern that might explain earlier spawning (NCDMF, unpublished data). Thus, we conclude that changes in age structure are not responsible for changes in river herring spawn times within the ASW.

Alewife and blueback herring population abundances in the ASW have decreased dramatically from the early 1970s to present and are currently at levels deemed to be overfished despite the absence of fishing pressures since 2007 (White et al. 2017). Thus, changes in abundance are one potential reason for changes in spawn timing. However, the relationship between population abundance and migration phenology has received very little study. Miller-Rushing et al. (2008) found that first arrival of several bird species in spring were related to population size since a larger population size would have a higher likelihood of detection. The earlier spawning in recent years is opposite of the pattern expected given decreased abundance levels. For anadromous fishes, there is potential for abundance levels to change the length of spawning time, but we did not find studies that examined this effect. Because river herring abundance declined in the ASW as vernal warming rate increased (see below), we cannot disentangle these two variables. We recommend research on the effects of abundance on spawning phenology in anadromous fishes.

Water temperature has repeatedly been identified as having an influence on spawning and migration timing for many anadromous species: striped bass (Peer and Miller 2014), Atlantic salmon (Juanes et al. 2004), American shad (*Alosa sapidissima*) (Quinn and Adams 1996), lake sturgeon (*Acipenser fulvescens*) (Bruch and Binkowski 2002), as well as alewife (Ellis and Vokoun 2009). Temperatures within the coastal mid-Atlantic region of the United States have been increasing over the past century (Polsky et al. 2000), with particularly larger changes observed in lower-order streams (Ding and Elmore 2015), such as those used by river herring as spawning habitat. Our results suggest that earlier vernal warming has led to an earlier spawning season for river herring in tributaries of the ASW. Our findings support the conclusions of Ellis and Vokoun (2009) for southern New England alewife. Their estimations of change in alewife ingress and peak migration were 13 and 12 days earlier, respectively, while our models predicted 16 and 12 days earlier. The strongest evidence for a temperature effect is that the temporal shift in egress dates predicted by the phenology models are similar to the changes in dates in which egress-associated temperatures (~17 °C) are reached. The temperature-predicted and observed egress dates in more recent decades were earlier and similar in timing for alewife (7 days apart) and blueback herring (1 day apart).

The egress temperatures we estimated for alewife and blueback herring (~17 °C) were similar to those observed in a river system ~300 km north. Ogburn et al. (2017) estimated the daily count of both upstream and downstream migrating alewife and blueback herring in the Choptank River, Maryland, for the 2014 spawning season using a dual-frequency identification sonar (DIDSON). Strong pulses of downstream migration in April and May appear to coincide with water temperatures near 17 °C. If the rate of vernal warming increases over time, water temperatures on river herring spawning grounds will reach 17 °C sooner and continue to shorten the spawning season if ingress timing remains the same or changes less than egress times. In fishes, climate change-driven shifts in phenology have been shown to negatively impact reproduction success and recruitment (Both et al. 2006; Watanuki et al. 2009). For river herring spawning within the ASW, shifts towards earlier egress dates has reduced time on the spawning grounds and may negatively impact spawning success and recruitment.

Trends in the phenological response to changing thermal regimes within a watershed were observed at the decadal scale; therefore, variation in population-level responses to relatively cool or warm springs for a given year within a decade might also be observable. Correlations between the interannual variation in the timing of egress and both the annual mean temperature and rate of temperature change across the range of predicted egress days were not significant. However, the correlations did trend towards earlier egress timing when mean annual water temperatures over the range of egress dates were warmer (Fig. S4[1]). Plasticity in migration timing, and subsequently spawning activity, could be optimized to avoid mismatches in resource availability (Cushing 1990). Phenological shifts in response to climate change have been observed in many inland fish populations (Lynch et al. 2016). However, research on brook trout (*Salvelinus fontinalis*) suggests that the rate of climate change can outpace compensatory responses and lead to a decline in population abundances (Bassar et al. 2016). More work is needed to understand the limits of adaptation to climate change by river herring.

## Comparing presence–absence and abundance data for spawning phenology metrics

The use of presence–absence data at multiple stations to measure changes in phenology is a novel method that required validation. The established approach to measuring timing of anadromous fishes is percent-of-run abundance percentiles using count data at stationary locations. Our predictions using presence–absence data were within ±7 days (mean ±3.5 days) of those using abundance data in a nearby system. These results show that presence–absence data, which are much less labor intensive and more readily accessible than abundance data, are a viable proxy for abundance data when estimating measures of phenology. We encourage further examination of other long-term datasets for signals in shifting phenology using presence–absence data when abundance data are unavailable.

### Implications

There has been increased interest in the incorporation of climate change effects (e.g., changes in phenology) into fisheries management strategies (Haak and Williams 2012; Peer and Miller 2014; Hare et al. 2016; Paukert et al. 2017). Management strategies for river herring so far have focused on the effects of increased fishing efforts and have attempted to mitigate historical overfishing through moratoria (but see Hare et al. 2016). While moratoria provide a major reduction in fishing mortality, it may not be sufficient to return stocks to historical levels of abundance in the face of warming waters and changing climate, particularly in the species' southern range (Tommasi et al. 2015). Current river herring stocks in North Carolina (White et al. 2017) and other Atlantic states (ASMFC 2017) remain in a depleted state.

Spawning phenologies of river herring in the ASW and recruitment should continue to be monitored. In the event that the fishery is re-opened, information on spawning migrations could be used in an adaptive management strategy framework (Peer and Miller 2014). It is important to note the differences between alewife and blueback herring spawning migration behaviors and apparent responses to increased vernal warming rate. Examining the shape of the phenology model curves provides insight into such differences (Fig. 2). Alewife have a much broader spawning migration season with evident pulses in migration, which appear as humps in the GAM (GAMs do not assume any particular shape). Comparatively, blueback herring spawning migrations follow a more unimodal distribution, despite also migrating upstream in pulses. The same patterns and contrasts in migration behavior have been seen in the Choptank River, Maryland, by Ogburn et al. (2017) when using DIDSON to monitor spawning runs. The shift in spawning migration phenology for alewife has resulted in an 11-day truncation of the spawning season over four decades (Table 1); however, considerable changes in ingress and egress timing have both occurred simultaneously (16 and 27 days, respectively). This is in strong contrast with blueback herring, which have maintained ingress timing (5-day change over three decades) but have egressed substantially earlier over time (23 days earlier over three decades). The variation in phenological changes may be due to different conditions encountered in preferred spawning habitat, as stream temperatures and water quality can vary widely throughout a watershed (Isaak et al. 2014). Generally, alewife prefer more lentic habitats compared with blueback herring (Loesch and Lund 1977). However, river herring in the ASW have a high degree of overlap in spawning habitat use, due in part to the slow-flowing tributaries (Walsh et al. 2005; S. Lombardo, personal observation), which makes spatial separation an unlikely driver of phenological variation. Physiological differences in thermal tolerances are most likely to influence spawning migration (Mullen et al. 1986).

The 30% reduction in spawning season length for blueback herring is concerning, considering their already depressed abundance in this region. The most recent stock assessment of blueback herring estimated the ASW population of age 3+ (sexually mature) fish to be 7.5 million fish in 2014, just 6% of the 127 million fish in 1976 (White et al. 2017). The truncation of time spent on the spawning grounds may have ramifications for recruitment through effects on adult spawning (i.e., reduced chances for optimal spawning conditions) or trophic or habitat mismatches for larvae and juveniles (Wright and Trippel 2009; Ohlberger et al. 2014). Tommasi et al. (2015) found that increased temperatures in June were associated with lower abundance levels of juvenile blueback herring in the Chowan River, North Carolina (a tributary of ASW); they hypothesized the decreased recruitment was due to temperatures exceeding an optimal temperature and predicted that future warming would lead to reduced recruitment in southern populations of river herring. In addition to more research on temperatures experienced by juveniles, we recommend research to test for a relationship between spawning phenology and recruitment in river herring.

## Acknowledgements

This research was funded by a North Carolina Division of Marine Fisheries Coastal Recreational Fishing License Fund grant (NCDENR Task Order No. 6426). We thank past and present members of the North Carolina Division of Marine Fisheries in Elizabeth City, North Carolina, for their work in data collection and entry. Special thanks to Milo Page for his input and suggestions in modeling these data.

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