# ABSTRACT

LOMBARDO, STEVEN MICHAEL. Phenological Characterization and Effects of Environmental Attributes on River Herring Spawning Migrations within the Albemarle Sound Watershed. (Under the direction of Dr. Jeffrey A. Buckel).

River herring, the collective name for alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), are anadromous fishes that are at or near historically low levels of abundance throughout their distributions. Historically, river herring supported one of the largest fisheries in North America. A combination of commercial pressure directly on the spawning grounds, offshore bycatch, and habitat degradation contributed to the collapse of river herring populations. Despite efforts to recover river herring stocks, which includes moratoria, bycatch caps, dam removal, and habitat restoration, stocks still have yet to rebound. We identified the spawning migration process as a potential bottleneck for recovery as it is particularly sensitive to environmental conditions. Our study objectives were to 1) characterize variation in the timing and duration of river herring spawning migrations within the Albemarle Sound watershed over a four-decade period and 2) elucidate whether agriculture/silviculture and development within the riparian zone impede the ability of river herring to migrate upstream, identify which habitat attributes are the most important for determining the suitability of habitat, and explore whether culverts are acting as a barrier for upstream migration.

Using logistic Generalized Additive Models (GAMs) and NC Division of Marine Fisheries (NCDMF) river herring spawning habitat survey data that spans four decades (1973 – 2016), we observed phenological changes in the timing and duration of spawning migrations for both alewife and blueback herring. When comparing the alewife spawning migration in the 1970s to migration in the 2010s, alewife arrive to the spawning grounds 16 d earlier, the spawning migration peaks 12 d earlier, the egress is 27 d earlier, and 11 d less are spent on the spawning grounds. When comparing the blueback herring spawning migration in the 1980s to the migration in the 2010s, blueback herring are arriving 5 d earlier, the peak of the migration is 13 d earlier, the egress occurs 23 d earlier, and 18 d less are spent on the spawning grounds. We hypothesized age structure, abundance, or vernal warming to be potential drivers of the observed change in phenology. Water temperature data suggest that an increased vernal warming rate in recent decades (2000s & 2010s vs 1970s & 1980s), specifically in April and May, is driving earlier egress times for both species.

In order to look at the effects of agriculture/silviculture, urbanization, and water quality on the ability of river herring to migrate upstream, we again used NCDMF river herring spawning habitat survey data (2007 – 2016) and logistic GAMs, in addition to 2010 land cover condition NOAA Coastal Change Analysis Program data. Presence/absence data from the NCDMF river herring spawning habitat survey was also used to evaluate culvert passability for river herring (observationally). We found no effect of agriculture/silviculture or development on upstream migration for either species. Water temperature and DO concentration were the two most important contributors for the presence of both alewife and blueback herring. The presence of culverts within the Albemarle Sound watershed currently does not appear to be restricting habitat availability or use. The 60 culverts sampled by the NCDMF were classified: 8 passable, 3 unpassable, 15 reached but undetermined passability, 1 potentially unpassable, 1 unknown, and 32 unreached. Overall, habitat conditions within the Albemarle Sound watershed appear suitable for river herring and efforts should be put forth to maintain those conditions.

# Phenological Characterization and Effects of Environmental Attributes on River Herring Spawning Migrations within the Albemarle Sound Watershed.

by
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# BIOGRAPHY

Steven Michael Lombardo was born on February 28, 1989 in Garfield Heights, Ohio. As a child, he was innately curious about nature and science in general; a trait his parents nurtured and urged him to pursue avidly. He attended Medina High School where he excelled in AP Biology and Chemistry. In 2007 he started working towards his bachelor's degree at Cuyahoga Community College in Parma, Ohio. He transferred to the University of Akron in 2009 as a biology major. While at the University of Akron, he began to focus his studies on aquatic biology. He pursued coursework in freshwater ecology (Lavrentyev), wetlands ecology (Mitchell), and marine ecology (Weeks & Moore). He also found great interest in comparative animal physiology and organic chemistry. As a junior, Steven began to work in the comparative animal physiology laboratory of Dr. Brain Bagatto, and worked closely with, then PhD student, Dr. Christopher Marks as part of the Tiered Mentoring Program. He completed two research projects on zebrafish ontogeny, one of which went on to be published. After graduating *magna cum laude* from the University of Akron in 2012 with a Biology degree, Steven spent two years as a wet/radiological chemist and field technician for Summit Environmental Technologies Inc. He returned to his passion of aquatic science, specifically fisheries, when he accepted a position as a creel clerk for the Ohio Department of Natural Resources Division of Wildlife at their Sandusky Fisheries Research Unit. He spent two seasons working on the shores of Lake Erie before accepting a master's position in 2015 at NC State University, in the laboratory of Dr. Jeffrey A. Buckel. He spent one semester in Raleigh where he completed coursework and worked as a Teaching Assistant for an undergraduate Biology course. In the spring of 2016, and subsequently the spring of 2017, he would move to Elizabeth City, NC in order to work directly with the NC Division of Marine Fisheries and their river herring spawning habitat survey crew.

While in Elizabeth City, he would take a full course load while collecting data that would be used in the two studies described below.  After his field seasons, he would move to Morehead City, NC where he would continue coursework, work on analyses, presentations, and writing. The research and coursework completed throughout his time at NC State University has contributed to his growth as a student, scientist, and person.  He will continue that growth as he transitions into a PhD position at Florida Atlantic University's Harbor Branch Oceanographic Institute to study juvenile bonefish habitat.  As he moves forward in his career, he hopes to continue to help fisheries managers devise strategies to achieve sustainability and protect valuable habitat.

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**CHAPTER 2**

# CHAPTER 1

# Evidence for Temperature-Dependent Shifts in Spawning Times of Anadromous Alewife (*Alosa pseudoharengus*) and Blueback Herring (*Alosa aestivalis*)

## Abstract

Alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), collectively known as river herring, are economically, ecologically, and culturally important fishes that are at low levels of abundance. Populations have remained in a depressed state since the 1970s in spite of fishing moratoria and habitat restoration efforts. We hypothesized that the timing and duration of river herring spawning has been influenced by the increased rate of vernal warming in northeastern North Carolina. We analyzed four decades (1970s, 1980s, 2000s, 2010s) of river herring presence/absence data collected by the North Carolina Division of Marine Fisheries in the Albemarle Sound watershed. We used logistic GAMs to characterize the ingress, peak, and egress timing of river herring within spawning habitat. Relative to the 1970s, estimates from the best fitting models show that alewife now arrive to spawning habitat 16 days earlier and leave 27 days earlier (peak 12 days earlier). Relative to the 1980s, blueback herring are arriving five days earlier and leaving 23 days earlier (peak 13 days earlier). The changes in ingress and egress times have shortened the spawning ground residency time 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 is ~49% faster during the last 20 years and is the most parsimonious explanation for changes in spawn times. The influence of a shortened spawning season on river herring recruitment in the Albemarle Sound watershed warrants further investigation.

## 1. Introduction

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. 2006; Miller-Rushing 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; Prieto et al. 2008; Richardson et al. 2013; Asch 2015). A species' ability to adapt their behavior to rapid environmental changes is imperative to ensuring the survival of oneself and their progeny.

Globally, averaged 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; Blanchard et al. 2005; Perry et al. 2005; Mieszkowska et al. 2006; Fogarty et al. 2008; Nye et al. 2009). Marine species whose life-history are solely dependent upon the marine or estuarine environment are capable of modifying their spatial distributions to stay within optimal thermal ranges for their various life stages. However, diadromous species that exhibit some degree of natal homing, such as river herring, may not be able to spatially account for environmental changes and are at greater risk of experiencing negative effects due to climate change (Hare et al. 2016).

River herring, the collective name for alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), are anadromous fishes that are at historically low levels of abundance (Hightower et al. 1996; ASMFC 2012, ASMFC 2017). River herring once supported large fisheries along the North American Atlantic coast from Nova Scotia down to the St. John's River, FL (Jackson 1944; Watts 2003; Hightower 2004). 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 & Odom 1989; Hall et al. 2010). Attempts to ameliorate the population decline include moratoria, offshore by-catch 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 (Hightower et al. 2004; 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 phenomenon.

In this paper, we examine the phenology of river herring spawning migration from the 1970s to present day. We use fisheries-independent data collected by the North Carolina Division of Marine Fisheries through their river herring spawning habitat survey, which is conducted within the Albemarle Sound, North Carolina watershed. We also evaluate potential mechanisms responsible for changes in the timing of spawning migrations. These include age structure, abundance, and the rate of spring warming.

## 2. Methods

### *2.1. Study Location and Monitoring*

The river herring spawning habitat survey has been conducted by the North Carolina Division of Marine Fisheries (NCDMF) 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 eight 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 Table 1 for sampling summary; Figure 1 for sampling stations). Although only 24 of the possible 43 years were sampled, sampling occurred in at least four years per decade in all decades with the exception of the 1990s (only one year of sampling). Prior to 2007, sampling was conducted at randomly selected stations throughout the Albemarle Sound watershed with varied spatial and temporal extents. 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 twelve additional Albemarle Sound 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 within any river system 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 in. and lengths ranging from 3 to 30 yd. Since 2007, the protocol has been standardized, providing more consistent use of bar mesh sizes of 1.38 in. during the alewife run and 1.25 in. 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 yd for floating gillnets, 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; detection probability for these sets was assumed similar to across channel sets. Gillnets were set on Mondays, checked every 24 hours, and removed over weekends and holidays due to logistical constraints. Water surface temperature, air temperature, pH, salinity, conductivity, and 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 February 4th to April 2nd, with a median start date of March 8th (Figure 2). Sampling end dates ranged from April 21st to May 8th, with a median end date of April 29th. From 2007 onward, sampling for alewife commenced when alewife were caught in the NCDMF striped bass (*Morone saxatilis*) independent gillnet survey, which is conducted within the Albemarle Sound at the mouths of the river systems. Starting dates ranged from January 12th to February 29th, with a median start date of February 6th. 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.

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 April 29th to May 30th, with a median end date of May 9th.

### *2.2. Analysis*

Studies on anadromous fish migrations characterize the phenology of the migration by identifying the initiation, peak, and completion (Quinn & Adams 1996; Juanes et al. 2004; Ellis & Vokoun 2009; Kennedy & 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 (Antonsson & Gudjonsson 2002; Kennedy & 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). Due to the variability in gill net sizes and amount of stream width covered by gill nets at each sampling location, we concluded that abundance data were not a good indicator of river herring phenology. Therefore, we used presence/absence data to characterize the phenology of river herring spawning.

We used generalized additive models (GAMs) with a logit link and a binomial distribution to model the effects of several variables on river herring presence and absence data. GAMs are useful in modeling nonparametric relationships typical of ecological data (Hastie & 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 non-significant variables to be removed from 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.

Due 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 daily sampling effort 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 can result in expeditious termination of the smoothed relationship. In modeling the presence of anadromous fish, which will roughly take the form a parabolic curve, the lack of data where absence was not established before and after the spawning period can yield biased predictions of presence probability. Due to river herring being anadromous, temporal extrapolation towards absence from the system (0% presence probability) can be justified as long as absences or near zero presence probabilities have been established. For instances where this condition is not met, a conservative estimation of ingress can be given as the first detection of presence (or earlier) and egress as the last detection of presence (or later). 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 (ESRI, Redlands, CA) and the USGS National Hydrography Dataset (NHD) (U.S. Geological Survey 2013). Upstream distances ranged from 101 to 188,478 meters. 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 (hereafter 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 modelling phenology with the complete dataset. The trends in presence at a subset of sample stations, created to reduce the spatial variability in sampling, was examined to evaluate whether any temporal changes in presence predicted by our models were still observed when spatial variability in sampling was reduced. 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. In order to obtain sufficient sampling resolution decades were binned 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 30 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 & 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 until the effective degrees of freedom were sufficiently different from k' (k -1). Akaike’s Information Criterion (AIC) was used to select the model with the best fit and fewest degrees of freedom (Burnham & 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 one-hundred (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 & Bell 1997; Pearce & 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, AUC = 0.7 – 0.8 is acceptable, AUC = 0.8 – 0.9 is excellent, and AUC = 0.9 – 1 is outstanding (Hosmer & Lemeshow 2000; Mandrekar 2010).

Model predictions were used to estimate three spawning migration reference points. These were: (1) initiation of ingress at 5% presence probability (herein referred to as ingress), (2) peak presence probability, and (3) completion of egress at 5% presence probability (herein referred to as egress). 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 spawning day for that decade. Conservative estimates of ingress or egress, equivalent to the first and last date of detection, are also given when the beginning or end of the spawning migration was not observed (presence probability $\nless$5%) and predictions are extrapolated >1 d. Confidence intervals were established for ingress, peak (unimodal), and egress using the presence probability CIs for the preceding and following ordinal days.

Temperature can be a particularly strong driver in movement of anadromous fishes (Antonsson & Gudjonsson 2002; Ellis & Vokoun 2009; Kennedy & Crozier 2010). We used associated water temperature data to explore temperature relationships with our modeled migration ingress and egress days. The 30 station subset of data used to evaluate the phenology models were also used to create linear models of water temperature across ordinal days. The decades were also binned into early decades (1970s – 1980s) and late decades (2000s – 2010s) to provide sufficient data for the regressions. Water temperature data in the early decades was sparser than the later decades, thus early decade water temperature data limited the decadal ingress and egress comparisons.  Water temperature data in the early decades did not cover the alewife ingress, so comparisons were made only for alewife egress and blueback herring ingress and egress.  Using the model predicted ingress and egress days for each species in the earliest decade estimated with the least additional uncertainty from extrapolation, we calculated the temperature estimated by the early temperature linear model.  We then compared the day that the early temperature occurred with the day that temperature occurred in the late decades.  The day the temperature occurred in the late decade was then compared to the ingress and egress days predicted by the phenology models.

## 3. Results

Over the 43-year time period (1973 – 2016), there were 12,839 sampling events made at 325 sample stations (see Figure 1 for stations).  A total of 2,241 alewife (17.5% catch rate) and 1,295 blueback herring (10.1%) were captured.  There was a general trend of decreasing presence probabilities over the sampling time period for alewife, and a slightly positive trend for blueback herring (Figure 3).  Alewife presence probability was highest in the 1970s, lowest in the 1980s, and remains at probability substantially lower than the 1970s.  Blueback herring presence probability was lowest in the 1970s, highest in the 1980s, and remains slightly higher probability than the 1970s.

### *3.1 Alewife Phenology*

The best model for alewife included distance proportion, day, decade, and the interaction between day and decade (Table 2).  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 3; Figure 4A). The changes are evident even with estimations based upon the first and last presences. In the 1970s, estimated alewife ingress (5% presence probability) was February 12, peaked at March 23, and completed their time on spawning ground by May 9 (egress estimate extrapolated one day). In the 2010s, these three dates were January 27, March 11, and April 12. The mean change in migration ingress and egress was -4 d per decade and -6.75 d per decade, with net-changes of -16 d and -27 d, respectively. The imbalanced shift in ingress and egress has reduced the time that the alewife population spent on the spawning grounds by -11 d. The date of peak catch probability occurred 12 d earlier over the four-decade time period.

The proportion of alewife presence detections at a subset of 30 sample stations that were consistently sampled in the early decades (1970s and 1980s) and late decades (2000s and 2010s) corroborate the modeled phenological changes (Figure 5A). 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.

### *3.2 Blueback Herring Phenology*

The best model for blueback herring included distance proportion, day, decade, and the interaction between day and decade (Table 2). Blueback herring showed the same phenological shifts as alewife, but with a muted change in the date of ingress and a larger shift in egress (Table 3; Figure 4B). 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 March 20, peaked at April 18, and completed their spawning migration by May 18. In the 2010s, these three dates were March 15, April 5, and April 25. The mean change in migration ingress and egress was -1.67 d per decade and ~-7.67 d per decade, respectively. The date of peak catch probability occurred 13 d earlier over the three-decade time period.

As with alewife, the proportion of blueback herring presence detections at the subset of 30 stations were examined and also corroborate the phenology model (Figure 5B). 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 to the higher and non-zero 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.

### *3.3 Effects of vernal warming rate on phenological shifts*

Water temperatures recorded at the 30 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 trends during the egress times of alewife and blueback herring. The rate of warming is ~49% greater for the 2001 – 2016 time period (slope = 0.150) compared to 1973 – 1988 (slope = 0.077) (Figure 6), and is significantly different when compared using an ANCOVA ($F = 61.51$, $df = 1, 3665$, $p < 0.001$). The increased rate of warming results in higher predicted temperatures from day 88 (March 29, at 14.0 C) onward. Elevated temperatures, or faster warming, from March 29 onward may be responsible for expediting the egress of both alewife and blueback herring. The alewife phenology model predicted a 1970s egress date of May 9 (day 129). The egress associated water temperature estimated on this date by the 1973 – 1988 regression was 17.2 C, which occurs on April 19 (day 109) in the 2001 – 2016 regression. The alewife phenology model predicts a 2010s egress date of April 12 (day 102) that is only seven days earlier than the estimate based on egress temperature. The blueback herring phenology model predicted a 1980s ingress date of March 20 (day 79). The ingress associated water temperature estimated on this date by the 1973 – 1988 regression was 13.3 C, which occurs on March 24 (day 83) in the 2001 – 2016 regression. The blueback herring phenology model predicts a 2010s ingress date of March 15 (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 (March 20 for 1973 – 1988 and March 24 for 2001 – 2016) and the similarities in dates for ingress predictions (March 20 in the 1980s vs March 15 in the 2010s). The blueback herring phenology model predicted a 1980s egress date of May 18 (day 138). The egress associated water temperature estimated on this date by the 1973 – 1988 regression was 17.9 C, which occurs on April 24 (day 114) in the 2001 – 2016 regression. The blueback herring phenology model predicts a 2010s egress date of April 25 (day 115) that is only one day later than the estimation using egress temperature.

## 4. Discussion

### *4.1. Changes in river herring spawn phenologies and potential causes*

Our analysis of river herring spawning migration phenology within the Albemarle Sound, North Carolina watershed found substantial shifts to earlier spawn times for both species. Our results are consistent with trends observed in other anadromous populations: southern New England alewife (Ellis & Vokoun 2009), Atlantic salmon (*Salmo salar*) (Juanes et al. 2004), and Pacific salmonids (*Oncorhynchus sp*.) (Kovach et al 2015), and Chesapeake Bay striped bass (Peer & Miller 2014). Similar to our work, Peer and Miller (2014) observed earlier shifts in spawning migration metrics (ingress, peak, and egress) of 800-899-mm female Chesapeake Bay striped bass, which share a spawning season with Albemarle Sound river herring. From 1991 to 2010, the striped bass arrived, peaked, and left 5, 6, and 14 days earlier. Shifts in the timing of anadromous spawning events can have cascading negative effects, such as trophic mismatches that have substantial impacts on the survival of offspring, nutrient influx, and especially food web dynamics in the case of forage fish such as river herring (Cushing 1990; Yako et al. 2000; Durant et al. 2007; Walters et al. 2009; Fortier & Gagné 2011). From the river herring perspective, the potential for negative effects on recruitment caused by a reduction in time where habitat conditions are suitable for spawning or the creation of trophic mismatches for early life history stages warrants future research.

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

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's observations led to the conclusion that larger, older fish arrived on the spawning grounds earlier than their smaller, younger conspecifics. It's not unreasonable to believe that the relationship between age-length and the timing of arrival upon the spawning grounds found in this confamilial apply to both alewife and blueback herring as well. The phenomenon has also been found in other anadromous species (Peer & Miller 2014). Thus, any shift towards an older age structure should manifest itself in earlier spawning migration times. However, we saw no change in alewife age structure (Figure 7). For blueback herring, there was a trend towards a younger age structure in recent decades which is opposite of the pattern that might explain earlier spawning. Thus, we conclude that changes in age structure are not responsible for changes in river herring spawn times within the Albemarle Sound watershed.

Alewife and blueback herring population abundances 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 (Hightower et al. 1996; White et al. 2017). Thus, changes in abundance are one potential reason for changes in spawn timing. However, the relationship between population abundance and 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. We found evidence for earlier shifts in spawning in recent years that 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 any studies that examined for this effect. Because river herring abundance declined 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 influence on spawning and migration timing for many anadromous species: striped bass (Peer & Miller 2014), Atlantic salmon (Juanes et al. 2004), American shad (*Alosa sapidissima*) (Quinn & Adams 1996), lake sturgeon (*Acipenser fulvescens*) (Bruch and Binkowski 2002), as well as alewife (Ellis & Vokoun 2009; Ogburn et al. 2017) and blueback herring (Ogburn et al. 2017). Temperatures within the coastal mid-Atlantic region of the United States have been increasing over the past century (Polsky et al. 2000s), with particularly larger changes observed in lower order streams (Ding & Elmore 2015) such as those used by river herring as spawning habitat. Our results suggest that an increased rate of warming within the tributaries of the Albemarle Sound in late spring is driving both river herring species towards earlier departures during their spawning seasons, a trend that has been observed in southern New England streams (Ellis & Vokoun 2009). The strongest evidence for this 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 are reached. For alewife, the temperature-predicted and observed egress (from model estimate) dates were earlier and only seven days apart; they were also earlier and only one day apart for blueback herring egress.

The temperatures we estimated for alewife and blueback herring egress (~17 C) are similar to those observed for egressing river herring Maryland (Ogburn et al. 2017). Ogburn et al. (2017) estimated the daily count of both upstream and downstream migrating alewife and blueback herring in the Choptank River 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. As the vernal warming rate increases over time, water temperatures on river herring spawning grounds will reach 17 C sooner and continue to shorten the spawning season. 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 Albemarle Sound watershed, shifts towards earlier egress dates, coupled with unequal changes in ingress, has reduced time on the spawning grounds and may be negatively impact spawning success, recruitment, and ultimately recovery.

### *4.2 Comparing presence/absence and abundance data for spawning phenology metrics*

We used presence data at multiple stations to examine for changes in phenology while others have used percent-of-run abundance percentiles at stationary nets/weirs/traps (see Antonsson & Gudjonsson 2002; Ellis & Vokoun 2009). We tested whether presence data are a good proxy for abundance by comparing our results to phenology results using river herring 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). For the most recent decade (2010), our phenology metrics derived from presence/absence data in Albemarle Sound match very closely with percent-of-run abundances of 5%, 50%, and 95%. For alewife in the Chickahominy River, percent-of-run abundance yields February 3, March 9, and April 6 as the dates of ingress, peak, and egress while our estimates are January 27, March 11, and April 12. The three percentiles for blueback herring in the Chickahominy River occur on March 16, March 31, and April 27 and our estimates are March 15, April 5, and April 25. Our predictions using presence/absence data were within ± 7 days of those using abundance data in a nearby system. Our results show that presence/absence data is a viable proxy for abundance-based estimations of phenology. We encourage further examination of other long-term datasets for signals in shifting phenology using presence/absence data when abundance data cannot be used.

### *4.3 Implications*

Researchers and fisheries managers have started to advocate for the incorporation of climate change effects and changes in phenology into their management strategies (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. While moratoria provide a significant 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. Current river herring stocks in North Carolina and other Atlantic states remain in a depressed state (White et al. 2017). We recommend future research test for the relationship between spawning migration time and recruitment.

If spawn timing is found to impact recruitment, state and federal management of river herring, and potentially other clupeid species, will need to account for shifts in spawning phenology and reductions in spawning season length when establishing commercial and recreational seasons. In order to ensure the future persistence of these species, and to potentially return stocks to historical levels as mandated, further work must be done to bolster river herring stocks and mitigate the rate at which stream waters are warming. Global regulation of carbon emissions is projected to slow the rate of global warming (IPCC 2014), and may help to ameliorate climate induced habitat degradation, but not stop it completely. Further regulation and the requirement natural riparian zone land cover, which is not currently regulated by North

Carolina within the Albemarle Sound watershed, may reduce solar insolation and thus temper the rate of warming for sensitive shallow, higher order streams. A review by Moore et al. (2005) reported that the effects of riparian zone deforestation, namely stream temperature regimes, can take as long as 10 years to recover, with many of the studies showing no recovery over their durations. The dominate anthropogenic influence on the Albemarle Sound watershed landscape is agriculture and silviculture, which may encroach upon important riparian zone habitat. The influence of anthropogenic activities within the Albemarle Sound watershed and their effects on water quality and habitat condition warrants further investigation.

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## Tables

Table 1. NC Division of Marine Fisheries river herring spawning habitat survey sampling history. Sampling was conducted within the tributaries and drainage areas of the listed rivers, creeks, or bays. AR = Alligator R., CH = Cashie R., CR = Chowan R., CS = Tull B., EB = Edenton B., LR = Little R., MC = Mackeys C., MR = Meherrin R., NR = North R., PK = Pasquotank R., PR = Perquimans R., RR = Roanoke R., SR = Scuppernong R., YR = Yeopim R.

| Decade | Years | River Systems | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | AR | CH | CR | CS | EB | LR | MC | MR | NR | PK | PR | RR | SR | YR |
| 1970 | | X | X | X | | X | X | X | | X | X | X | X | | X |
| | 1973 | | | X | | | X | X | | X | X | X | | | X |
| | 1974 | | | X | | | X | | | X | X | X | X | | X |
| | 1975 | | | | | X | | | | | | X | | | X |
| | 1976 | | | X | | | | X | | | | | | | |
| | 1977 | X | | | | | | | | | | | | | |
| | 1978 | | X | | | | | | | | | | X | | |
| | 1979 | | | X | | | | | | | | | | | |
| | | | | | | | | | | | | | | | |
| 1980 | | | | X | X | | X | | X | | X | X | | | |
| | 1980 | | | X | | | | | X | | | | | | |
| | 1982 | | | | X | | | | | | | | | | |
| | 1983 | | | X | | | | | | | | | | | |
| | 1987 | | | | | | X | | | | X | X | | | |
| | 1988 | | | | | | X | | | | X | X | | | |
| | | | | | | | | | | | | | | | |
| 2000 | | | | X | | X | | X | X | | | | X | X | X |
| | 2001 | | | X | | X | | | | | | | X | | |
| | 2007 | | | | | | | | | | | | | | X |
| | 2008 | | | X | | X | | | X | | | | | | |
| | 2009 | | | X | | X | | X | | | | | | X | |
| | | | | | | | | | | | | | | | |
| 2010 | | X | X | X | | X | X | X | X | X | X | X | X | X | X |
| | 2010 | | | X | | X | X | | | | | X | | | |
| | 2011 | X | | X | | X | | | | | | | | | |
| | 2012 | | X | X | | X | | | | | | | X | | |
| | 2013 | | | X | | X | | | | X | X | | | | |
| | 2014 | | | X | | X | | | | | | | | | X |
| | 2015 | | | X | | X | | | X | | | | | | |
| | 2016 | | | X | | X | | X | | | | | | X | |

Table 2. Model selection for the generalized additive models for alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*) in the Albemarle Sound, North Carolina watershed, 1973 – 2016. Models were assessed using Akaike Information Criterion (AIC), weighted AIC (AICw), and Receiver Operating Characteristic Area Under the Curve (AUC). The most parsimonious model is highlighted.

| Model | AIC | ΔAIC | AICw | AUC | % Dev Exp |
|---|---:|---:|---:|---:|---:|
| **Alewife** | | | | | |
| Full | 9876.90 | 0.00 | 1.00 | 0.78 | 17.35 |
| *-o*d* | 10078.23 | 201.33 | 0.00 | 0.77 | 15.59 |
| *-dp* | 10191.59 | 314.69 | 0.00 | 0.75 | 14.59 |
| *-d-o*d* | 10378.99 | 502.09 | 0.00 | 0.74 | 13.01 |
| *-o-o*d* | 11255.85 | 1378.95 | 0.00 | 0.66 | 5.51 |
| Null | 11891.48 | 11891.48 | 0.00 | 0.50 | <0.00 |
| | | | | | |
| **Blueback Herring** | | | | | |
| Full | 6285.50 | 0.00 | 1.00 | 0.86 | 25.56 |
| *-od* | 6487.33 | 201.86 | 0.00 | 0.84 | 45.16 |
| *-d-o*d* | 6514.21 | 228.73 | 0.00 | 0.84 | 44.88 |
| *-dp* | 6772.35 | 483.88 | 0.00 | 0.82 | 44.30 |
| *-o-o*d* | 7839.43 | 1553.95 | 0.00 | 0.70 | 42.38 |
| Null | 8398.15 | 2112.68 | 0.00 | 0.50 | 41.94 |

**Note**: Full is $x_{o,d,(dp)} = i + g_1(d) + g_2(o) + g_3(o*d) + g_4(dp) + e_{o,d(dp)}$ where $x$ = river herring presence probability, $i$ = intercept, $g$ = nonparametric smoothing function, $d$ = decade, $o$ = ordinal day, *dp = distance proportion*.

Table 3. Logistic GAM-derived migration metrics for alewife and blueback herring spawning in the Albemarle Sound, NC watershed. Metrics are ingress (5% probability of presence on left hand side of the distribution), egress, peak (maximum presence probability in a unimodal curve or mean day of maximum presence probabilities in bimodal/plateaued curve), and season length estimations (differences between ingress and egress). Some temporal comparisons within and across decades use extrapolated predictions. Predictions influenced by extrapolation are denoted with *. Conservative estimates based upon the first presence and last presence are given in brackets. The 95% confidence interval is give in parenthesis.

**Alewife**

| Decade | Ingress | Egress | Peak | Season Length |
|---|---:|---:|---:|---:|
| 1970 | 43 (39-46) | 129 (127-144) | 82 | 86 |
| 1980 | 48 [<55]* | 122 (119-124) | 81 | 74 [>67] |
| 2000 | 24 [<34]* | 107 (106-108) | 70 (68-72) | 83 [>73] |
| 2010 | 27 (25-29) | 102 (101-103) | 70 (68-72) | 75 |

| | Ingress Diff | Egress Diff | Peak Diff | Season Diff |
|---|---:|---:|---:|---:|
| 1970s vs 2010s | -16 | -27 | -12 | -11 |
| Per Decade | -4 | -6.75 | -3 | -2.75 |

**Blueback Herring**

| Decade | Ingress | Egress | Peak | Season Length |
|---|---:|---:|---:|---:|
| 1970 | 76 (74-77) | >150 [>128]* | 117 (108-133) | >74 [>52] |
| 1980 | 79 (77-80) | 138 [>126]* | 108 (102-114) | 59 [>47] |
| 2000 | 71 (70-72) | 117 (116-118) | 95 (90-100) | 46 |
| 2010 | 74 (73-75) | 115 (114-116) | 95 (91-99) | 41 |

| | Ingress Diff | Egress Diff | Peak Diff | Season Diff |
|---|---:|---:|---:|---:|
| 1980s vs 2010s | -5 | -23 [<-9] | -13 | -18 [<-6] |
| Per Decade | -1.67 | -7.67 [<-3] | -4.33 | -6 [<-2] |

## Figures

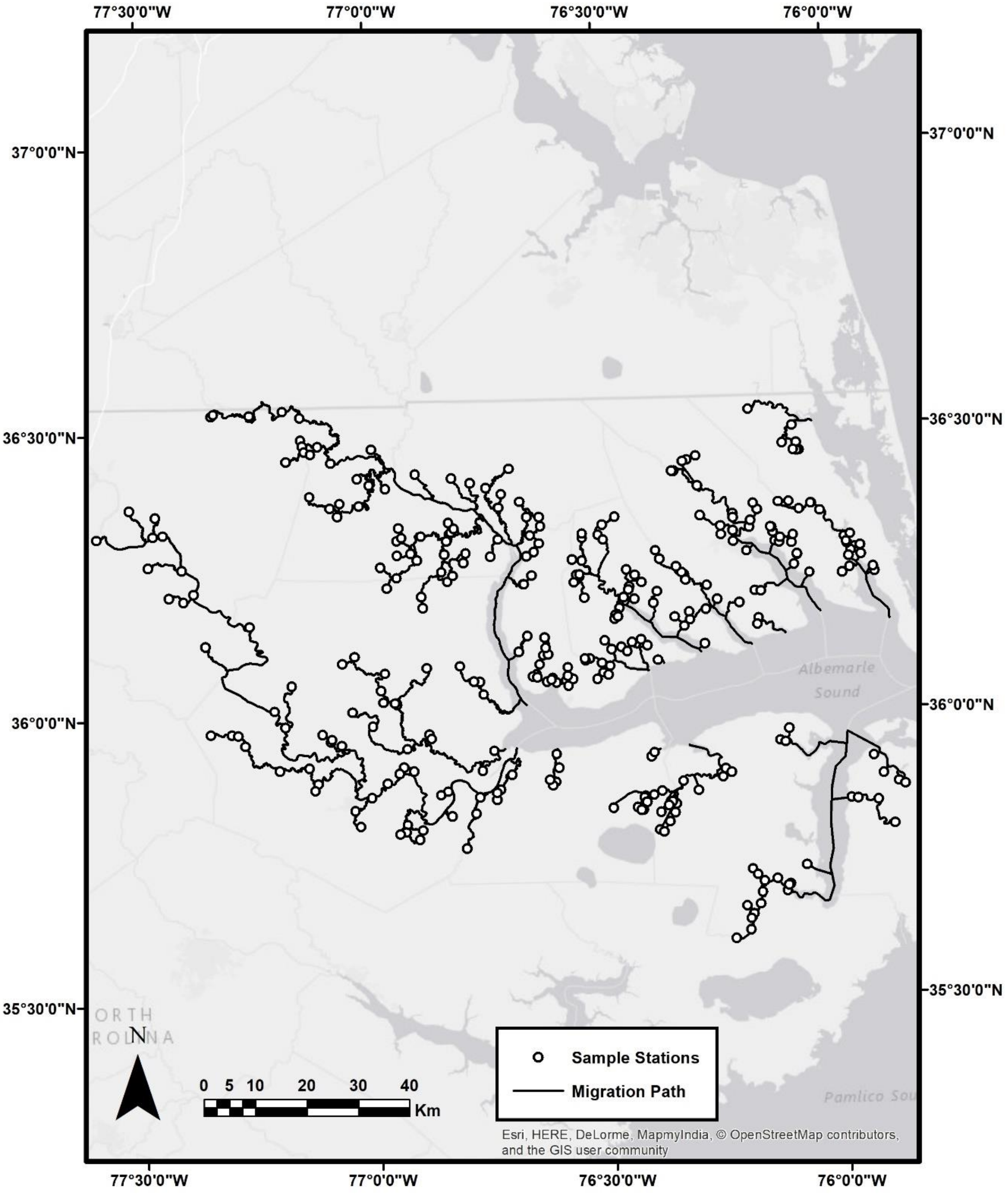

Figure 1. The North Carolina Division of Marine Fisheries river herring spawning habitat survey has been conducted from 1973 – 2016 and has sampled at 325 locations throughout the Albemarle Sound, North Carolina watershed.

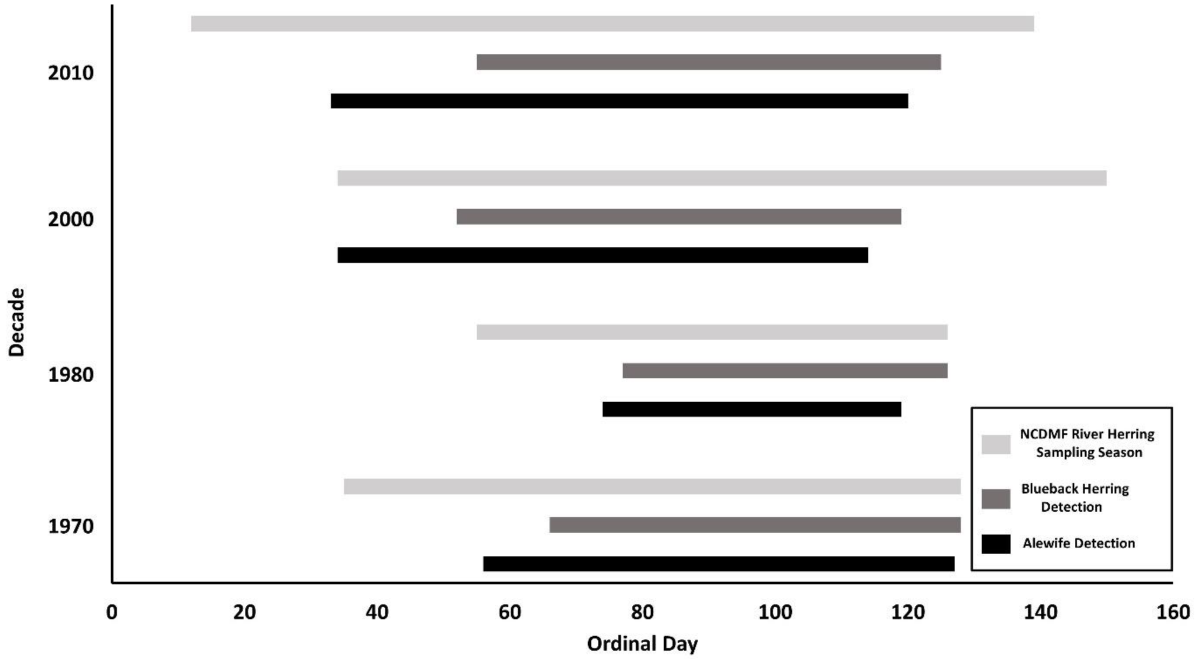

Figure 2. The timing and length of the North Carolina Division of Marine Fisheries river herring spawning habitat survey have fluctuated across decades. The span of the first and last detections for alewife and blueback are plotted to show the sampling coverage for the river herring run.

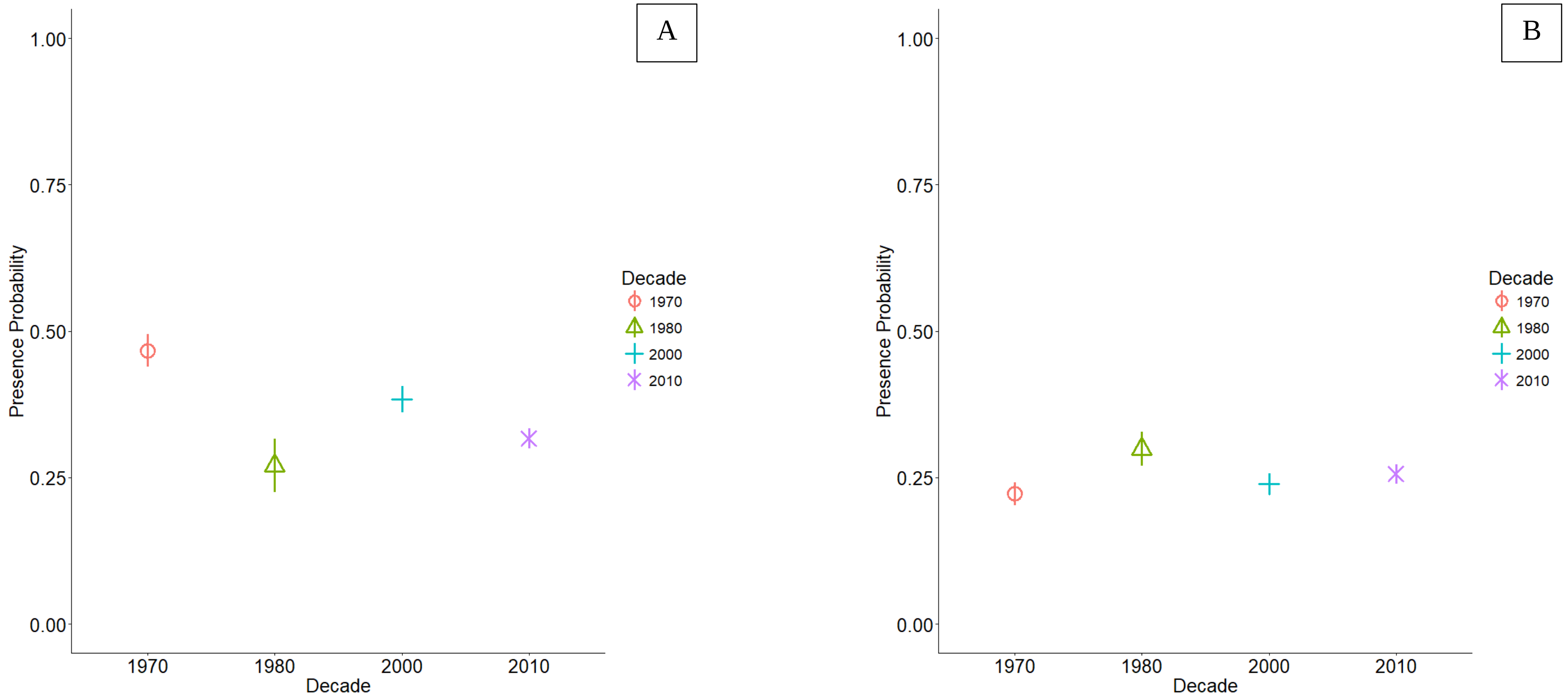

Figure 3. Logistic GAM-derived predictions of (A) alewife presence probability and (B) blueback herring presence probability across decades. Probabilities were modeled using ordinal day, decade, distance proportion, and ordinal day * decade for samples collected in the NC Division of Marine Fisheries river herring spawning habitat survey throughout the Albemarle Sound, NC watershed. 95% CI indicated by vertical line.

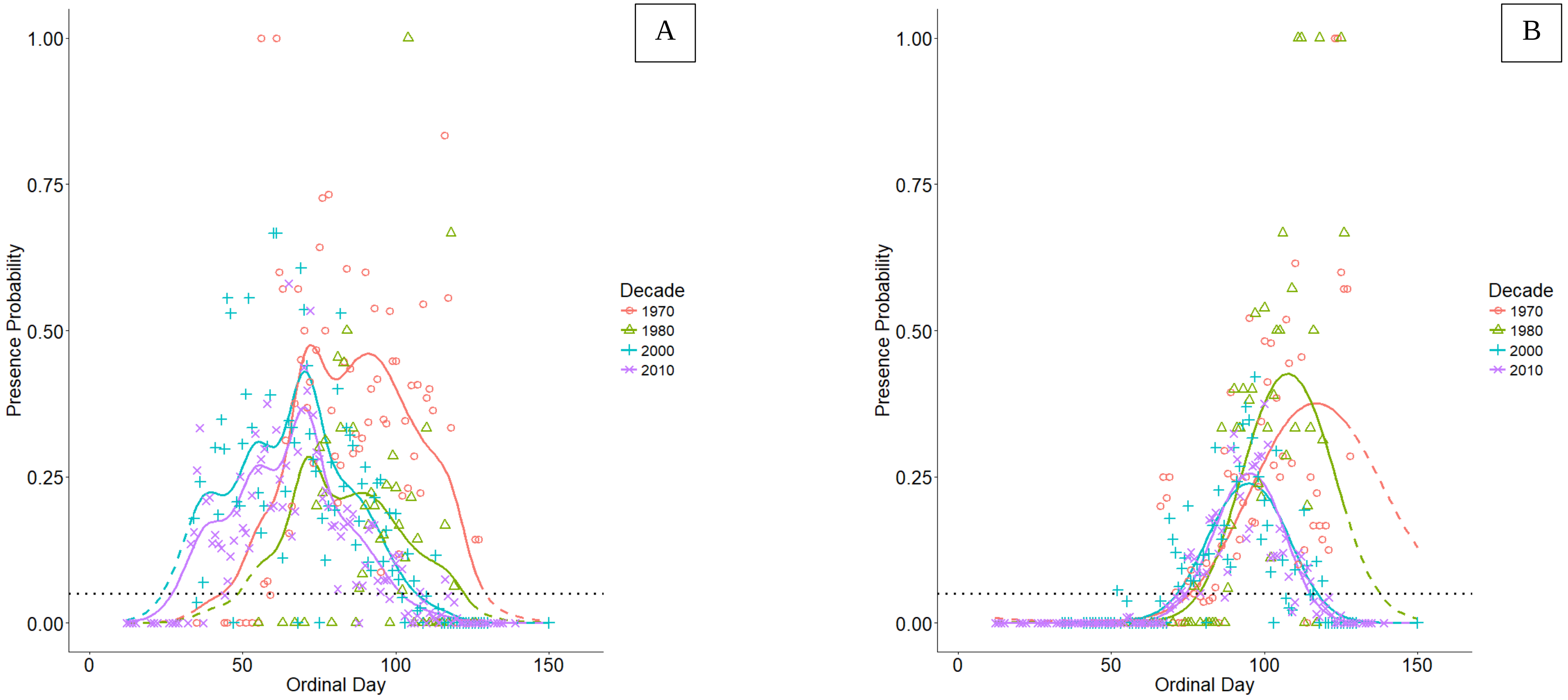

Figure 4. Logistic GAM-derived predictions of (A) alewife and (B) blueback herring presence probability. Solid curves are model predictions from dates sampled, dotted curves are extrapolated predictions. Probabilities were modeled using ordinal day, decade, distance proportion, and ordinal day * decade for samples collected in the NC Division of Marine Fisheries river herring spawning habitat survey throughout the Albemarle Sound, NC watershed. Points represent the raw proportion of presences for all nets set on each day of the decade. Black horizontal line at 5% for estimates of ingress and egress.

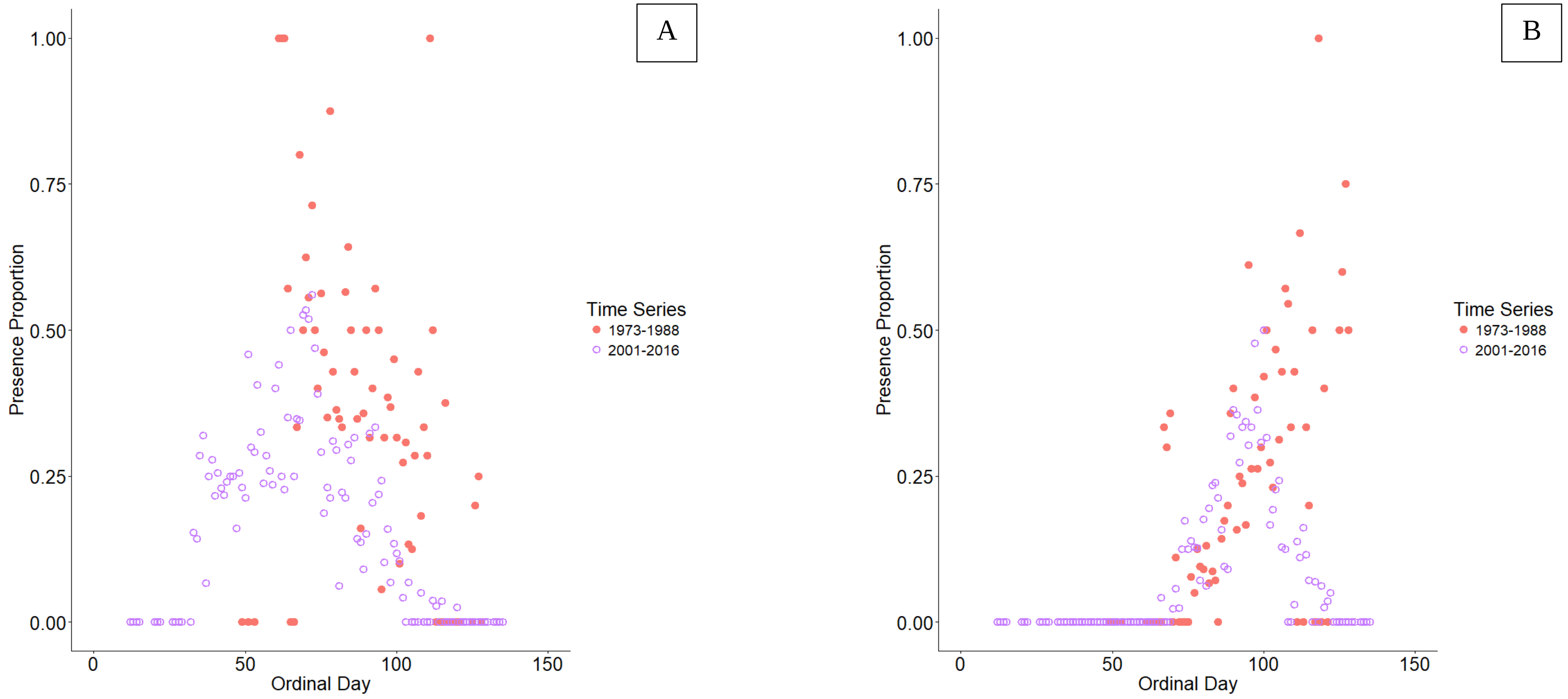

Figure 5. Presence proportions for (A) alewife and (B) blueback herring at 30 sampling locations regularly sampled across four decades of NCDMF river herring sampling. Proportions are calculated from samples taken on any given day within the early (1973 – 1988) or late (2001 – 2016) time periods.

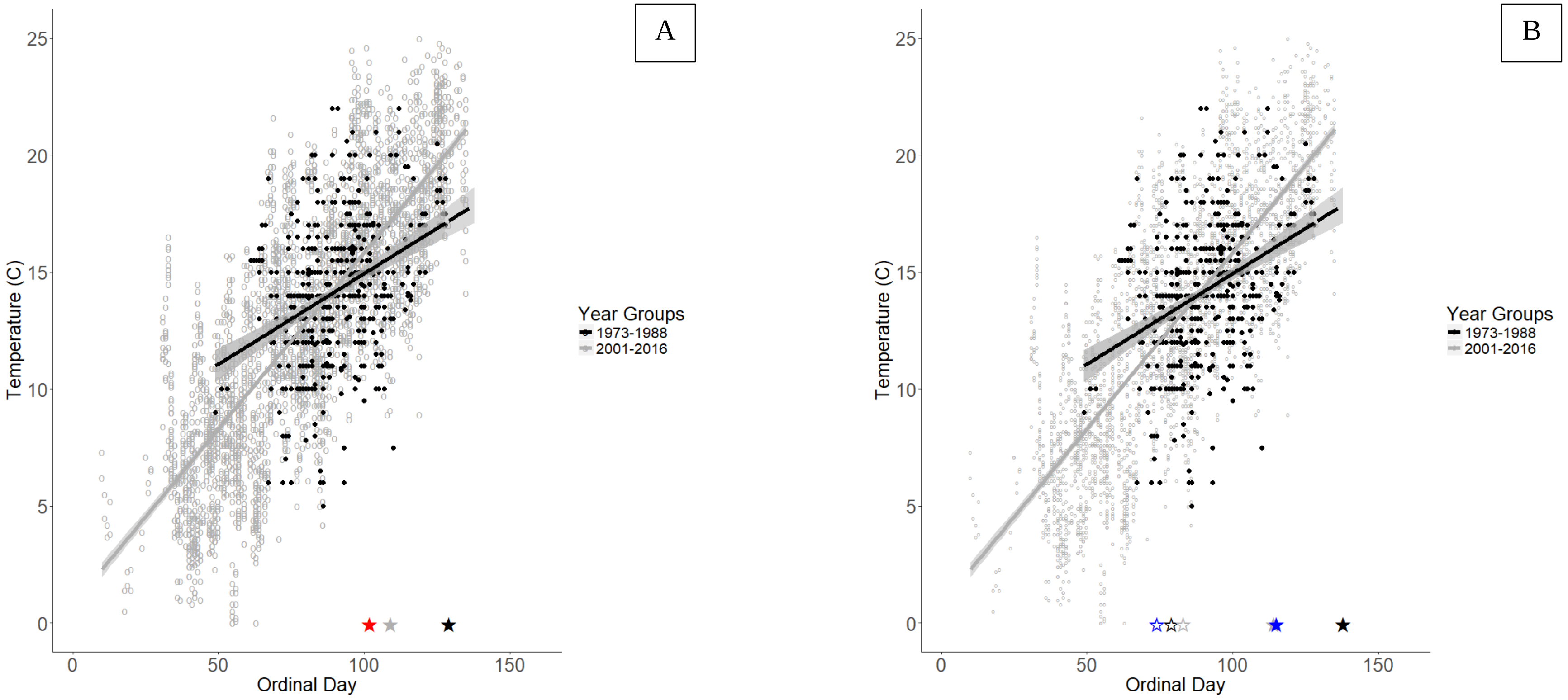

Figure 6. Water temperature data for 30 stations regularly sampled throughout four decades of NCDMF river herring sampling were divided into early (1973 – 1988) and late (2001 – 2016) time periods, with the early temperature trend extrapolated out to the latest egress date predicted by the phenology models (dotted line). Water temperatures (early data above) associated with the predicted egress dates (solid black star) for (A) alewife (1970s) and (B) blueback herring (1980s) were identified (17.2 C for alewife and 17.9 C for blueback herring). The 2001 – 2016 dates associated with these 1973 – 1988 egress temperatures were then identified as a temperature-dependent egress date (solid gray star; day 109 for alewife and day 114 for blueback herring). The predicted egress dates from the 2010s phenology model are plotted for alewife (solid red star; day 102) and blueback herring (solid blue star; day 115). Blueback herring ingress was also examined using the same approach described for egress (see open stars). The 1973-1988 temperature on the date of ingress (day 79; open black star) in the 80s was 13.3 C; that temperature gave an estimate of ingress based on the 2001-2016 temperature data of day 83 (open gray star) and was similar in time to the model-predicted ingress date (open blue star; day 74). The gray shading represents the 95% CI.

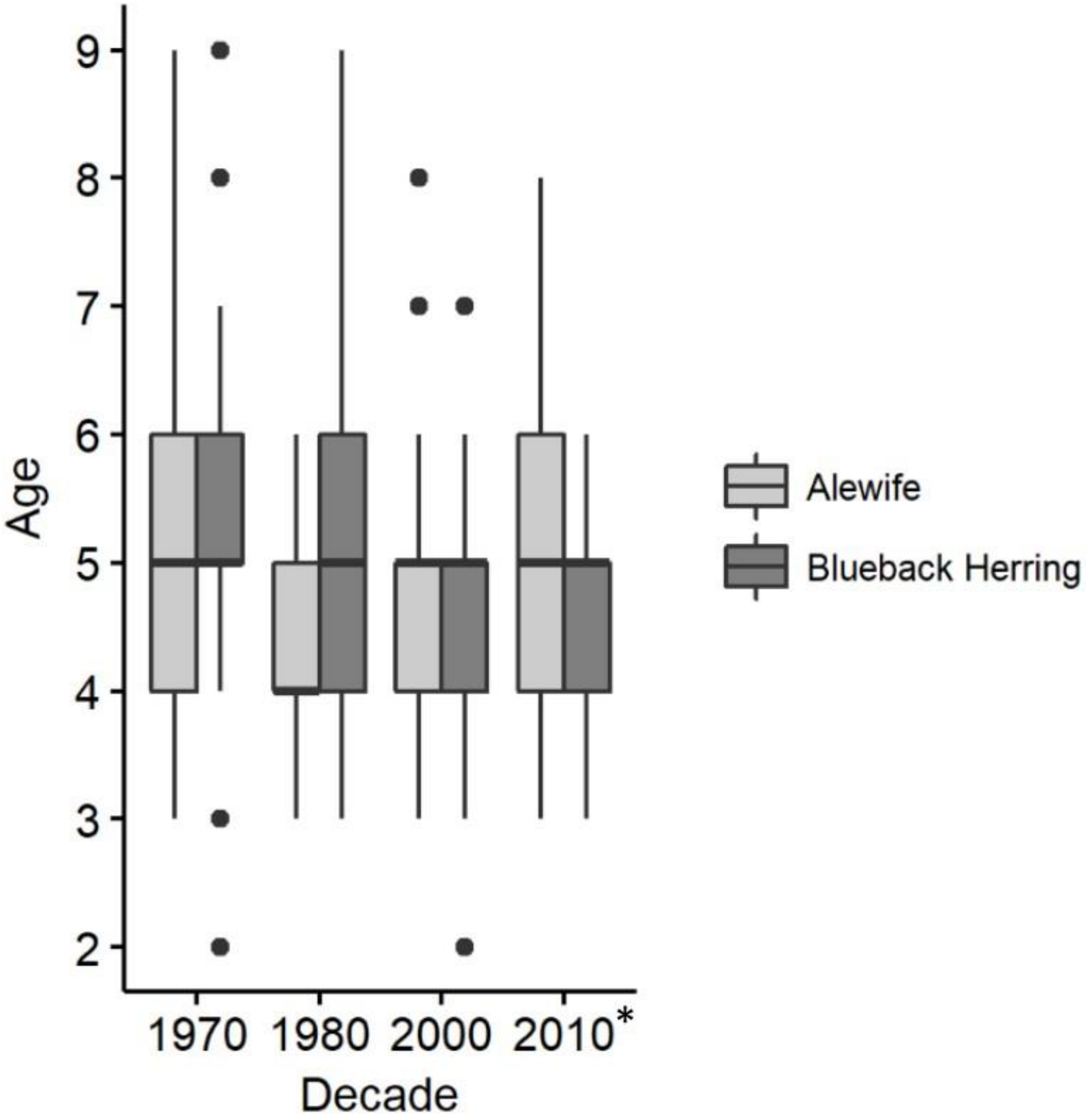

Figure 7. Age distribution of alewife and blueback herring caught from 1973 to 2010 in the NC Division of Marine Fisheries river herring spawning habitat survey, Albemarle Sound, North Carolina watershed. Box lower and upper limits represent the interquartile range (IQR) of ages, median age is indicated by the thick black line, tails are 1.5 * IQR, dots are outliers. *Aging data for the 2010 decade was limited to 2010.

# CHAPTER 2

# Examining the Influence of Anthropogenic Riparian Zone Land Cover on River Herring Catch within the Albemarle Sound Watershed, NC

## Abstract

Alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), collectively known as river herring, are economically, ecologically, and culturally important fishes that are at low levels of abundance. Populations have remained in a depressed state since the 1970s in spite of fishing moratoria and habitat restoration efforts. We hypothesized that anthropogenic modifications within the riparian zones (agriculture/silviculture and development) has created conditions that impede river herring movement to spawning habitat. We analyzed spawning habitat survey data collected from 2007 to 2016 by the NC Division of Marine Fisheries to determine if riparian zone land cover (measured along the migration route to specific sampling sites) has influenced the presence of river herring throughout the Albemarle Sound watershed. The influence of agriculture/silviculture on alewife and blueback herring was non-linear, but generally negative. There was no clear indication of a development effect on river herring presence as both positive and negative effects were observed; however, it is important to point out that there was very little contrast in percent development. Additionally, road culverts were not found to be an impediment to river migration. Water quality metrics (temperature, DO, and pH) strongly influence the presence of river herring. Overall, the watershed's riparian zones are dominated by forested and wetland habitats that are typically suitable for spawning activity. Under current habitat and fish abundance conditions, we found limited evidence for

anthropogenic modifications to impede the ability of river herring to migrate to spawning habitats within the Albemarle Sound watershed.

## 1. Introduction

Riparian zones are the interface between aquatic and terrestrial ecosystems. Riparian zones are biologically diverse ecotones that span from the river's edge through the floodplain and are comprised of vegetation that are tolerant to variably hydrated soils (Cowardin et al. 1979). Riparian zones act as disturbance buffers, performing critical ecosystem services such as stabilizing river banks, preventing erosion from flood events, and sequestering nutrient runoff from nonpoint source pollution (Gregory et al. 1991; Sweeney et al. 2004). Complete and partial deforestation of the riparian zone has been shown to reduce, if not completely, eliminate these ecosystem services (Sweeney et al. 2014). Nutrient pollution is regularly cited as the greatest threat to water quality and the stability of inland aquatic ecosystems (Smith 2003; Dudgeon et al. 2006; Vörösmarty et al. 2010; Brooks et al. 2015). Agricultural and urban activities can significantly increase nutrient concentrations in neighboring aquatic systems, causing dramatic declines in water quality. This includes toxic algal blooms, hypoxia, changes in pH, increased turbidity, destruction of submerged aquatic vegetation, and fish kills (Carpenter et al. 1998).

Anthropogenic modification of habitat has been identified as a significant contributor to the decline of marine and coastal biodiversity and abundance, accounting for an estimated 37% (Dulvy et al. 2003) to 39% of local extinctions (Lotze et al. 2006). Of the fishes examined by Lotze et al. (2006), diadromous fishes showed the most precipitous decline in abundance and were the most vulnerable due to the ease of access for harvest, and their exposure to degraded habitat conditions encountered throughout their migratory life histories. A meta-analysis by

Limburg and Waldman (2009) found 24 examples of diadromous populations that have decreased in relative abundance by >90%. Alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), collectively known as river herring, are two species of anadromous fishes that have shown dramatic decreases in abundance across their entire North American range due to fishing pressure, habitat destruction, and possibly climate change (Hightower et al. 1996; ASMFC 2012; NCDMF 2015; ASMFC 2017; See Chapter 1). River herring populations found in the Albemarle Sound, North Carolina watershed were historically plentiful, with commercial pound-net landings averaging 5.4 million kilograms between 1880 and 1970 (Chestnut & Davis 1975). By 1987, landings had decreased to under one million kilograms, and in 2006, the last year before North Carolina enacted a fishing moratorium on river herring, landings were just over one thousand pounds with CPUE matching the decline in landings (NCDMF 2015). In 2006, the National Marine Fisheries Service identified river herring as a species of concern, and in 2007 North Carolina enacted a river herring fishing moratorium. In spite of this moratorium, the river herring population remains at historically low levels of abundance (ASMFC 2017) and prompts further investigation into the condition of spawning habitat and migration pathways for river herring within the Albemarle Sound watershed.

The Albemarle Sound watershed is located in the northeast region of North Carolina, extending its drainage area into Virginia. The watershed is dominated by wetland forests with large plots of agriculture and silviculture, and small pockets of urban areas mostly positioned along the higher order tributaries. Nine large, blackwater rivers feed into the Albemarle Sound (North R., Pasquotank R., Little R., Perquimans R., Chowan R., Roanoke R., Scuppernong R., Alligator R., Yeopim R.). The Chowan River has the largest run of river herring (Hightower et al. 1996), and constitutes the largest portion of the NC Department of Environmental Quality’s

Strategic Habitat Area (SHA) within the Albemarle Sound region (NCDEQ 2016). The SHA designates habitat that is vital to successful reproduction, recruitment, and survival of many aquatic species, including river herring, and is comprised of main rivers, tributaries, swamps, and floodplains. Many of the waters within the Albemarle Sound watershed are also designated as SHA, and have been classified as nutrient sensitive by the North Carolina Department of Environmental & Natural Resources (NCDENR 2007).

Nutrient sensitive waters are susceptible to algal blooms and subsequent hypoxic periods. Hypoxia has been shown to make habitats untenable for fish species, especially in estuarine environments where human activity has expanded. Wannamaker and Rice (2000) demonstrated hypoxia detection avoidance behaviors in seven North Carolina estuarine species. A result of the avoidance of hypoxic conditions can be habitat compression, which has been observed in the Neuse River, NC (Eby & Crowder 2002). Little information exists on the responses of adult river herring to hypoxic conditions. Alewife have been shown to tolerate dissolved oxygen conditions as low as 0.5 mg/L for up to five minutes, as long as post-exposure conditions were greater than 3.0 mg/L, and experience a mortality rate of 33% when exposed to DO concentrations between 2.0 mg/L and 3.0 mg/L for 16 hours (Dorfman & Westman 1970). Blueback herring have been reported to require DO concentrations 5.0 mg/L for spawning activity (Jones et al. 1978). Avoidance responses by river herring to anthropogenically induced hypoxic conditions during their spawning migration may result in impassable waters and reductions in habitat use.

Excess nitrogen and phosphorus can be introduced by non-point sources such as agriculture/silviculture and urbanization. Removal of these nutrients can prevent the occurrence of hypoxic conditions. Riparian buffer width has been shown to be the most important characteristic in retention of pollutants (Phillips 1989). Prior to 1997, North Carolina did not mandate any requirements for the existence of riparian zone buffers. In response to large scale fish kills associated with increased levels of nitrogen and phosphorus in the Neuse River, North Carolina legislature enacted a law to require riparian buffer regions of 50 feet for the Neuse River (ARCD 2016). Further riparian zone mandates within the state have only been made on a case-by-case basis with six watersheds protected, none of which are within the Albemarle Sound watershed. The 2012 Annual Progress Report on the Neuse Agricultural Rule (15 A NCAC 2B.0238) showed marked decreases in nitrate levels with increases in riparian zone buffer distance, from 20 ft to 100+ ft (NC Environmental Management Commission 2012). Further evidence for greater riparian zone buffers to remove nitrogen has been found in a meta-analysis by Mayer et al. (2007), which shows that riparian zones > 50 m more consistently remove nitrogen than those from 0-25 m. A second meta-analysis by Sweeney & Newbold (2014) determined that lower order streams should have buffers ≥30 m. In spite of evidence for the implementation of riparian zone regulation, North Carolina has yet to require the presence of riparian zone buffers within the Albemarle Sound watershed. Riparian zone buffers in North Carolina have actually been declining. From 2012 – 2015, North Carolina has shown consistent losses in riparian buffer acreage and linear feet of streams, losing ~34 ac of riparian buffer and ~36,400 ft of streams per-year (NCDEQ 2016). The loss of riparian zone buffers to agriculture/silviculture and urban development may be negatively effecting water quality, and impeding river herring from reaching their spawning grounds.

In this paper, we examine the effects of riparian zone agriculture/silviculture and development on the ability of river herring to migrate upstream within the Albemarle Sound watershed. We use fisheries-independent data collected by the North Carolina Division of

Marine Fisheries through their river herring spawning habitat survey. We also examine trends in water quality, and whether culverts, a prevalent construction technique for road crossings, may be restricting river herring spawning movements.

## 2. Methods

### *2.1 Study Location and River Herring Monitoring*

River herring monitoring was conducted by the North Carolina Division of Marine Fisheries (NCDMF) through their river herring spawning habitat survey. The survey is intended to identify the extent of stream habitats used for both alewife and blueback herring spawning in nine river systems and their associated tributaries that feed into the Albemarle Sound. Monitoring began in 1973 and is still currently active as of 2017, with 24 of the possible 43 years sampled. For our analysis, we used NCDMF data from 2007 to 2016, which temporally aligned with the most recent land cover data available through NOAA (detailed below). In 2007, only the Yeopim River system was sampled. From 2008 to 2016, sampling consisted of the entirety of the river herring spawning run within the Chowan River and Edenton Bay watersheds plus one of twelve additional Albemarle Sound river systems on a rotating basis. Additional river systems were sampled if travel time to and from sampling stations was not limiting.

Migration progress for both species was concurrently monitored using gillnets. Staked or floating gillnets of 1.38 in. bar mesh were used during the alewife run, and 1.25 in. bar mesh for the blueback herring run. Net lengths of 5, 8, and 10 yd were used for staked gillnets, while floating gillnets were 5, 8, 10, 20, and 30 yd. Both gillnet types were 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; detection probability for these sets was assumed similar to across channel sets. Gillnets were set on Mondays, checked every 24 hours, and removed over weekends and holidays due to logistical constraints. Water surface temperature, air temperature, pH, salinity, conductivity, and DO were taken at each sampling station upon net inspection using a YSI Professional Plus.

Sampling for alewife commenced when staging alewife were caught in the NCDMF striped bass independent gillnet survey, which is conducted within the Albemarle Sound at the mouths of the river systems. Nets were reset to their furthest downstream positions when the first blueback herring was caught in any of the alewife survey nets. 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).

## *2.2 Analyses*

### *2.2.1 GIS construction of migration pathways and riparian zones*

Pathways for river herring migration to sampling stations were determined and assembled into stream networks for each river system using United States Geological Survey National Hydrography Dataset (USGS NHD) flowline vector data (U.S. Geological Survey 2013) and ArcGIS Network Analyst. NHD data were reduced to only vectors representing pathways that river herring would migrate along, from the confluence of the river system and the Albemarle Sound up to the sample station. Pathways were constrained to the highest order streams and natural waterways, only using lower order streams and channelized waterways when no alternative migration route was viable to reach the sample station. The migration pathway distance was measured within the Network Analyst tool.

In order to assess the riparian zone land cover at a constant riparian zone width, stream widths needed to be accounted for. Stream widths were incorporated into the migration pathways by creating polygon representations from NCDEQ Estuarine Shoreline – Coastal North Carolina vector polylines (North Carolina Department of Coastal Management 2012). Some sections of shoreline were absent from the dataset and thus required digitization. Digitization was conducted over ESRI World Imagery (ESRI et al. 2017) at a scale of 1:1000 m. Stream polygons were clipped to the extent of the pathway leading to a given sample station and tributaries downstream of the sample station were removed. Riparian zone buffers of 100 m, as recommended by Hawes and Smith (2005) for effective prevention of pesticide, litter and debris input, were applied to the paired migration pathway vectors and polygons. The paired buffers were then merged, resulting in unique 100 m riparian zones for the migration pathways leading to the 234 sampling stations throughout the Albemarle Sound watershed. Land cover classifications, represented by the most recent (2010) NOAA Coastal-Change Analysis Program raster dataset: NOAA C-CAP 2010 Regional Land Cover Change Data – Coastal United States (NOAA 2013), within each of the 100 m riparian zone buffers were extracted, and the percent cover for each classification was calculated. NOAA C-CCAP classifies land covers into 21 classifications at a 30 m resolution. The 2010 land cover classifications were used to represent the land conditions throughout the 2007 – 2016 time-period due to its temporal positioning at roughly the mid-point in our dataset. The 2010 land cover classification is also cited as more accurate (84.0%) than the 2006 dataset and the 2006 – 2010 land cover change dataset (NOAA 2014).

### *2.2.2 River herring and habitat relationships*

Using river herring presence/absence data collected from 2007 – 2016 through the NCDMF river herring spawning habitat survey, we created generalized additive models (GAMs) with a logit link and a binomial distribution to model the effects of habitat and water quality variables on river herring presence and absence. GAMs are useful in modeling nonparametric relationships typical of ecological data (Hastie & Tibshirani 1990). Penalized thin plate splines with shrinkage parameters were used as smoothers. The inclusion of shrinkage parameters allows for non-significant variables to be removed from the model by reducing the splined term to zero (Wood 2006).

Because the spatial coverage of the survey changed across time, with non-Chowan River systems being sampled on a rotating basis, and the presence of river herring can change with distance upstream, spatial variability needed to be accounted for. We created a proportion in order to standardize the upstream distance of the sample stations within each river system; the distance between the tributary mouth and each sample station to the maximum distance a river herring was observed in the tributary (hereafter referred to as distance proportion). An additional model for each species was created to evaluate our results and to control for the variation in river systems sampled. We used a subset of data from the Chowan River system and the Edenton Bay watershed, which were sampled for all but one year in the time series (not sampled in 2007).

Land covers were binned into four general classifications: forest, wetland, agriculture/silviculture, and developed. A Spearman’s rho test was used to screen for correlation among general land cover classification, water quality variables (pH, DO, water temperature), site specific parameters (distance proportion, depth), and year. 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). Akaike's Information Criterion (AIC) was used to select the model with the best fit and fewest degrees of freedom (Burnham & Anderson 2002). Percent deviance explained was calculated by subtracting the model deviance from the null deviance then dividing by the null deviance times one-hundred (Stoner et al. 2001).

The ability for river herring to pass through culverts found within the Albemarle Sound watershed was also assessed using the presence/absence data for the whole time series (1973 – 2017). Observations were made regarding whether river herring were reaching the culverts (presence at the culvert downstream side) and whether passage was possible (presence immediately upstream of the culvert or at the next upstream sampling station).

## 3. Results

Aggregating land cover classifications along river herring migration pathways into four categories (wetland, forest, agriculture/silviculture, and developed) reveals that the riparian zone landscape within the Albemarle Sound watershed is largely undisturbed (Figure 1). The migration pathways within our sample universe range from 0.1 – 188 km, and sum to 15,312 km of rivers and streams, and 284,076 acres of riparian zone. Of the 284,076 acres of riparian habitat, 282,782 acres (99.54%) are wetlands, 418 acres are forest (0.15%), 710 acres are agriculture/silviculture (0.25%), and 166.35 acres are developed (0.06%). Table 1 summarizes the riparian zone composition of the 14 drainage areas studied.

Six out of 14 river systems/watersheds have agriculture or silviculture cover comprising 5% or more of the riparian zone land cover and only in one system does development make up ≥5% of the riparian zone. The drainage area of Edenton Bay has the highest levels of anthropogenic modification within the riparian zone. Agriculture and silviculture make up 10.96% of the riparian cover, and development covers 6.32% of the riparian zone. The two creek systems that make-up the Edenton Bay drainage area, Pembroke Creek and Queen Anne Creek, both have agriculture/silviculture riparian coverage of 9.53% and 16.22%, respectively. Developed areas account for 7.21% of the riparian cover within the Pembroke Creek sampling area. The Chowan River system, which makes up the main spawning grounds within the Albemarle Sound watershed, can be divided into nine drainage areas where lower-order tributaries feed into the Chowan River from the west or the east. None of the nine drainage areas within the Chowan River watershed had anthropogenic modification comprising ≥5% of the riparian zone.

The Spearman's rho test showed a strong correlation between percent developed land and percent wetland cover ($r = -0.82$, $p < 0.001$), and between percent agriculture/silviculture cover and percent forested land ($r = 0.63$, $p < 0.001$). Since we were interested in the effects of anthropogenic modification of the riparian zone, we included percent agriculture/silviculture and percent developed into our model selection process. No other variables had correlations of $r > 0.60$ or $r < -0.60$. The best models (ranked by AIC) for alewife and blueback herring (all data) retained all land cover, water quality, and site specific variables (Table 2). The best models for alewife and blueback herring using the Chowan River and Edenton Bay data also retained all variables (Table 3).

### *3.1 Alewife Habitat Model*

Overall, greater percentages of agriculture/silviculture within riparian zones were associated with decreased alewife presence (Figure 2). Non-linearities in the relationship between agriculture/silviculture and alewife presence resulted in significant negative effects when agriculture/silviculture riparian zone cover was between 8% and 11%, 16% and 21%, and 26% and 29%. Of the 234 migration paths examined, 79 contained agriculture/silviculture within these ranges. Conversely, the percent of development within the riparian zone shows a non-linear positive relationship with the presence of alewife. Non-linear effects for percent agriculture/silviculture and percent development are also observed when looking at just the Chowan River and Edenton Bay watersheds (Figure 3).

Temperature (along with the temperature * year interaction) and dissolved oxygen were the strongest drivers of variation in alewife presence as indicated by the largest increases in AIC when dropped from the model, with increases of 341.46 and 328.71, respectively (Table 2). Temperature had a dome-shaped relationship with alewife presence. Temperature had a positive relationship from 7.6 – 15.3 C, and a negative relationship from -0.1 – 5.9 C and 16.4 – 27.1 C. Alewife were caught at temperatures as low as 0 C and as high as 24 C, with the mean at 11.3 C. Half of all alewife were caught in water temperatures of 5.4 C – 13.6 C. Dissolved oxygen shows an overall positive relationship with alewife presence, with DO having a positive effect from 5.2 – 14.4 mg/L and a negative effect from 0 – 4.2 mg/L. Alewife were caught at DO concentrations as low as 0.1 mg/L and up to 15 mg/L, with the mean at 7.1 mg/L. Half of all alewife caught were in waters with DO concentrations of 5.4 – 8.7 mg/L. The third water quality variable, pH, was the least important contributor to the model. Overall, pH had a mostly neutral relationship with alewife presence. Significant positive effects were seen from 6.5 – 6.8, and negative effects from 3.9 – 5.9. Alewife were caught in acidic to slightly basic waters between 2.7 and 9.5, with the mean at 6.8 and 53% caught between 6.5 and 7.1. Depth, a sample station specific variable, showed an overall positive relationship. Depth negatively affected alewife presence from 0.1 – 1.4 m, and positively affected presence from 1.9 – 5.6 m. Alewife were caught at sample stations with depths of 0.2 – 6 m, with the mean sample station depth at 2.3 m and 53% caught at sample station depths between 1.5 m and 2.7 m. The other sample station specific variable, distance proportion, was inconsistently related to alewife presence. Negative effects were seen from sample stations positioned at distance proportions of 0 – 0.3, 0.6 – 0.7, and 1 – 1.3, and positive effects were seen from 0.4 – 0.5 and 0.7 – 1. The mean sample station distance proportion for alewife catches was 0.7, with 50% caught at distance proportions between 0.7 and 0.9. Year (along with the interaction between year and temperature) was minimally influential in predicting the presence of alewife. Year was positively related with alewife catch between 2007 and 2008, and in 2016, while a negative relationship was seen in 2009, 2011, 2012, 2014, and 2015.

### *3.2 Blueback Herring Habitat Model*

Blueback herring responded similarly to alewife in response to anthropogenic disturbances within the riparian zone. Overall, there was a negative relationship between the percentage of agriculture/silviculture within riparian zones and blueback herring presence (Figure 4). Non-linearities in the relationship between agriculture/silviculture and blueback herring presence resulted in significant negative effects when agriculture/silviculture riparian zone cover was between 11% and 21% and 29% and 35%. Of the 234 migration paths examined, 72 contained agriculture/silviculture within these ranges. Conversely, the percent of development within the riparian zone shows a non-linear positive relationship with the presence of blueback herring. We found the same negative relationship between percent agriculture/silviculture and blueback herring presence when looking at just the Chowan River and Edenton Bay watersheds (Figure 5).

Temperature (along with the temperature * year interaction) was the strongest driver of variation in blueback herring presence as indicated by the largest increase in AIC when dropped from the model, with an increase of 646.98 (Table 2). Temperature had a dome-shaped relationship with blueback herring presence. Temperature had a negative relationship from -0.1 – 10.6 C, and a positive relationship from 11.7 – 22.2 C. Blueback herring were caught at temperatures as low as 3.6 C and as high as 25 C, with the mean at 15.4 C. Half of all blueback herring were caught in water temperatures of 13.5 C – 17.3 C. Dissolved oxygen was the next most important water quality variable, but overall was less important than the inclusion of both riparian agriculture/silviculture and development, depth. Dissolved oxygen shows an overall positive relationship with blueback herring presence, with DO having a positive effect from 5.2 – 14.4 mg/L and a negative effect from 0 – 4.2 mg/L. Blueback herring were caught at DO concentrations as low as 1.1 mg/L and up to 13.3 mg/L, with the mean at 6.0 mg/L. Half of all blueback herring were caught in waters with DO concentrations of 4.3 – 7.5 mg/L. The third water quality variable, pH, was the least important contributor to the model. Overall, pH had a mostly neutral relationship with blueback herring presence. Significant positive effects were seen from 6.6 – 7.3, and negative effects from 2.9 – 6.2. Blueback herring were caught in slightly acidic to slightly basic waters between 5.7 and 8.5, with the mean at 6.8 and 54% caught between 6.6 and 7.1. Depth, a sample station specific variable, showed an overall positive relationship. Depth negatively affected blueback herring presence from 0.1 – 1.5 m, and positively affected presence from 1.8 – 4.8 m. Blueback herring were caught at sample stations with depths of 0.3 – 6 m, with the mean sample station depth at 2.4 m and 57% caught at sample station depths between 1.9 m and 3 m. The other sample station specific variable, distance proportion, was inconsistently related to blueback herring presence. Negative effects were seen from sample stations positioned at distance proportions of 0 – 0.2 and 1 – 1.4, and positive effects were seen from 0.5 – 1. The mean sample station distance proportion for blueback herring catches was 0.6, with 50% caught at distance proportions between 0.3 and 0.9. Year (along with the interaction between year and temperature) was minimally influential in the predicting the presence of blueback herring. Year was positively related with blueback herring catch between 2008 and 2009, and 2014 and 2016, while a negative relationship was seen between 2010 and 2013.

### *3.3 Culvert Analysis*

From 1973 – 2017, sampling occurred for river herring near 60 culverts from twelve of fourteen systems (Table 4; Figure 6). Culverts were assessed for passability based upon observations of river herring being caught upstream. Six categories were assigned to capture the different patterns in river herring sampling and catch around culverts. The categories were: 1 – Passable (catches at the downstream side and immediate upstream or next upstream sample station), 2 – Unpassable (catches at the downstream side but not immediately upstream), 3 – Potentially unpassable (river herring caught at downstream side, but not at next upstream station (no sampling immediately upstream of culvert), 4 – Reached but unknown (catches at the downstream side, but no upstream sampling occurred), 5 – Unreached (no catches at downstream side), 6 – Unknown (one culvert was sampled only at the upstream side with no catches).

Just over half of the sampled culverts (32 out of 60) were unreached. Of the remaining 28 culverts, fifteen were reached but had no upstream sampling (it is unknown if they are passable) and one had only upstream sampling with zero catch. For the remaining twelve culverts that were reached with sampling both up and downstream: eight were categorized as passable (three of these were in the Chowan River, two in Edenton Bay, and one in each of the Perquimans River, Scuppernong River, and Yeopim River); three were categorized as unpassable (one each in the Chowan River, Edenton Bay, and Little River); and one in the Pasquotank was categorized as potentially unpassable. Thus, many of the culverts in the Albemarle watershed are not reached by river herring; of those culverts that are reached with sampling on both sides, the majority were passable.

## 4. Discussion

Anthropogenic influences within Albemarle Sound watershed riparian zones are minimal, with less than 0.5% of riparian zone coverage being modified (Table 1). Our analyses showed some indication of non-linear relationships between anthropogenic influences and river herring presence. However, relationships were weak and inconsistent, and there was little contrast in anthropogenic variables. We found no strong evidence for an effect of agriculture/silviculture and development within the Albemarle Sound watershed on the ability of river herring to migrate upstream to spawning habitat.

Our riparian zone analysis corroborates similar geospatial studies conducted within the Albemarle Sound watershed. McNaught et al. (2010) created a GIS modeling tool to delineate and identify quality habitat for river herring within the Chowan River watershed. They used larval river herring sample data collected by the NCDMF and land cover between 1996 and 2001 (soil erodibility and nutrient condition calculated from land cover proxies; culvert, bridge, and dam locations; and road and river networks) to construct a habitat identification tool that accounted for land cover within each sub-watershed. They determined that the Chowan River basin provides 93,757 acres of river herring habitat and that 90,961 acres is intact and available. A comparison between adult river herring presence data collected by the NCDMF to quality habitats identified by McNaught et al. shows that river herring are still not making it to unobstructed, quality habitats. Two locations in Salmon Creek, NCDMF Stations CR014 and CR015 are located at bridge crossings in quality, accessible habitat. However, only one alewife in each of 2008, 2015, and 2016 made it upstream to CR015, and none made it to CR014. In Chinkapin Creek, CR069 is positioned above and at accessible, quality habitat where no river herring have been detected while sampling in 2008, 2009, 2015, and 2016. Conversely, EB002 and EB007 located in Pembroke Creek are the second and third most heavily urbanized riparian zones in our study system (27.8% and 27.3%, respectively) where blueback herring have been caught 85.7% and 40% of the time those stations were sampled, respectively. PK033, located in the Pasquotank River, is the sixth most agrarian riparian zone but has a relatively high catch rate for alewife at 23.8%. Despite having heavily modified riparian zones, the sampling stations exceed the mean presence proportions for alewife (15.8%) and blueback herring (6.5%). These comparisons suggest that river herring habitat selection is more complex than the riparian zone based models we presented and the sub-watershed models constructed by McNaught et al.

The Albemarle Sound, Chowan River, Little River, and Perquimans River have recently experienced algal blooms in 2015, 2016, and 2017. Algal blooms are typically caused by large nitrogen influxes and subsequently result in lower dissolved oxygen content. Organic nitrogen levels are monitored in the Chowan River by the EPA, and have been steadily increasing since

1998 (ARCDC 2017). Measures of nutrient concentration were not taken at sampling locations, but DO concentration was. DO concentration was the second most important contributor to both species' habitat models. While both species were observed in DO concentrations down to ~1.0 mg/L, most catches were in waters with >~4.0 mg/L, which corroborates the findings presented in the 2009 Atlantic States Marine Fisheries Commission's Habitat Management Series 9 (ASMFC 2009). Adult river herring appear to be able handle hypoxic conditions (DO <3.0 mg/L), but this may only be tolerable for short periods during upstream migration. Of all samples taken between 2007 and 2016, ~18% were <3.0 mg/L. Some of the low DO concentrations may be attributable to natural swamp runoff (NCDENR 2007), but anthropogenic activities or warming waters may also be contributing to low DO.

Water temperature was the most important contributor in both habitat models. Movement and spawning behavior in anadromous fishes has been repeatedly linked to water temperatures and warming rates (Quinn & Adams 1996; Bruch and Binkowski 2002; Juanes et al. 2004; Peer & Miller 2014). This includes river herring (Loesch & Lund 1977; Schmidt et al. 2003; Ellis & Vokoun 2009; Ogburn et al. 2017). Previous work by Lombardo et al. (See Chapter 1) suggests that increased vernal warming rates in recent decades may be strong enough to cause earlier egress relative to prior decades. Reduction in riparian zone coverage can disrupt thermal regimes, further exacerbating climatic shifts (Pusey & Arthington 2003). Studies have shown that riparian zone reduction can result in increased summer water temperatures (Lynch et al. 1984; Pearson & Penridge 1992; Quinn et al. 1992), lower winter water temperatures (Lynch et al. 1984; Armour et al. 1991), and more rapid transitions in water temperatures both temporally and spatially (Lynch et al. 1984). While the riparian zones within the Albemarle

Sound watershed remain mostly intact, further exploration on the influences of riparian zone condition on vernal warming should be examined.

Culverts have been identified as a cause of riverine habitat fragmentation for various fish species (Belford & Gould 1989; Warren Jr & Pardew 1998; Gibson et al. 2005), including river herring (Collier & Odom 1989; Castro-Santos 2004). Culverts can cause fragmentation through river disconnect via an elevated outfall or through the creation of velocity barriers by reducing the effective channel width. Culverts have also been suspected to act as a barrier for river herring due to their propensity to avoid lighting conditions below 1.4% of the ambient light intensity when given a choice (Moser and Terra 1999). NCDMF sampling was not designed to explicitly address culvert passage, but we were able to determine that many culverts are not reached by river herring and of those that were reached and sampled, the majority (8 out of 12) were passable. We did not identify differences between passable and unpassable culverts. For example, culvert 505 is a completely submerged box culvert in a 2 m deep still water creek and is unpassable. However, a culvert of the same construction and condition is passable (culvert 513, Brooks Creek – Chowan River). Further investigation at these stations is recommended.

Generally, river herring have not migrated far enough upstream to reach the majority of the culverts within the watershed. More than half of the culvers sampled were not reached by river herring. At this time, and at current levels of abundance, river herring do not seem to be threatened by culverts within the Albemarle Sound watershed. Further refinement of the culvert passage assessment should be made, as there is potential for error when using the NCDMF river herring spawning habitat survey methods. The survey design repeatedly samples stations until a running ripe female is caught. Only then does sampling proceed upstream. Waiting for a running ripe female at stations downstream of the culvert may prevent the tracking of fish migrating further upstream, potentially beyond the culvert. More direct sampling at culverts will help to assess the passability with a high degree of certainty. We suggest further examination of these culverts by sampling the downstream and upstream sides of culverts simultaneously when river herring are encountered, independent of spawning condition. Results from such studies may provide further refinement to culvert designs that are optimized for fish passage in wetland dominated landscapes.

Adult river herring do not appear to be impacted by changes in habitat connectivity or alterations within the Albemarle Sound watershed. It is important to point out that our analysis does not account for earlier, more vulnerable life stages. Adult river herring are more resilient to variation in water conditions than earlier life stages (ASMFC 2009), which may limit spawn survival. However, recent studies on river herring eggs and larvae in the Chowan River watershed suggest that water quality is not likely to be an issue, even for these more vulnerable life stages. Waters and Hightower (2007) conducted a hatching study and found that water quality within the Albemarle Sound watershed is unlikely to account for the mortality of blueback herring eggs. They observed hatch rates greater than 50% in ten of eleven sites, with hatch rates unaffected by higher amounts of agriculture within the watersheds. Butler (2012) found that larval abundance of river herring in the Chowan River was positively correlated to chlorophyll-a, phosphate, and potassium concentrations, while water quality conditions do not affect nutritional condition. The results from these studies suggest that recent water quality conditions and land cover are not negatively affecting the survival of river herring in their most vulnerable life-stages.

The findings in this paper indicate that anthropogenic modification of the riparian zone itself has not negatively impacted the passage of river herring within the Albemarle Sound watershed for the time period between 2007 and 2016, and that any effects of culverts appear minimal. Further refinement of our model may help to alleviate the strong non-linearities associated with riparian zone land cover. Examining relationships at different spatial extents, such as accounting for upstream drainage area will better represent the connectivity of a fluvial system. Identifying higher resolution land cover data and exploring the relationship between canopy cover and radiative warming of waters will also help to better describe how anthropogenic modification to riparian zones are impacting river herring habitat use. We suggest future monitoring and inclusion of nutrient concentrations in models used to examine habitat selection by river herring. Chlorophyll-a, nitrogen, phosphorus concentrations, and turbidity are a direct measure of water quality and are strongly influenced by anthropogenic input (Lenat & Crawford 1994; Bolstad & Swank 1997; Tong & Chen 2002). While these metrics may not directly impede the upstream progress of adult river herring, or reduce the survival of early life-stages, they can help to predict hypoxic conditions and monitor the continued progress of land management and waste water management.

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## Tables

Table 1. Land cover classifications delineated by NOAA were grouped into four general land cover groups. Acreage of each classification is given for the cumulative sampling area (Albemarle Sound Watershed) and all of the drainage areas that it is comprised of. Anthropogenic alterations of > 5% of the within system riparian zone acreage are in bold.

| System | Agriculture/ Silviculture | Development | Forest | Wetland |
|---|---|---|---|---|
| Albemarle Sound Watershed | 710.44 | 166.35 | 417.57 | 282781.77 |
| Alligator R. | 8.10 | 3.02 | 3.58 | 14431.25 |
| Big Flatty | **8.50** | 0.29 | 2.25 | 144.25 |
| Cashie R. | 11.85 | 4.74 | 9.85 | 842.27 |
| Chowan R. | 173.31 | 22.66 | 172.67 | 3862.03 |
| Bennetts C. | 5.72 | 0.71 | 5.49 | 212.25 |
| Cole-Sarem C. | 0.04 | 0.09 | 0.31 | 101.11 |
| Deep Swamp B. | 0.78 | 0.07 | 4.38 | 68.3 |
| Indian C. | 2.94 | 0.49 | 2.11 | 160.26 |
| Rockyhock C. | 2.85 | 0.00 | 0.51 | 81.67 |
| Salmon C. | 7.07 | 1.00 | 7.27 | 160.01 |
| Stumpy C. | 0.78 | 0.13 | 0.85 | 17.77 |
| Warwick-Trotman C. | 4.14 | 0.16 | 2.49 | 351.78 |
| Wiccacon R. | 39.07 | 1.82 | 39.59 | 888.45 |
| Edenton Bay | **24.51** | **14.12** | 3.76 | 181.20 |
| Pembroke C. | **16.66** | **12.61** | 2.94 | 142.58 |
| Queen Anne C. | **8.38** | 1.58 | 0.87 | 40.82 |
| Little R. | **50.71** | 6.52 | 20.73 | 714.83 |
| Mackeys C. | 4.78 | 4.03 | 3.87 | 154.08 |
| North R. | 4.83 | 1.31 | 3.27 | 5393.87 |
| Pasquotank R. | **73.01** | 42.19 | 29.09 | 1169.32 |
| Perquimans R. | **112.95** | 17.19 | 31.42 | 1059.69 |
| Roanoke R. | 83.71 | 20.24 | 83.13 | 5340.94 |
| Scuppernong R. | 66.92 | 8.65 | 12.70 | 2678.36 |
| Tulls Bay | 37.14 | 4.20 | 13.21 | 3317.32 |
| Yeopim R. | **50.48** | 17.32 | 28.04 | 471.56 |

Table 2. Model selection for the generalized additive models for alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*) within the Albemarle Sound, North Carolina watershed, 2007 – 2016. Models were assessed using Akaike Information Criterion (AIC), weighted AIC (AICw), and percent deviance explained. The most parsimonious model is highlighted.

| Model | AIC | ΔAIC | AICw | % Dev Exp |
|---|---:|---:|---:|---:|
| **Alewife** | | | | |
| Full | 6706.28 | 0.00 | 1.00 | 21.34 |
| *-ph* | 6721.06 | 14.78 | 0.00 | 21.07 |
| -y*t | 6728.58 | 22.30 | 0.00 | 20.93 |
| *-dev* | 6786.85 | 80.57 | 0.00 | 20.13 |
| _-y-y*t_ | 6833.69 | 127.41 | 0.00 | 19.48 |
| *-ag* | 6871.44 | 165.16 | 0.00 | 18.96 |
| *-dp* | 6949.76 | 243.48 | 0.00 | 18.27 |
| *-d* | 7016.22 | 309.94 | 0.00 | 17.46 |
| *-ag-dev* | 7026.14 | 319.86 | 0.00 | 16.89 |
| *-do* | 7034.99 | 328.71 | 0.00 | 19.48 |
| _-t-y*t_ | 7047.74 | 341.46 | 0.00 | 17.01 |
| Null | 8632.50 | 1926.22 | 0.00 | <0.00 |
| | | | | |
| **Blueback Herring** | | | | |
| Full | 3431.37 | 0.00 | 1.00 | 37.52 |
| *-ph* | 3449.52 | 18.16 | 0.00 | 37.09 |
| _-y*t_ | 3461.69 | 30.32 | 0.00 | 36.84 |
| *-ag* | 3467.78 | 36.41 | 0.00 | 36.62 |
| _-y-y*t_ | 3549.20 | 117.83 | 0.00 | 35.04 |
| *-dev* | 3608.04 | 176.68 | 0.00 | 34.07 |
| *-dp* | 3609.50 | 178.13 | 0.00 | 33.76 |
| -do | 3672.15 | 240.78 | 0.00 | 35.61 |
| -d | 3685.60 | 254.23 | 0.00 | 32.50 |
| *-ag-dev* | 3704.97 | 273.60 | 0.00 | 31.97 |
| _-t-y*t_ | 4078.34 | 646.98 | 0.00 | 25.22 |
| Null | 5583.50 | 2152.13 | 0.00 | <0.00 |

**Note**: Full is $x(y, t, y*t, do, ph, d, dp, ag, dev) = i + g_1(y) + g_2(t) + g_3(y*t) + g_4(do) + g_5(ph) + g_6(d) + g_7(dp) + g_8(ag) + g_9(dev) + e(y, t, y*t, do, ph, d, dp, ag, dev)$ where x = river herring presence probability, *i* = intercept, *g* = nonparametric smoothing function, *y* = year, *t* = temperature, *do* = dissolved oxygen, *ph* = pH, *d* = depth, *dp* = distance proportion, *ag* = proportion of riparian zone agriculture/silviculture, *dev* = proportion of riparian zone development.

Table 3. Model selection for the generalized additive models for alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*) in the Chowan River system and Edenton Bay watershed, 2008 – 2016. Models were assessed using Akaike Information Criterion (AIC), weighted AIC (AICw), and percent deviance explained. The most parsimonious model is highlighted.

| Model | AIC | ΔAIC | AICw | % Dev Exp |
|---|---:|---:|---:|---:|
| **Alewife** | | | | |
| Full | 3994.13 | 0.00 | 0.99 | 27.60 |
| *-ph* | 4005.02 | 10.89 | 0.01 | 27.37 |
| -y*t | 4009.44 | 15.31 | 0.00 | 27.07 |
| *-dev* | 4010.72 | 16.59 | 0.00 | 27.20 |
| *-ag* | 4064.37 | 70.24 | 0.00 | 26.22 |
| _-y-y*t_ | 4101.09 | 106.96 | 0.00 | 25.15 |
| *-do* | 4132.32 | 138.19 | 0.00 | 27.23 |
| *-d* | 4143.16 | 149.03 | 0.00 | 24.59 |
| *-dp* | 4167.79 | 173.66 | 0.00 | 24.21 |
| *-ag-dev* | 4253.49 | 259.36 | 0.00 | 22.40 |
| _-t-y*t_ | 4294.26 | 300.13 | 0.00 | 21.57 |
| Null | 5548.36 | 1554.23 | 0.00 | 0.00 |
| | | | | |
| **Blueback Herring** | | | | |
| Full | 2420.39 | 0.00 | 0.99 | 41.72 |
| *-ph* | 2430.29 | 9.90 | 0.01 | 41.31 |
| *-dev* | 2431.80 | 11.41 | 0.00 | 41.36 |
| _-y*t_ | 2449.66 | 29.27 | 0.00 | 40.60 |
| *-d* | 2472.12 | 51.73 | 0.00 | 40.56 |
| *-ag* | 2490.96 | 70.57 | 0.00 | 39.74 |
| _-y-y*t_ | 2534.67 | 114.28 | 0.00 | 38.21 |
| *-dp* | 2559.64 | 139.25 | 0.00 | 37.99 |
| *-do* | 2582.40 | 162.01 | 0.00 | 40.74 |
| *-ag-dev* | 2609.23 | 188.84 | 0.00 | 36.55 |
| _-t-y*t_ | 2975.10 | 554.71 | 0.00 | 27.41 |
| Null | 4192.76 | 1772.37 | 0.00 | <0.00 |

**Note**: Full is $x(y, t, y*t, do, ph, d, dp, ag, dev) = i + g_1(y) + g_2(t) + g_3(y*t) + g_4(do) + g_5(ph) + g_6(d) + g_7(dp) + g_8(ag) + g_9(dev) + e(y, t, y*t, do, ph, d, dp, ag, dev)$ where x = river herring presence probability, *i* = intercept, *g* = nonparametric smoothing function, *y* = year, *t* = temperature, *do* = dissolved oxygen, *ph* = pH, *d* = depth, *dp* = distance proportion, *ag* = proportion of riparian zone agriculture/silviculture, *dev* = proportion of riparian zone development.

Table 4. Culvert passability was assessed using NCDMF river herring spawning habitat survey data from 1973 – 2017. Culvert categories: 1 – Passable (catches at the downstream side and immediate upstream or next upstream sample station), 2 – Unpassable (catches at the downstream side but not immediately upstream), 3 – Potentially unpassable (river herring caught at downstream side, but not at next upstream station (no sampling immediately upstream of culvert), 4 – Reached but unknown (catches at the downstream side, but no upstream sampling occurred), 5 – Unreached (no catches at downstream side), 6 – Unknown (one culvert was sampled only at the upstream side with no catches). System abbreviations: CH = Cashie R., CR = Chowan R., EB = Edenton B., LR = Little R., MC = Mackeys C., MR = Meherrin R., PK = Pasquotank R., PR = Perquimans R., RR = Roanoke R., SR = Scuppernong R., YR = Yeopim R.

| System | Culvert ID | Lat. | Lon. | Category |
|---|---:|---:|---:|---:|
| CH | 488 | 36.086 | -76.885 | 5 |
| CR | 218 | 36.229 | -76.672 | 1 |
| | 511 | 36.365 | -76.724 | 1 |
| | 513 | 36.322 | -76.828 | 1 |
| | 505 | 36.279 | -76.665 | 2 |
| | 18 | 36.347 | -76.636 | 4 |
| | 177 | 36.418 | -76.825 | 4 |
| | 20 | 36.286 | -76.648 | 5 |
| | 29 | 36.247 | -76.826 | 5 |
| | 31 | 36.285 | -76.796 | 5 |
| | 37 | 36.192 | -76.892 | 5 |
| | 65 | 36.340 | -76.834 | 5 |
| | 76 | 36.332 | -76.941 | 5 |
| | 77 | 36.314 | -76.934 | 5 |
| | 90 | 36.284 | -76.945 | 5 |
| EB | 3 | 36.068 | -76.581 | 1 |
| | 9 | 36.104 | -76.634 | 1 |
| | 6 | 36.068 | -76.657 | 2 |
| | 1 | 36.050 | -76.579 | 4 |
| | 5 | 36.082 | -76.581 | 4 |
| | 506 | 36.105 | -76.623 | 4 |
| | 2 | 36.061 | -76.571 | 5 |
| LR | 510 | 36.230 | -76.322 | 2 |
| | 334 | 36.195 | -76.255 | 4 |
| | 327 | 36.175 | -76.316 | 5 |
| | 330 | 36.283 | -76.386 | 5 |
| | 337 | 36.189 | -76.208 | 5 |
| MC | 254 | 35.882 | -76.612 | 4 |
| | 255 | 35.907 | -76.605 | 4 |

Table 4 Continued.

| System | Culvert ID | Lat. | Lon. | Category |
|---|---|---|---|---|
| MR | 121 | 36.401 | -76.967 | 5 |
| | 123 | 36.420 | -77.028 | 5 |
| PK | 367 | 36.271 | -76.080 | 3 |
| | 364 | 36.305 | -76.087 | 4 |
| | 338 | 36.150 | -76.169 | 5 |
| | 361 | 36.320 | -76.136 | 5 |
| | 362 | 36.319 | -76.133 | 5 |
| | 366 | 36.271 | -76.080 | 5 |
| PR | 507 | 36.169 | -76.470 | 6 |
| | 512 | 36.251 | -76.450 | 4 |
| | 508 | 36.173 | -76.472 | 1 |
| | 509 | 36.171 | -76.475 | 4 |
| | 299 | 36.231 | -76.563 | 5 |
| | 320 | 36.167 | -76.348 | 5 |
| | 321 | 36.149 | -76.327 | 5 |
| | 309 | 36.316 | -76.544 | 5 |
| | 313 | 36.228 | -76.418 | 5 |
| RR | 465 | 35.974 | -77.353 | 5 |
| SR | 235 | 35.794 | -76.390 | 5 |
| | 248 | 35.843 | -76.418 | 1 |
| | 252 | 35.835 | -76.437 | 4 |
| | 256 | 35.923 | -76.405 | 5 |
| | 247 | 35.829 | -76.430 | 5 |
| | 284 | 36.124 | -76.441 | 4 |
| YR | 274 | 36.097 | -76.534 | 1 |
| | 282 | 36.128 | -76.422 | 5 |
| | 281 | 36.091 | -76.386 | 4 |
| | 278 | 36.116 | -76.464 | 5 |
| | 271 | 36.068 | -76.493 | 4 |
| | 273 | 36.093 | -76.542 | 5 |
| | 280 | 36.108 | -76.452 | 5 |

**Figures**

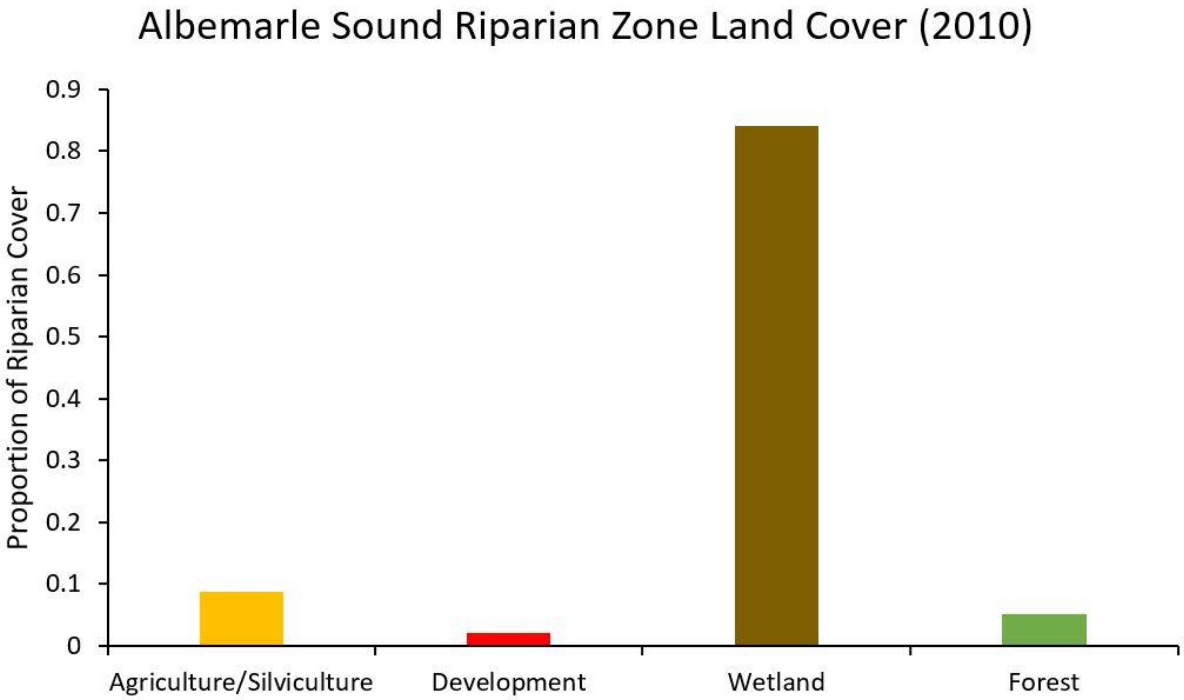
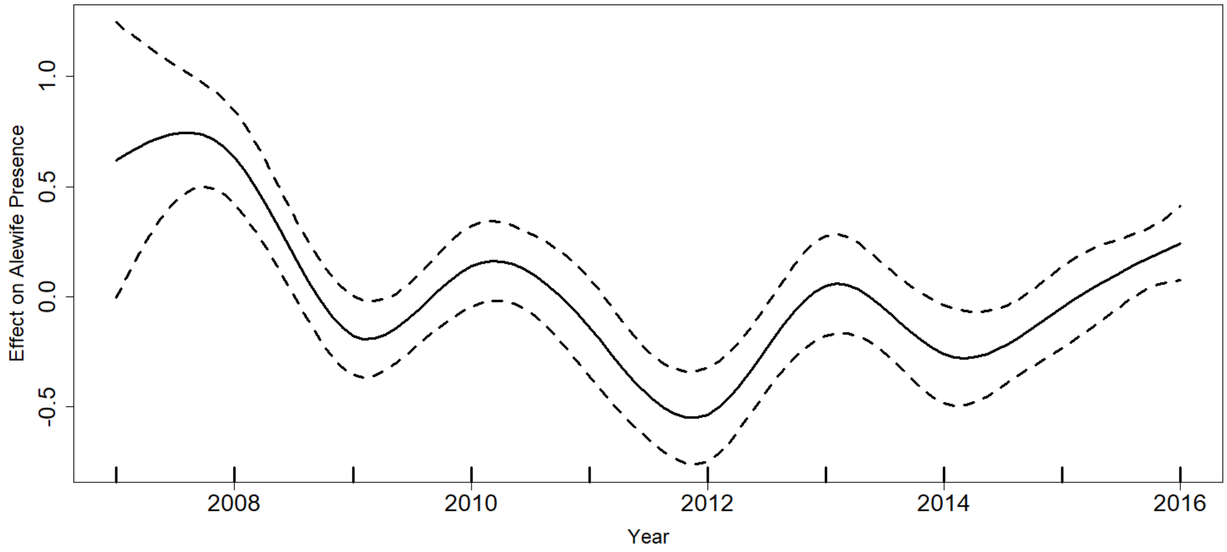
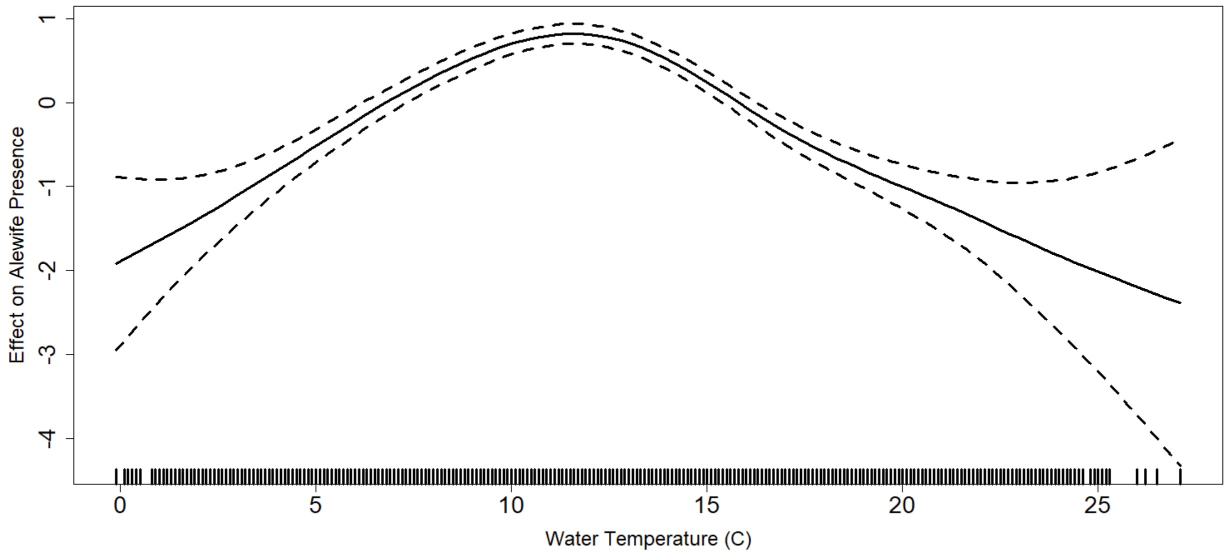
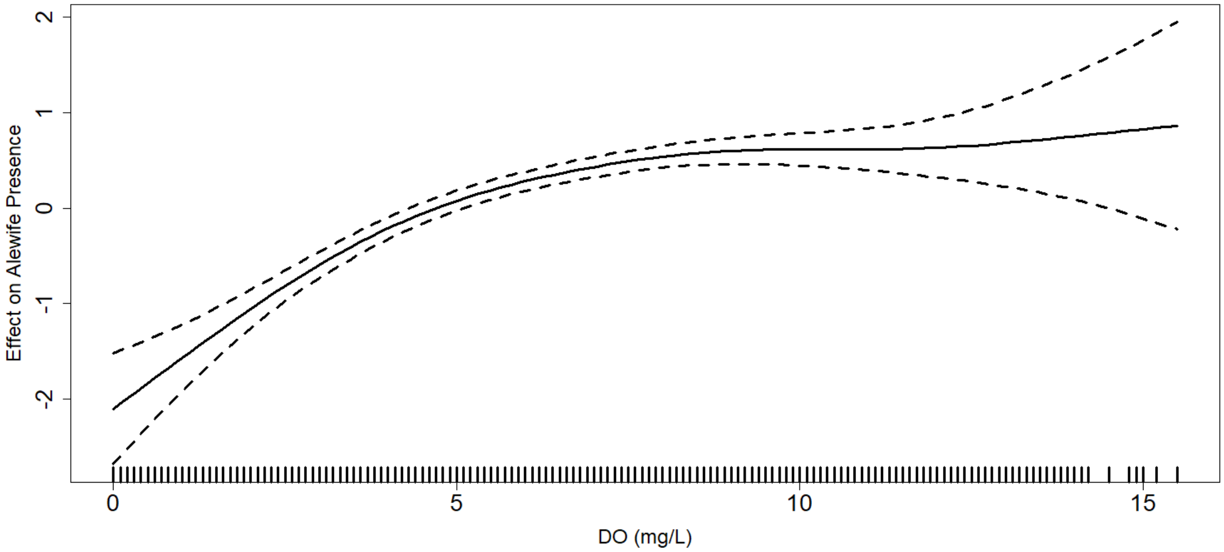


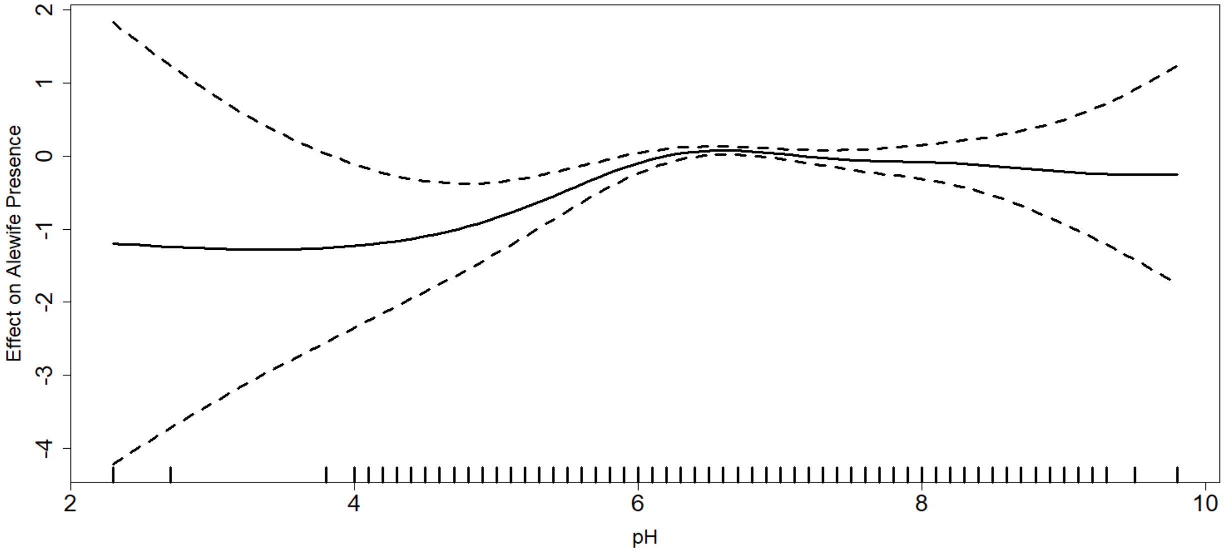
Figure 1. Summary of riparian zone land cover areas for the migration paths taken to reach each of the 236 sample stations. Wetlands dominate the riparian zone throughout the Albemarle Sound watershed.

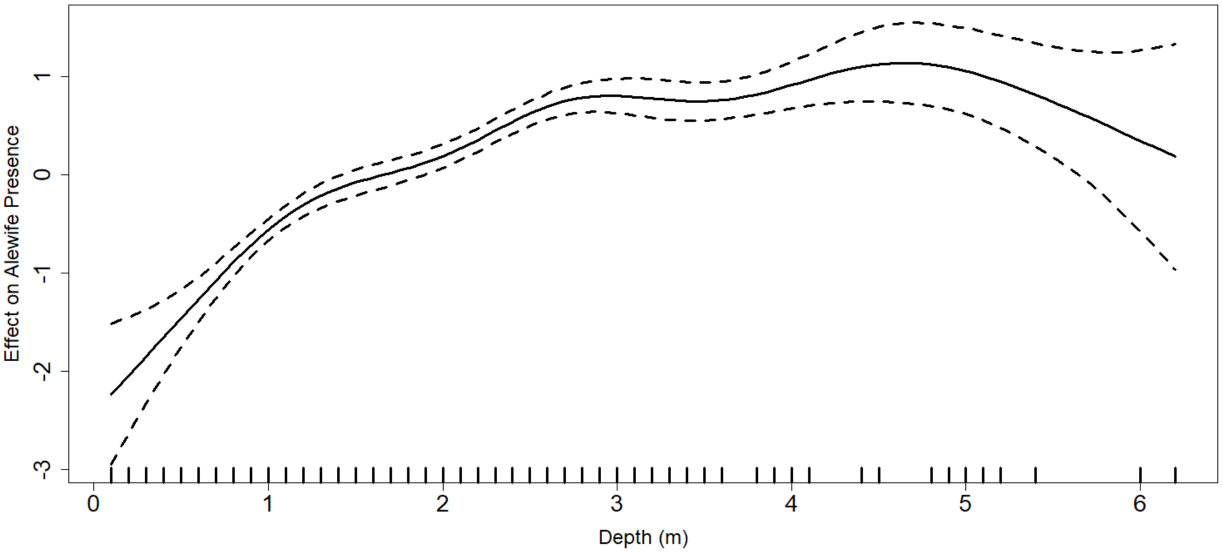
Figure 2. Logistic GAM-derived effects of year, water temperature, DO, pH, depth, distance proportion, proportion of agriculture/silviculture land cover in the riparian zone, and proportion of developed land cover in the riparian zone on the presence of alewife in the Albemarle Sound watershed. Dashed lines indicated the 95% CI. Tick marks on the x axis represent sampling intensity.

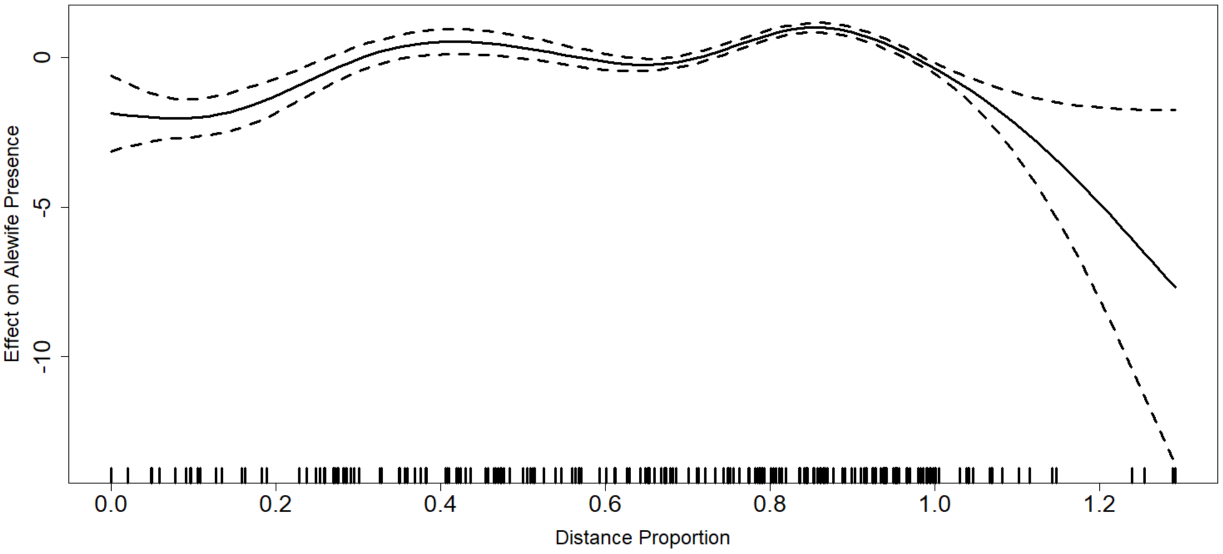

Effect on Alewife Presence
-0.5
0.0
0.5
1.0
2008
2010
2012
2014
2016
Year

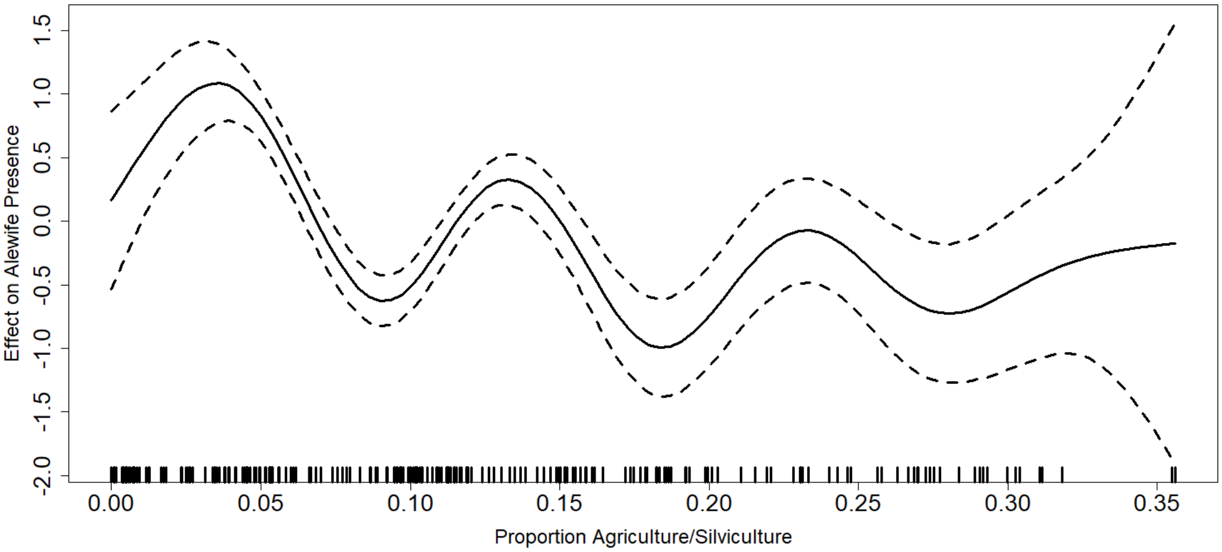

Effect on Alewife Presence
-4
-3
-2
-1
0
1
0
5
10
15
20
25
Water Temperature (C)

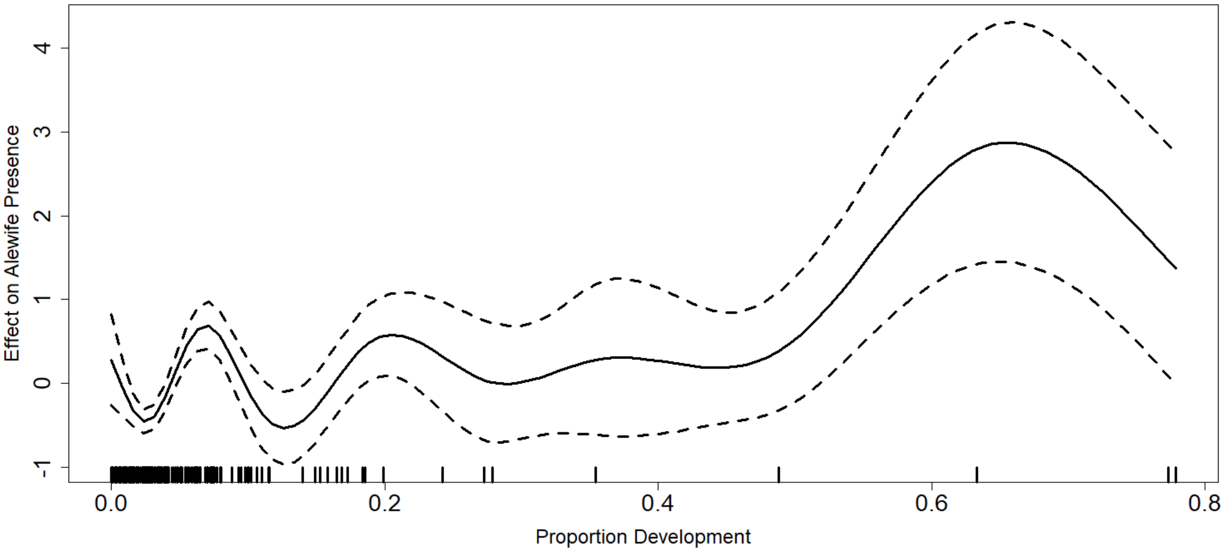

Effect on Alewife Presence
2
1
0
-1
-2
0
5
10
15
DO (mg/L)


Effect on Alewife Presence
2
1
0
-1
-2
-3
-4
2
4
6
8
10
pH


Effect on Alewife Presence
-3
-2
-1
0
1
0
1
2
3
4
5
6
Depth (m)


Effect on Alewife Presence
-10
-5
0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Distance Proportion


Effect on Alewife Presence
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
Proportion Agriculture/Silviculture


Effect on Alewife Presence
-1
0
1
2
3
4
0.0
0.2
0.4
0.6
0.8
Proportion Development

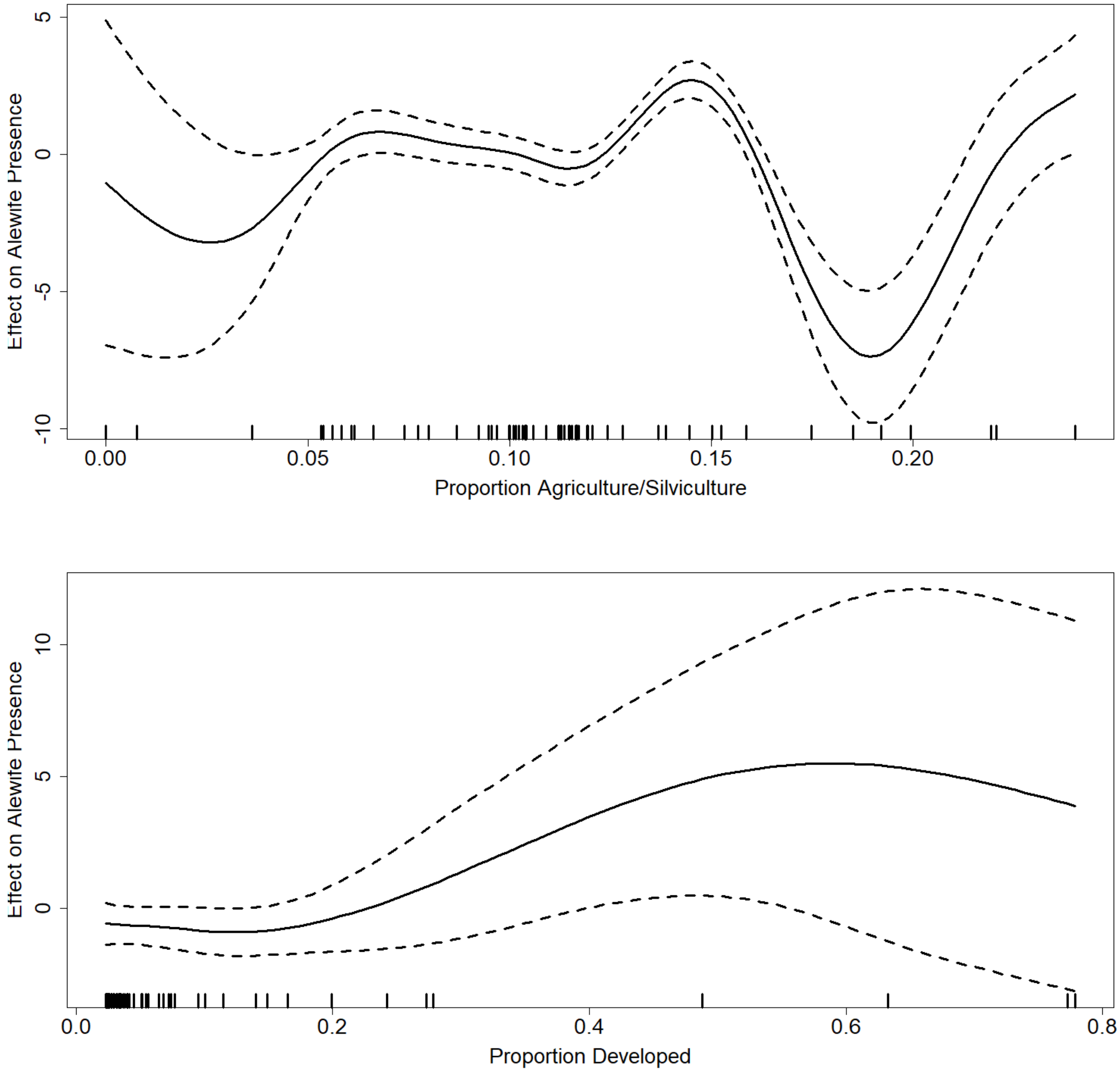
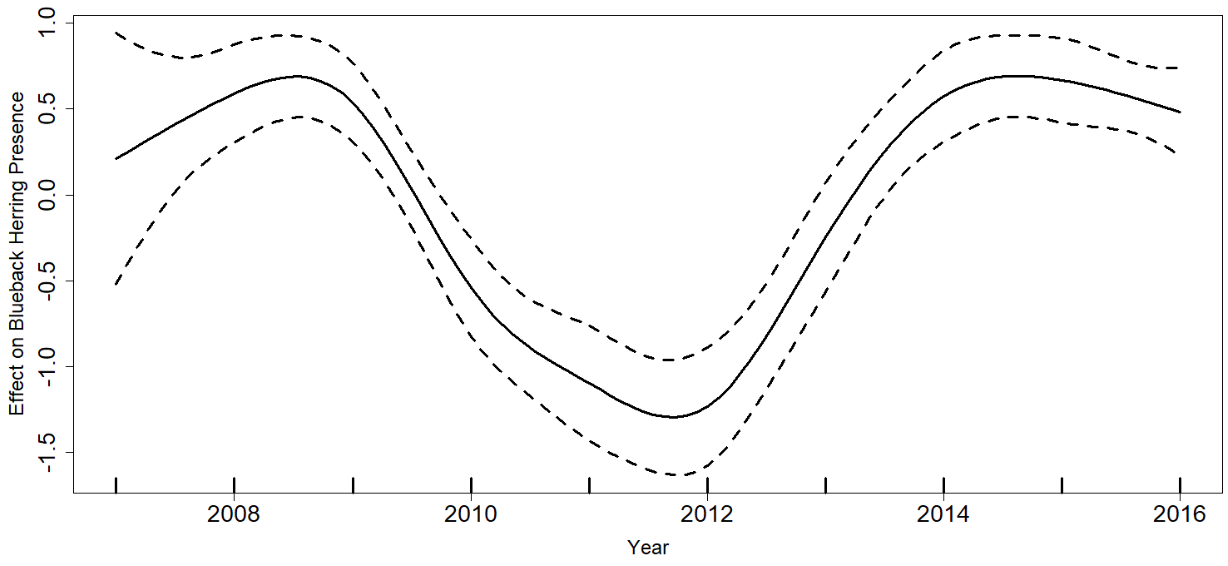
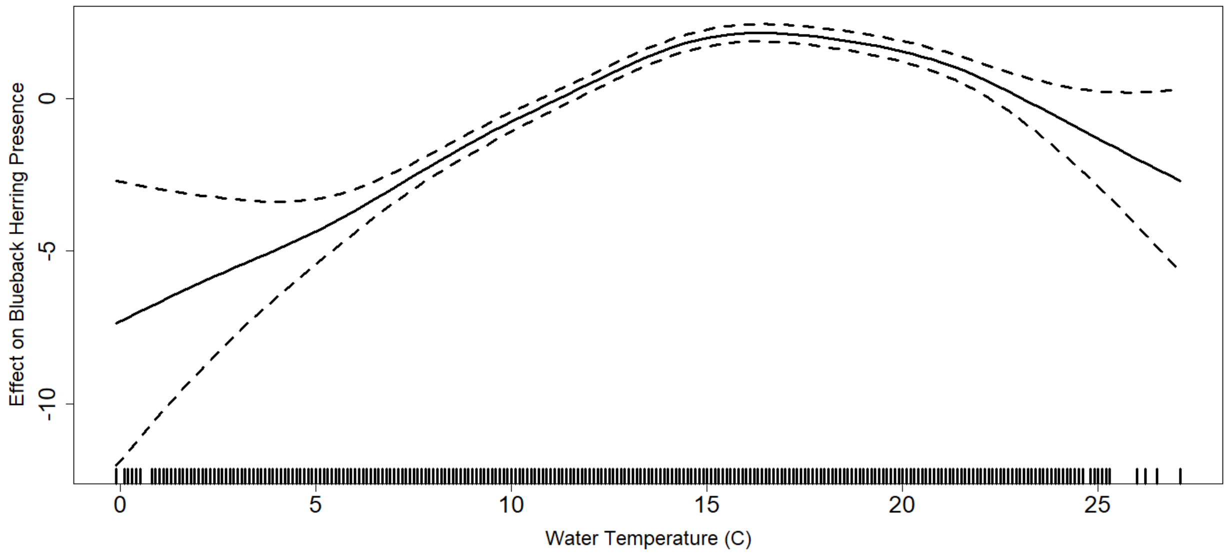
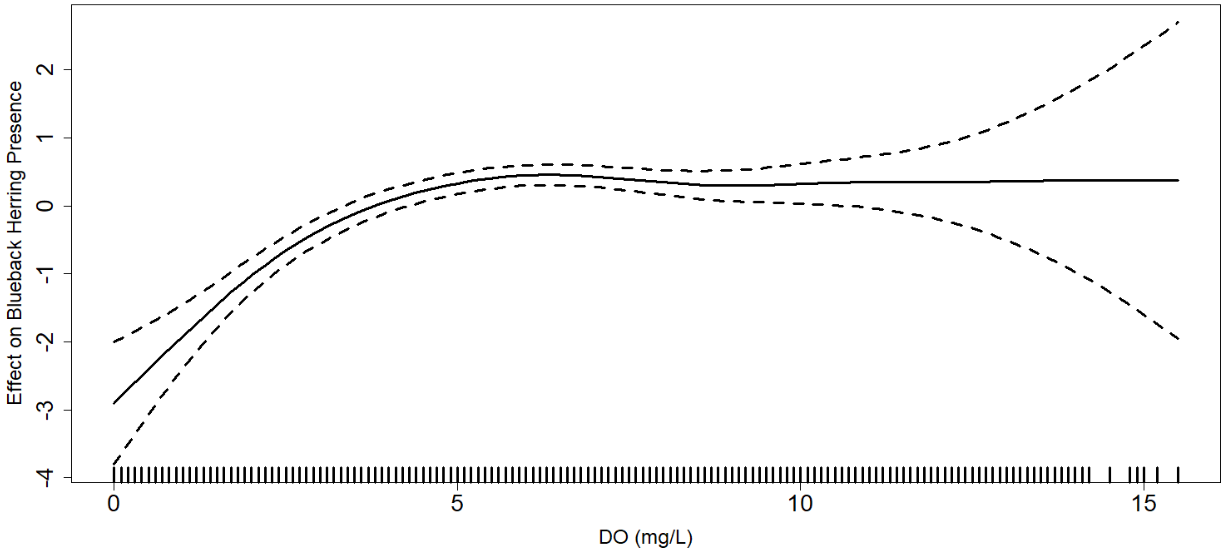


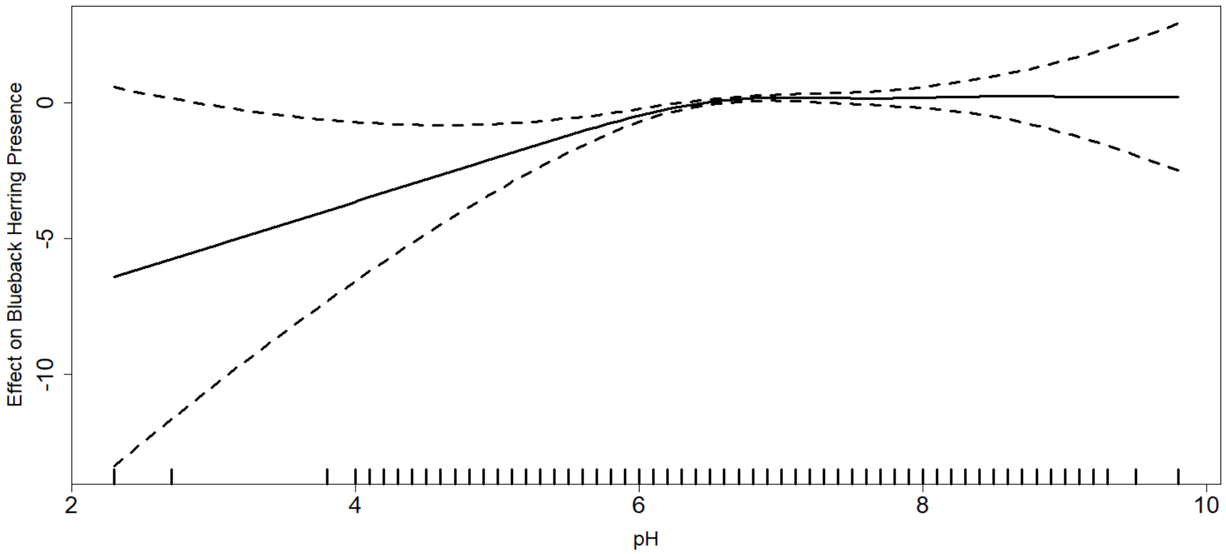
Figure 3. Logistic GAM-derived effects of proportion of agriculture/silviculture land cover in the riparian zone, and proportion of developed land cover in the riparian zone on the presence of alewife in the Chowan River and Edenton Bay. Dashed lines indicated the 95% CI. Tick marks on the x axis represent sampling intensity.

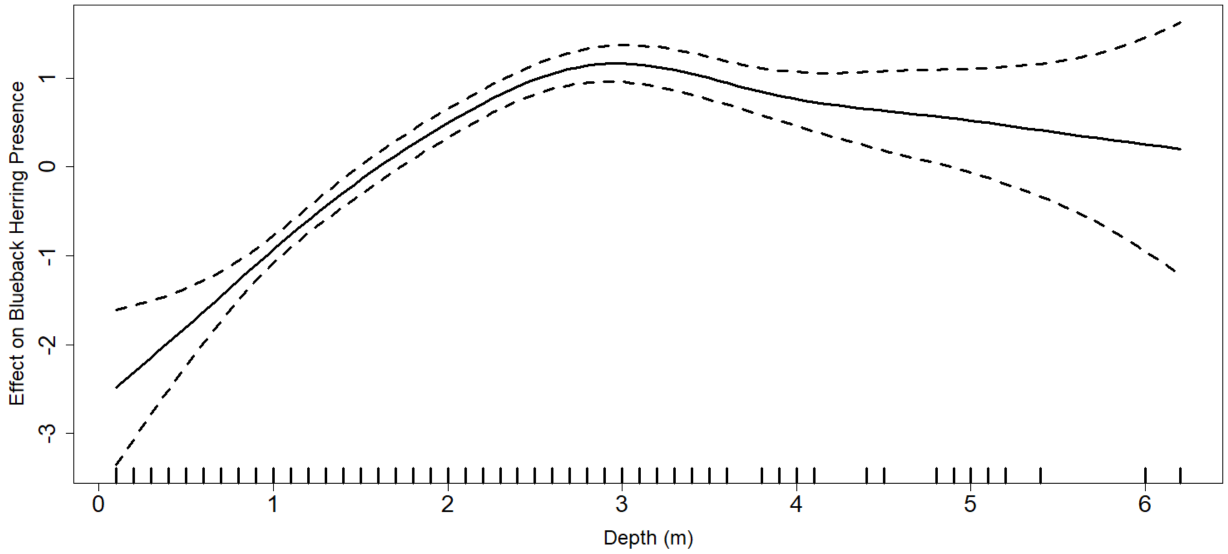
Figure 4. Logistic GAM-derived effects of year, water temperature, DO, pH, depth, distance proportion, proportion of agriculture/silviculture land cover in the riparian zone, and proportion of developed land cover in the riparian zone on the presence of blueback herring in the Albemarle Sound watershed. Dashed lines indicated the 95% CI. Tick marks on the x axis represent sampling intensity.

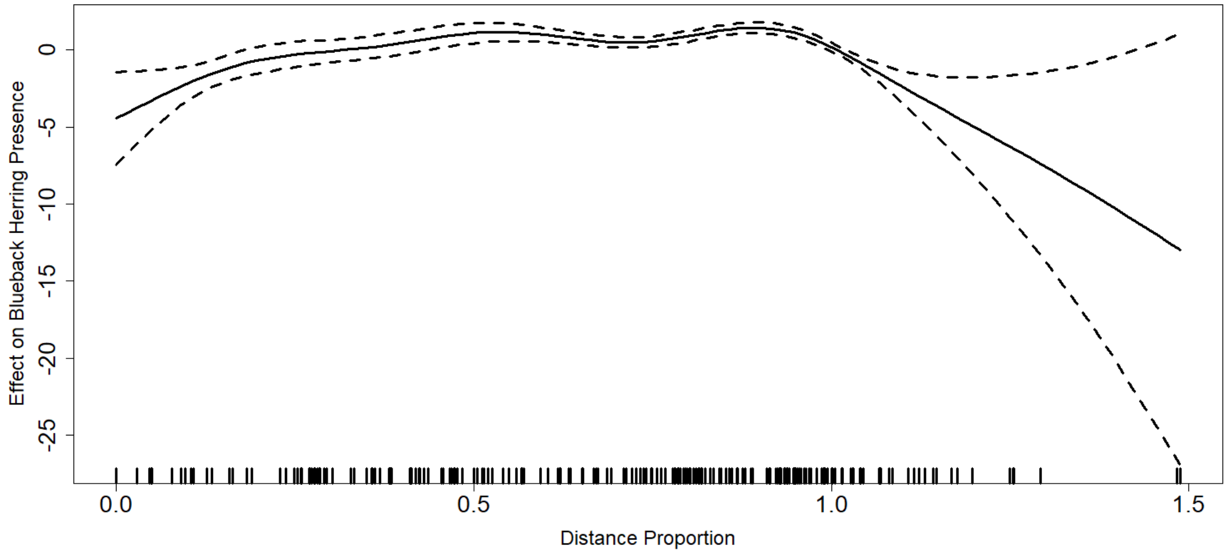

Effect on Blueback Herring Presence
1.0
0.5
0.0
-0.5
-1.0
-1.5
2008
2010
2012
2014
2016
Year

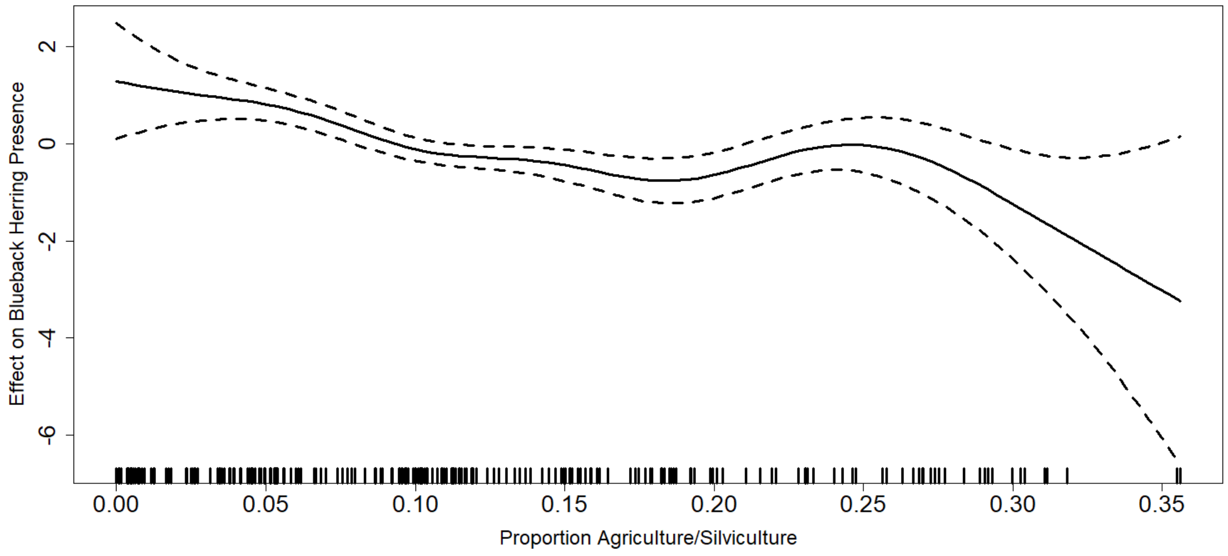

Effect on Blueback Herring Presence
0
-5
-10
0
5
10
15
20
25
Water Temperature (C)

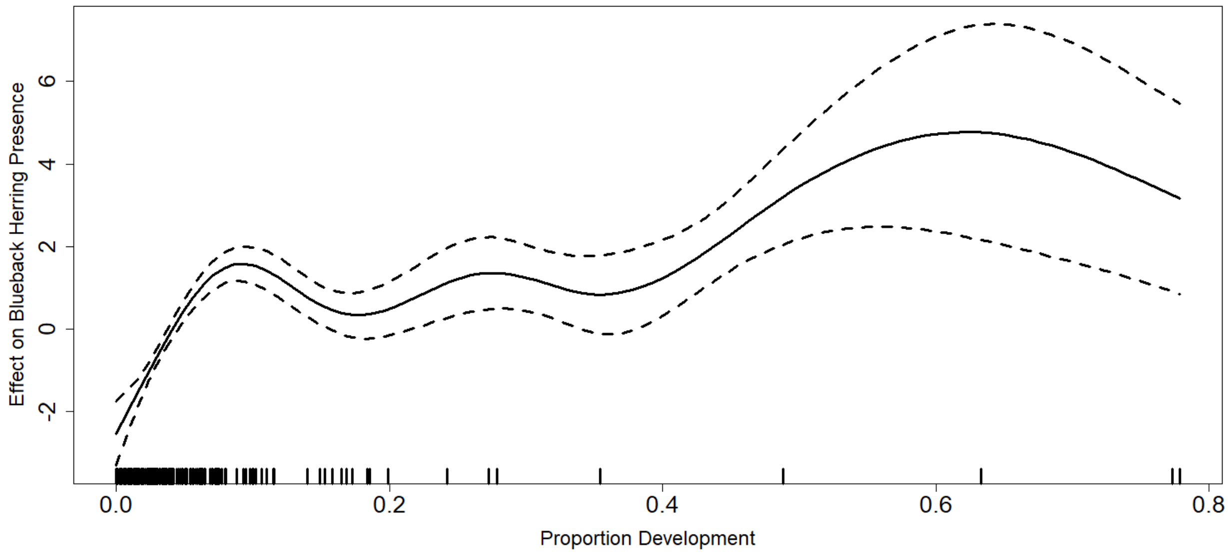

Effect on Blueback Herring Presence
2
1
0
-1
-2
-3
-4
0
5
10
15
DO (mg/L)


Effect on Blueback Herring Presence
0
-5
-10
2
4
6
8
10
pH


Effect on Blueback Herring Presence
1
0
-1
-2
-3
0
1
2
3
4
5
6
Depth (m)


Effect on Blueback Herring Presence
0
-5
-10
-15
-20
-25
0.0
0.5
1.0
1.5
Distance Proportion


Effect on Blueback Herring Presence
2
0
-2
-4
-6
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
Proportion Agriculture/Silviculture


Effect on Blueback Herring Presence
6
4
2
0
-2
0.0
0.2
0.4
0.6
0.8
Proportion Development

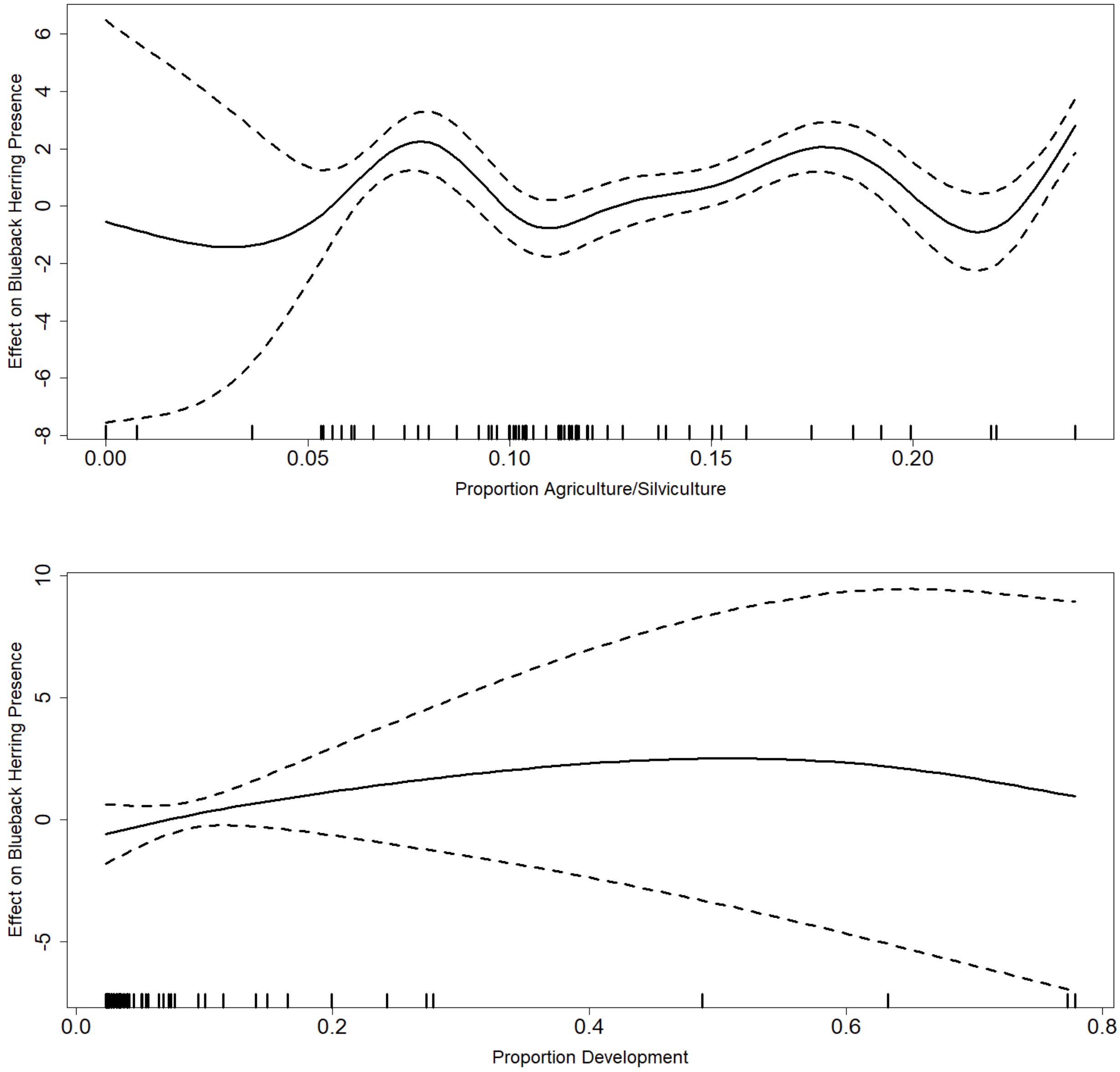
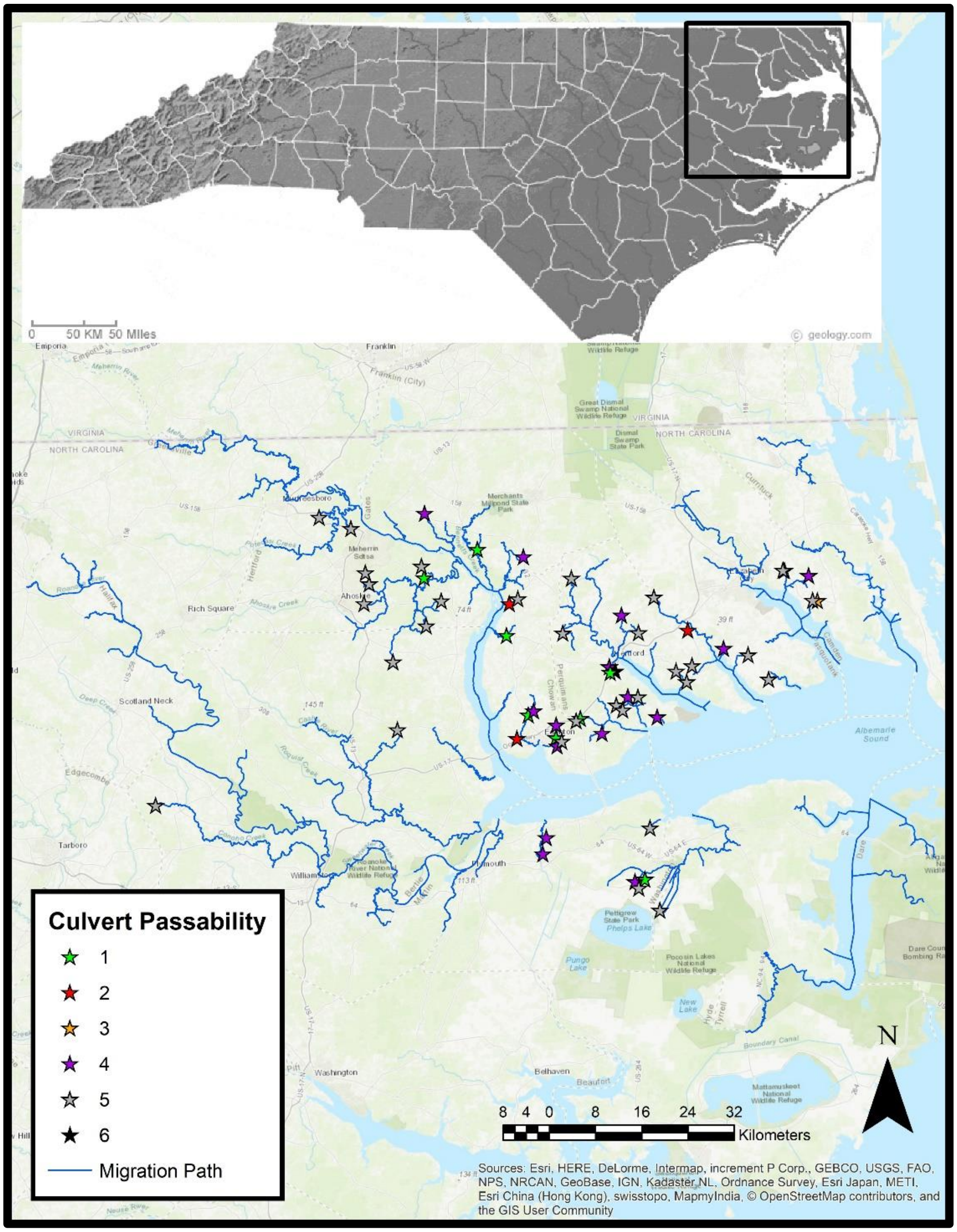


Figure 5. Logistic GAM-derived effects of proportion of agriculture/silviculture land cover in the riparian zone, and proportion of developed land cover in the riparian zone on the presence of blueback herring in the Chowan River and Edenton Bay. Dashed lines indicated the 95% CI. Tick marks on the x axis represent sampling intensity.



Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure 6. Culvert passability was assessed using NCDMF river herring spawning habitat survey data (1973 – 2017). Culvert categories: 1 – Passable (catches at the downstream side and immediate upstream or next upstream sample station), 2 – Unpassable (catches at the downstream side but not immediately upstream), 3 – Potentially unpassable (river herring caught at downstream side, but not at next upstream station (no sampling immediately upstream of culvert), 4 – Reached but unknown (catches at the downstream side, but no upstream sampling occurred), 5 – Unreached (no catches at downstream side), 6 – Unknown (one culvert was sampled only at the upstream side with no catches).