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

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## Manuscripts

1  **Evidence for temperature-dependent shifts in spawning times of anadromous alewife**

2  **(*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*)**

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24   **Abstract** We analyzed four decades of presence/absence data from a fishery-independent survey

25   to characterize the long-term phenology of river herring (alewife *Alosa pseudoharengus* and

26   blueback herring *Alosa aestivalis*) spawning migrations in their southern distribution.  We used

27   logistic generalized additive models to characterize the average ingress, peak, and egress timing

28   of spawning.  In the 2010s, alewife arrived to spawning habitat 16 days earlier and egressed 27

29   days earlier (peak 12 days earlier) relative to the 1970s.  Blueback herring arrived five days

30   earlier and egressed 23 days earlier (peak 13 days earlier) in the 2010s relative to the 1980s.  The

31   changes in ingress and egress timing have shortened the occurrence in spawning systems by 11

32   days for alewife over four decades and 18 days for blueback herring over three decades.  We

33   found that the rate of vernal warming was faster during 2001 to 2016 relative to 1973 to 1988

34   period and is the most parsimonious explanation for changes in spawning phenology.  The

35   influence of a shortened spawning season on river herring population dynamics warrants further

36   investigation.

37 **Introduction**

38 Globally, average temperatures have increased steadily from 1880 to 2012, with the three most

39 recent decades having been successively warmer than any preceding decade since 1850 (IPCC

40 2014).  A meta-analysis by Chen et al. (2011) linked range shifts and warming climate for 23

41 terrestrial species groups to higher latitudinal distributions and higher elevations.  Poleward

42 shifts in distribution have also been observed in marine species across taxa (Murawski 1993;

43 Blanchard et al. 2005; Perry et al. 2005; Mieszkowska et al. 2006; Fogarty et al. 2008; Nye et al.

44 2009).  Marine species whose life histories are solely dependent upon marine or estuarine

45 environments are often capable of modifying their spatial distributions to stay within optimal

46 thermal ranges for their various life stages (Perry et al. 2005; Poloczanska et al. 2013).

47 However, diadromous species that exhibit some degree of natal homing may not be able to

48 spatially adapt to environmental changes and are at greater risk of experiencing negative effects

49 due to climate change (Hare et al. 2016), but could temporally adapt their behavior to maintain

50 accessibility to preferred temperatures in response to changes in thermal regime.

51 Phenology is the study of seasonal or cyclical biological processes and how they are

52 influenced by climate, environment, and species interactions.  Plants and animals alike rely upon

53 external stimuli to optimize the timing of migrations, blooms, molts, and reproduction (Newton

54 1966; White et al. 1997; Sherry et al. 2006; Miller-Rushing et al. 2008).  Climate change has

55 disrupted the natural timing of such biological processes for many species through intensified

56 rates of warming, prolonged seasons of precipitation or drought, amplification of weather events,

57 and cascading effects through trophic interactions (Cushing 1990; Zhang et al. 2005; Ciannelli et

58 al. 2007; Prieto et al. 2008; Richardson et al. 2013; Asch 2015).  For diadromous fishes, changes

59 in thermal regime have already been shown to impact the phenology of spawning migrations

60    (Quinn and Adams 1996; Crozier et al. 2008; Kovach et al. 2013, Otero et al. 2014; Peer and

61    Miller 2014; Kovach et al. 2015).

62          River herring, the collective name for alewife (*Alosa pseudoharengus*) and blueback

63    herring (*Alosa aestivalis*), are anadromous fishes that are at historically low levels of abundance

64    (Hightower et al. 1996; ASMFC 2012, ASMFC 2017).  River herring once supported large

65    fisheries along the North American Atlantic coast from Nova Scotia down to the St. Johns River,

66    FL (Jackson 1944; Watts 2003; Hightower 2004).  Declines in river herring stocks have been

67    attributed to overfishing (Hightower et al. 1996), offshore bycatch (ASMFC 2012; Bethoney et

68    al. 2013; Cournane et al. 2013), and loss of spawning habitat due to obstructions and degradation

69    (Collier and Odom 1989; Hall et al. 2011).  Attempts to ameliorate the population decline

70    include moratoria, offshore by-catch caps, offshore spatial/temporal closures in the Atlantic

71    herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) fisheries, and dam removal, all of

72    which have been ineffective at recovering stocks (Hightower et al. 2004; ASMFC 2012;

73    Bethoney et al. 2013; Cournane et al. 2013).

74          While the decline of river herring was likely caused by a combination of fishing pressures

75    and habitat loss, the continued depression of population levels may result from other ecological

76    mechanisms, including climatological phenomenon.  For example, Lynch et al. (2015) provide

77    evidence that river herring are vulnerable to ocean warming off the northeast US shelf, reducing

78    the amount of suitable habitat, and that the population may be more sensitive to climate effects at

79    low levels of abundance.  Furthermore, a vulnerability assessment of 82 Northeast Atlantic

80    marine fish and invertebrate species by Hare et al. (2016) identified both alewife and blueback

81    herring as species of the highest concern for negative effects of climate change, citing water

82    temperature and the limited periodicity and spatial constraints of their anadromous spawning

83  strategy as the most critical environmental and biological factors.  A tagging study by Jessop

84  (1994) in the Saint John's river system shows that river herring exhibit high inter-annual

85  spawning site fidelity (63-97% return rate), a process likely driven by olfactory natal homing

86  (Thunberg 1971).  In freshwater systems utilized by river herring as spawning and nursery

87  habitat, river flow conditions and water temperature are the dominant influencers of stock

88  recruitment (Tommasi et al. 2015).  Early studies in New England at fish weirs and dams have

89  shown the timing and behavior of pre- and post-spawning migration river herring to be tightly

90  coupled with stream temperatures and insolation (Collins 1952; Saila et al. 1972; Beltz 1975).

91  Ellis and Vokoun (2009) provided the first suggestion that alewife spawning migrations may be

92  occurring earlier due to higher water temperatures in recent time periods.  However, they did not

93  have historical and modern fish count data in the same watershed.  Both Lynch et al. (2016) and

94  Tommasi et al. (2015) suggest further examination of the climatological effects on river herring

95  in freshwater systems, and specifically on adult spawning migrations.  Despite colloquial and

96  managerial grouping of alewife and blueback herring, the two sympatric species display different

97  behaviors with alewife spawning migrations happening earlier than blueback herring.  Whether

98  migrating blueback herring display the same response to climatological changes as alewife, as

99  suggested by Ellis and Vokoun (2009), has yet to be examined.

100      Here, we test the hypothesis that the phenology of adult alewife and blueback herring has

101  independently changed by examining river herring catch data during the spawning migration

102  from 1973 to 2016 in the Albemarle Sound watershed (hereafter referred to as ASW).  After

103  describing the temporal variation in spawning migrations, we also evaluate potential mechanisms

104  responsible for the changes including: age structure, abundance, and water temperature.  Our

105  work aims to further characterize the response of river herring to shifting climate norms in their

106    southern distribution and to provide life history information to better inform management

107    decisions as the environment continues to change.

108    **Methods** *Study Location and Monitoring* The North Carolina Division of Marine Fisheries

109    (NCDMF) has conducted a river herring spawning habitat survey since spring of 1973.  The goal

110    of the survey is to identify the annual extent of stream habitats used by both alewife and

111    blueback herring for spawning in nine river systems and their associated tributaries that feed into

112    the AS.  Sampling for river herring was intermittent in years between 1973 and 2001 but has

113    been annual since 2007 (See Table S1 for sampling summary; Fig 1 for sampling stations).

114    Although only 24 of the possible 43 years were sampled, sampling occurred in at least four years

115    per decade in all decades with the exception of the 1990s (only one year of sampling).  Prior to

116    2007, sampling was conducted at randomly selected stations throughout the ASW with varied

117    spatial and temporal extents (See Fig S1).  Beginning with 2008, the methods were standardized

118    to sample the entirety of the river herring spawning run within the Chowan River and Edenton

119    Bay watershed plus at least one of twelve additional ASW river systems on a rotating basis.

120    Additional systems were sampled if travel time to and from sampling stations was not limiting.

121    In 2007, the sampling design changed from random sampling to sampling that tracked the

122    migration progress of river herring through the watershed.  Beginning in 2012, sample stations

123    located at the nearest road crossing to the mouths of five Chowan River tributaries became fixed

124    sampling stations that are sampled each week throughout the entire river herring spawning

125    season.

126          The presence of river herring was monitored with staked or floating gillnets.  Gillnet

127    dimensions have varied over the time series with bar meshes ranging from 1.13 to 1.88 in. and

128    lengths ranging from 3 to 30 yd.  Since 2007, the protocol has been standardized, providing more

129    consistent use of bar mesh sizes of 1.38 in. during the alewife run and 1.25 in. during the

130    blueback herring run.  Net lengths were also restricted to 5, 8, and 10 yards for staked gillnets, 5,

131    8, 10, 20, and 30 yd for floating gillnets, fished at a maximum depth of 2.1 m where possible.

132    Staked gillnets were stretched across the channel width on the effluent side of the furthest

133    downstream bridge or culvert and moved upstream to the next road crossing when running ripe

134    females were encountered.  Navigable waterways were sampled with gillnet lengths that left

135    watercraft passage uninterrupted.  Gillnets were set on Mondays, checked every 24 hours, and

136    removed over weekends and holidays due to logistical constraints.  Water surface temperature,

137    air temperature, pH, salinity, conductivity, and DO were taken at each sampling station upon net

138    inspection.

139          Prior to 2007 sampling was random in start date, end date, and location, and mostly

140    focused on monitoring the blueback herring spawning migration.  Starting dates ranged from

141    February 4 to April 2, with a median start date of March 8 (Fig S1).  Sampling end dates ranged

142    from April 21 to May 8, with a median end date of April 29.  From 2007 onward, sampling for

143    alewife commenced when alewife were caught in the NCDMF striped bass (*Morone saxatilis*)

144    fisheries-independent gillnet survey, which is conducted within the ASW at the mouths of the

145    river systems.  Starting dates ranged from January 12 to February 29, with a median start date of

146    February 6.  The sampling protocol for 2007 onward began sampling at the most downstream

147    stations and only moved to upstream locations after a running ripe alewife was caught, with the

148    exception of the five fixed nets (2012 – present).  Nets were reset to their original starting

149    positions when the first blueback herring was caught in any of the alewife survey nets and then

150    moved upstream again as running ripe blueback herring were caught.  Sampling ceased when

151    catches of blueback herring in the NCDMF Chowan River pound-net survey, conducted in the

152     main stem of the Chowan River, became sporadic (<10 fish per week).  The end dates ranged

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

154     *Phenology* Studies on anadromous fish migrations characterize the phenology of the migration

155     by identifying the initiation, peak, and completion (Quinn and Adams 1996; Juanes et al. 2004;

156     Ellis and Vokoun 2009; Kennedy and Crozier 2010).  Migration progress is typically delineated

157     by identifying the day of the year that 25%, 50%, and 75% of yearly abundance is observed as

158     reference points for the initiation, peak, and completion of the migration (Antonsson and

159     Gudjonsson 2002; Kennedy and Crozier 2010; Otero et al. 2014).  However, 5% of the run

160     abundance has been used to identify the initiation of alewife spawning migrations in New

161     England (Ellis and Vokoun 2009) and the Chesapeake Bay (Ogburn et al. 2017).  Due to the

162     variability in gill net sizes and amount of stream width covered by gill nets at sampling locations

163     across years, presence/absence data were used instead of abundance data to characterize the

164     phenology of river herring spawning.

165         We used generalized additive models (GAMs) with a logit link and a binomial

166     distribution to examine the effects of several variables on river herring presence and absence

167     data.  GAMs are useful in modeling nonparametric relationships typical of ecological data

168     (Hastie and Tibshirani 1990) and have been shown to be a more accurate representation of

169     phenology than first appearance dates or alternative measures (Moussus et al. 2010).  Penalized

170     thin plate and tensor product splines with shrinkage parameters were used as smoothers.  The

171     inclusion of shrinkage parameters allows for completely smoothed predictors to be selected out

172     of the model by reducing the splined term to zero (Wood 2006).  Environmental (surface

173     temperature, DO, pH, conductivity, upstream distance) and temporal (ordinal day and decade)

174     variables were screened for correlation and brought into the models *a priori* based upon

175 knowledge of the environmental cues that river herring use to initiate migratory behavior and

176 inspection of plots of river herring presence probability and potential variables. Because of

177 correlation with ordinal day, we dropped water quality parameters and retained ordinal day.

178 Due to the sampling procedures and efforts varying across the 43-year time series, some

179 special considerations needed to be made when constructing and making inferences from the

180 models. Upon inspection of the data, we determined that sampling was too sparse to model the

181 phenological trends at a yearly resolution. Modeling at a broader scale, using decade, allowed

182 for a wider range of days for the model to be fitted to and more precise measures of fish presence

183 within the system. It is important to note that similar changes in phenology (described below)

184 were observed when using year instead of decade. Decadal differences in the first and last dates

185 of sampling resulted in GAM predictions occurring outside of the dates where sampling

186 occurred. Extrapolation is not recommended without ecological justification and results should

187 be evaluated critically (Merow et al. 2014). Thuiller et al. (2004) showed that extrapolating from

188 a restricted range of data (i.e., not capturing leading and trailing absences) can result in

189 disruption of smoothed relationships and more conservative or liberal predictions depending on

190 the information available to inform the model. Due to river herring being anadromous, temporal

191 extrapolation trending towards egress from the system (5% presence probability) can be

192 ecologically and statistically justified as long as predictions are not extrapolated beyond the

193 temporal bounds of sampling for the entire time-series (i.e., the first and last ordinal days

194 sampled). For instances where predictions are extrapolated, a second estimate of ingress can be

195 made as the first detection of presence and egress as the last detection of presence. These latter

196 estimates based on observations are biased late for ingress and biased earlier for egress given that

197 sampling during these periods was limited.

198    Additionally, the changes in experimental design in 2007 could lead to changes in spatial

199    coverage of the survey in recent years.  Because the presence of river herring can change with

200    distance upstream, we accounted for variability in the distance upstream that samples were taken.

201    Distances from the mouth of the river systems to the sample stations were measured using

202    ArcMap 10.3.1 (ESRI, Redlands, CA) and the USGS National Hydrography Dataset (NHD)

203    (U.S. Geological Survey 2013).  Upstream distances ranged from 101 to 188,478 meters.  Spatial

204    variation was accounted for by creating a proportion; the distance between the tributary mouth

205    and each sample station to the maximum distance a river herring was observed in the tributary

206    (hereafter referred to as distance proportion).

207    Although we used distance proportion as a variable to correct for any changes in

208    sampling design over the decades, the variability in sampling locations during the spawning run

209    (i.e., from changing sampling protocol in 2007) was a source of uncertainty in modelling

210    phenology with the complete dataset.  The trends in presence at a subset of sample stations that

211    were less impacted by spatial variability in sampling was examined to ensure our results using all

212    data were not biased by changes in sampling protocol.  Criteria for the subset selection was that

213    sampling should span the spawning migrations of both alewife and blueback herring as best as

214    possible, and that at least 10 unique days were sampled.  In order to obtain sufficient sampling

215    resolution decades were binned into an "early" set (1970s and 1980s) and a "late" set (2000s and

216    2010s).  The reduction in degrees of freedom caused by binning decades prevented the creation

217    of spline fitted models similar to those created with the full dataset.  The criteria used resulted in

218    a subset of 36 sample stations.

219    Trends in daily presence (present = 1 or absent = 0) at the sampling event level for the

220    1970s (1973 to 1979), 1980s (1980, 1982, 1983, 1987, 1988), 2000s (2001 and 2007 to 2009),

221    and 2010s (2010 to 2016) were modeled separately for alewife and blueback herring.  The

222    variables included in the models were distance proportion, ordinal day, decade, and the ordinal

223    day and decade interaction.

224        Final variable selection and model fitting using restricted maximum likelihood (REML)

225    was done within the R package MGCV (Wood 2011).  Models were constructed with variables

226    having associated smoothers, no smoothers (linear predictor), and tensor product interaction

227    smooths with the interaction and main effects.  Interactions were constructed with tensor product

228    interaction smooths which are more stable and interpretable than using full tensor product

229    smooths that remove the main effects (Wood 2017).  The basis dimensions (k), which control the

230    number of basis functions and sets the maximum degrees of freedom for smooth terms in the

231    model, were evaluated using the gam.check() function from the R package MGCV.  The basis

232    dimensions were adjusted to balance computational efficiency and reduce overfitting.  Akaike's

233    Information Criterion (AIC) was used to select the model with the best fit and fewest degrees of

234    freedom (Burnham and Anderson 2002).  Percent deviance explained was calculated by

235    subtracting the model deviance from the null deviance then dividing by the null deviance and

236    multiplying the result by one-hundred (Stoner et al. 2001).

237        Model prediction success was evaluated using receiver operating characteristics (ROC)

238    plots generated in the R packages ROCR and pROC (Sing et al. 2005; Robin et al. 2011).  The

239    ROC uses a series of misclassification matrices computed for a range of presence probability cut-

240    offs from 0 to 1, then plots the true positive fraction against the false positive fraction (Fielding

241    and Bell 1997; Pearce and Ferrier 2000; Brotons et al. 2004).  The area under the curve (AUC) is

242    a measure of model performance, where an AUC = 0.5 yields the same predictive capacity as

243     chance and increases above 0.5 represent increases in predictive capacity (Hosmer and

244     Lemeshow 2000; Mandrekar 2010).

245          Model predictions were used to estimate three spawning migration reference points.

246     These were: (1) *ingress* at 5% presence probability, (2) *peak* presence probability, and (3) *egress*

247     at 5% presence probability.  Where no single, clearly defined peak existed (i.e. a plateau or

248     bimodal curve), the mean day along the plateau or between the peaks was designated as the peak

249     (i.e., central measure) spawning day for that decade.  There were instances where the beginning

250     or end of the spawning migration was not sampled and predictions from the model would have to

251     be extrapolated >1 d to reach 5% presence probabilities; in these cases, estimates of ingress and

252     egress were made using the first and last date of observed detections.  Confidence intervals were

253     established for ingress, peak (unimodal), and egress using the presence probability CIs for the

254     preceding and following ordinal days.

255     *Drivers of Phenology Changes* Temperature can be a particularly strong driver in movement of

256     anadromous fishes (Antonsson and Gudjonsson 2002; Ellis and Vokoun 2009; Kennedy and

257     Crozier 2010).  We used associated water temperature data to determine temperatures that

258     triggered migrations and if those were consistent across decades.  The 36 station subset used to

259     evaluate the phenology models was also used in a two-way ANOVA to examine the effect of the

260     interaction between ordinal day and time period on temperature.  The annual data were binned

261     into early- (1970s – 1980s) and late-decades (2000s – 2010s) to provide sufficient data for

262     regression.  Water temperature data in the early decades were sparse, particularly in the early

263     spring, relative to later decades; thus, we limited our temperature and migration analysis to

264     egress only for alewife.  We estimated the water temperature on the days when ingress (blueback

265     herring only) and egress occurred in the early-decades (alewife: 1970s; blueback herring: 1980s)

266    using the early-decades temperature fit.  We then estimated the ordinal day when that

267    temperature occurred in the late-decades temperature fit and compared it to the ingress and

268    egress days predicted by the later-decade phenology models.  To ensure our results were not

269    biased by non-overlapping periods, we also ran the regression only using data from the same

270    ordinal day range.

271            Although we detected decadal shifts in ingress and egress timing (see Results below), we

272    were interested in whether we could link annual variability in river herring migrations to annual

273    variability in mean water temperature or rate of temperature change.  This analysis was limited to

274    2008 to 2016 because of limitations with water temperature data for earlier years.  Furthermore,

275    estimates of ingress for alewife were not possible for all of these years so we limited our analysis

276    to egress timing only for blueback herring and alewife.  A subset of Chowan River and Edenton

277    Bay catch data from 2008 – 2016 were used to create both alewife and blueback herring GAM

278    models with the same structure and interpretation of egress as the full dataset phenology models.

279    Rates of water temperature change for each year between 2008 and 2016 were estimated by

280    creating linear regression models over the range of days that egress was predicted for 2008 –

281    2016.  Mean water temperature for each year from 2008 to 2016 was calculated as the mean

282    water temperature over the range of days that egress was predicted for each species (Alewife:

283    April 4 – April 18, and blueback herring: April 15 – April 30; See Results below).  Correlation

284    between days of egress and the two water temperature metrics was assessed by Pearson's r.

285    *Comparison of Presence/Absence with Abundance Data* We used presence/absence data at

286    multiple stations to examine for changes in phenology while others have used percent-of-run

287    abundance percentiles at stationary locations (see Antonsson & Gudjonsson 2002; Ellis &

288    Vokoun 2009). We tested whether presence/absence data are a good proxy for abundance by

289    comparing the ASW 2010s decade phenology metrics with phenology metrics calculated using

290    2016 river herring spawning run abundance data from the nearby (~140 km to the North)

291    Chickahominy River, Virginia.  The Virginia Institute of Marine Science (VIMS) operates a

292    fishery-independent alosine monitoring program for this river (Hilton et al. 2017).  We compared

293    ingress (ingress 5% presence probability vs 5% run abundance), peak (peak presence probability

294    vs 50% run abundance), and egress (egress 5% presence probability vs 95% run abundance).

295    **Results** Over the 43-year time period (1973 – 2016), there were 12,839 sampling events made at

296    325 sample stations (see Fig 1 for stations).  A total of 8,970 alewife were caught (40.4% female,

297    58.1% male) in 2,241 net sets (17.5% catch rate) and 8,609 blueback herring were caught (51.2%

298    female, 47.8% male) in 1,295 net sets (10.1% catch rate).

299    *Alewife Phenology* AIC selection strongly favored the full model, which included distance

300    proportion, day, decade, and the interaction between day and decade (Table S2).  The decadal

301    change in timing on the spawning grounds is dramatic with a clear shift in ingress, peak, and

302    egress and a resulting shortening of time on spawning grounds (Table 1; Fig 2a).  The changes

303    are evident even with estimations based upon the first and last presences.  In the 1970s, estimated

304    alewife ingress (5% presence probability) was February 12, peaked at March 23, and completed

305    their time on spawning ground by May 9 (egress estimate extrapolated one day).  In the 2010s,

306    these three dates were January 27, March 11, and April 12.  The mean change in migration

307    ingress and egress was -4 d per decade and -6.75 d per decade, with net-changes of -16 d and -27

308    d, respectively.  The imbalanced shift in ingress and egress has reduced the time that the alewife

309    population spent on the spawning grounds by 11 d. The date of peak catch probability occurred

310    12 d earlier over the four-decade time period.

311    The proportion of alewife presence detections at a subset of 36 sample stations that were

312    consistently sampled in the early decades (1970s and 1980s) and late decades (2000s and 2010s)

313    corroborate the modeled phenological changes (Fig 3a).  During ingress time periods in the early

314    decades (around day 43), presence proportions were much greater in the later decades.  During

315    the egress time periods in the early decades (around day 129), presence proportions were zero or

316    near-zero in the later decades and substantially lower than the presence proportions in the early

317    decades.  Thus, changes in sampling design between the early and late decades does not explain

318    the changes in phenology of alewife spawning.

319    *Blueback Herring Phenology* AIC selection strongly favored the full model, which included

320    distance proportion, day, decade, and the interaction between day and decade (Table S2).

321    Blueback herring showed the same phenological shifts as alewife, but with a smaller change in

322    the date of ingress and a larger shift in egress (Table 1; Fig 2b).  Decadal comparisons were not

323    made with the 1970s because sampling or model extrapolation could not be done for the egress

324    period.  However, egress was captured by extrapolation in the 1980s, and decadal comparisons

325    can be made for all 1980s migration metrics.  In the 1980s, blueback herring arrived at March 20,

326    peaked at April 18, and completed their spawning migration by May 18.  In the 2010s, these

327    three dates were March 15, April 5, and April 25.  The mean change in migration ingress and

328    egress was -1.67 d per decade and ~-7.67 d per decade, respectively.  The date of peak catch

329    probability occurred 13 d earlier over the three-decade time period.

330    As with alewife, the proportion of blueback herring presence detections at the subset of

331    36 stations were examined and also corroborate the phenology model (Fig 3b).  During ingress

332    time periods in the early decades (around day 79), presence proportions were marginally greater

333    in the later decades.  During the egress time periods in the early decades (around day 138),

334    presence proportions were much lower or zero in the later decades compared to the higher and

335    non-zero presence proportions in the early decades.  Thus, changes in sampling design between

336    the early and late decades do not explain the changes in phenology of blueback herring

337    spawning.

338    *Effects of vernal warming rate on phenological shifts* Water temperatures recorded at the 36

339    station subset for both the early decades (1973 – 1988) and the late decades (2001 – 2016)

340    provide the best data coverage to describe late spring warming trends during the egress times of

341    alewife and blueback herring.  The rate of vernal warming during 2001 to 2016, 0.152 C*d$^{-1}$

342    (95% CI 0.119-0.191) was significantly higher than warming rate (0.077 C*d$^{-1}$, 0.060-0.095)

343    during springs of 1973 – 1988 (ordinal day * time period; $F_{3,3665}$ = 65.23; $p < 0.001$) (Fig 4).  A

344    second comparison of warming rate between the two time periods but limited to the same range

345    of ordinal days maintains this trend ($F_{3,3140}$ = 72.92; $p < 0.001$; Fig S2).  The increased rate of

346    warming results in higher predicted temperatures from day 88 (March 29, at 14.0 C) onward.

347    Elevated temperatures, or faster warming, from March 29 onward may be responsible for

348    expediting the egress of both alewife and blueback herring.  The alewife phenology model

349    predicted a 1970s egress date of May 9 (day 129).  The egress associated water temperature

350    estimated on this date for 1973 – 1988 was 17.2 C, which occurred on April 19 (day 109) in

351    2001 – 2016 (estimates from temperature vs ordinal day regressions).  The alewife phenology

352    model predicts a 2010s egress date of April 12 (day 102) that is only seven days earlier than the

353    estimate based on temperature.  The blueback herring phenology model predicted a 1980s egress

354    date of May 18 (day 138).  The egress associated water temperature estimated on this date for

355    1973 – 1988 was 17.9 C, which occurred on April 24 (day 114) in 2001 – 2016.  The blueback

356    herring phenology model predicts a 2010s egress date of April 25 (day 115) that is only one day

357    later than the estimation using egress temperature.  The blueback herring phenology model

358    predicted a 1980s ingress date of March 20 (day 79).  The ingress associated water temperature

359    estimated on this date in 1973 – 1988 was 13.3 C, which occurred on March 24 (day 83) in 2001

360    – 2016.  The blueback herring phenology model predicts a 2010s ingress date of March 15 (day

361    74).  Although this represents a difference of 9 days, it is important to point out the similarities in

362    dates for 13.3 C water in the two time periods (March 20 for 1973 – 1988 and March 24 for 2001

363    – 2016) and the similarities in dates for ingress predictions (March 20 in the 1980s vs March 15

364    in the 2010s).

365        We examined the relationship between annual timing of river herring egress and annual

366    water temperature metrics from 2008 to 2016.  AIC model selection strongly favored the full

367    model structure (Table S3).  Within the Chowan River and Edenton Bay systems, alewife were

368    predicted to egress between April 4 and April 18 (Table S4; Fig S3).  Mean water temperatures

369    over these days ranged from 13.8 C to 17.9 C and the rate of temperature change ranged from -

370    0.32 to 0.52 C*d$^{-1}$.  The relationships between alewife egress date and both water temperature

371    metrics were slightly negative (Fig S4), but neither correlation was significant (temperature: r = -

372    0.09, $df$ = 7, $p$ = 0.82; rate: r = -0.04, $df$ = 7, $p$ = 0.92).  Blueback herring were predicted to

373    egress between April 15 and May 1.  Mean water temperatures over these days ranged from 15.4

374    C to 19.8 C and the rate of temperature change ranged from -0.63 to 0.56 C*d$^{-1}$.  The

375    relationships between blueback herring egress and both temperature metrics were also not

376    significant (temperature: r = -0.46, $df$ = 7, $p$ = 0.22; rate: r = 0.27, $df$ = 7, $p$ = 0.48; Fig S4).

377    Thus, we did not find evidence of temperature metrics influencing egress dates for alewife and

378    blueback herring during the 2008 to 2016 period.

379    *Comparing presence/absence and abundance data for spawning phenology metrics* For the most

380    recent decade (2010), our presence probability derived phenology metrics for river herring in the

381    ASW match closely with the percent-of-run abundance phenology metrics (5%, 50%, and 95%)

382    calculated for the 2016 river herring spawning run in the Chickahominy River.  For alewife in

383    the Chickahominy River, percent-of-run abundance yields February 3, March 9, and April 6 as

384    the dates of ingress, peak, and egress while our estimates are January 27, March 11, and April

385    12.  The three percentiles for blueback herring in the Chickahominy River occur on March 16,

386    March 31, and April 27 and our estimates are March 15, April 5, and April 25.  Thus, our

387    migration metric predictions using presence/absence data were within ± 7 days (average ± 3.5) of

388    those using abundance data in a nearby system.

389    **Discussion** *Changes in river herring spawn phenologies and potential causes* We provide

390    evidence that the spawning migrations of alewife and blueback herring have shifted to earlier

391    dates in recent decades within the ASW, with substantial truncation of blueback herring

392    spawning season length.  Our results are consistent with trends observed in other anadromous

393    populations: southern New England alewife (Ellis and Vokoun 2009), Atlantic salmon (*Salmo*

394    *salar*) (Juanes et al. 2004), Pacific salmonids (*Oncorhynchus sp.*) (Kovach et al 2015), and

395    Chesapeake Bay striped bass (Peer and Miller 2014).  Ellis and Vokoun (2009) found that

396    changes in spring temperatures across ~4 decades was associated with alewife migrations that

397    occurred ~12 days earlier.  Peer and Miller (2014) observed earlier shifts in spring-spawning

398    migration metrics (ingress, peak, and egress) of 800-899 mm female Chesapeake Bay striped

399    bass.  From 1991 to 2010, the striped bass arrived, peaked, and left 5, 6, and 14 days earlier.

400    Shifts in the timing of anadromous spawning events can have cascading negative effects such as

401    reduced population resiliency through decreases in phenotypic variation (Sgrò et al. 2011),

402    trophic mismatches that have substantial impacts on the survival of offspring (Cushing 1990;

403    Durant et al. 2007; Fortier and Gagné 2011), nutrient influx (Walters et al. 2009), and especially

404    food web dynamics in the case of forage fish (Yako et al. 2000).  Management strategies, such as

405    seasonal harvest closures, can also become less effective due to shifts in migration timing (Peer

406    and Miller 2014).

407        Changes in the phenologies of migration and spawning across animal groups have been

408    attributed to changes in age structure (Lambert 1987; Hutchings and Myers 1993; Trippel and

409    Morgan 1994), changes in species abundance (Miller-Rushing et al. 2008), and shifts in

410    environmental cues due to climate change (Quinn and Adams 1996; Ellis and Vokoun 2009). We

411    examined the possibility for each of these for alewife and blueback herring in the ASW.

412        The relationship between the timing of spawning runs and age structure has not been

413    addressed in the literature for river herring.  Lambert (1987) detailed this relationship with

414    another clupeid species, Atlantic herring, in both the Atlantic and Pacific stocks.  Lambert (1987)

415    concluded that larger, older fish arrived on the spawning grounds earlier than their smaller,

416    younger conspecifics.  It is reasonable to believe that the relationship between age-length and the

417    timing of arrival upon the spawning grounds found in this confamilial apply to both alewife and

418    blueback herring as well.  The phenomenon has also been found in another anadromous species,

419    striped bass (Peer and Miller 2014).  Thus, any shift towards an older age structure should

420    manifest itself in earlier spawning migration times.  However, no change in alewife age structure

421    was observed and blueback herring age structure trended towards a younger age structure in

422    recent decades, which is opposite of the pattern that might explain earlier spawning (NCDMF

423    unpublished data).  Thus, we conclude that changes in age structure are not responsible for

424    changes in river herring spawn times within the ASW.

425    Alewife and blueback herring population abundances in the ASW have decreased

426    dramatically from the early 1970s to present and are currently at levels deemed to be overfished

427    despite the absence of fishing pressures since 2007 (White et al. 2017).  Thus, changes in

428    abundance are one potential reason for changes in spawn timing.  However, the relationship

429    between population abundance and migration phenology has received very little study.  Miller-

430    Rushing et al. (2008) found that first arrival of several bird species in spring were related to

431    population size since a larger population size would have a higher likelihood of detection.  The

432    earlier spawning in recent years is opposite of the pattern expected given decreased abundance

433    levels.  For anadromous fishes, there is potential for abundance levels to change the length of

434    spawning time but we did not find studies that examined this effect.  Because river herring

435    abundance declined in the ASW as vernal warming rate increased (see below) we cannot

436    disentangle these two variables.  We recommend research on the effects of abundance on

437    spawning phenology in anadromous fishes.

438    Water temperature has repeatedly been identified as having an influence on spawning and

439    migration timing for many anadromous species: striped bass (Peer and Miller 2014), Atlantic

440    salmon (Juanes et al. 2004), American shad (*Alosa sapidissima*) (Quinn and Adams 1996), lake

441    sturgeon (*Acipenser fulvescens*) (Bruch and Binkowski 2002), as well as alewife (Ellis and

442    Vokoun 2009).  Temperatures within the coastal mid-Atlantic region of the United States have

443    been increasing over the past century (Polsky et al. 2000), with particularly larger changes

444    observed in lower order streams (Ding and Elmore 2015) such as those used by river herring as

445    spawning habitat.  Our results suggest that earlier vernal warming has led to an earlier spawning

446    season for river herring in tributaries of the ASW.  Our findings support the conclusions of Ellis

447    and Vokoun (2009) for southern New England alewife.  Their estimations of change in alewife

448    ingress and peak migration were 13 and 12 days earlier, respectively, while our models predicted

449    16 and 12 days earlier.  The strongest evidence for a temperature effect is that the temporal shift

450    in egress dates predicted by the phenology models are similar to the changes in dates in which

451    egress-associated temperatures (~17 C) are reached.  The temperature-predicted and observed

452    egress dates in more recent decades were earlier and similar in timing for alewife (7 d apart) and

453    blueback herring (1 d apart).

454         The egress temperatures we estimated for alewife and blueback herring (~17 C) were

455    similar to those observed in a river system ~300 km north.  Ogburn et al. (2017) estimated the

456    daily count of both upstream and downstream migrating alewife and blueback herring in the

457    Choptank River, MD for the 2014 spawning season using a dual-frequency identification sonar

458    (DIDSON).  Strong pulses of downstream migration in April and May appear to coincide with

459    water temperatures near 17 C.  If the rate of vernal warming increases over time, water

460    temperatures on river herring spawning grounds will reach 17 C sooner and continue to shorten

461    the spawning season if ingress timing remains the same or changes less than egress times.  In

462    fishes, climate change driven shifts in phenology have been shown to negatively impact

463    reproduction success and recruitment (Both et al. 2006; Watanuki et al. 2009).  For river herring

464    spawning within the ASW, shifts towards earlier egress dates has reduced time on the spawning

465    grounds and may negatively impact spawning success and recruitment.

466         Trends in the phenological response to changing thermal regimes within a watershed

467    were observed at the decadal scale; therefore, variation in population level responses to relatively

468    cool or warm springs for a given year within a decade might also be observable.  Correlations

469    between the inter-annual variation in the timing of egress and both the annual mean temperature

470    and rate of temperature change across the range of predicted egress days were not significant.

471    However, the correlations did trend towards earlier egress timing when mean annual water

472    temperatures over the range of egress dates were warmer (Fig S4).  Plasticity in migration

473    timing, and subsequently spawning activity, could be optimized to avoid mismatches in resource

474    availability (Cushing 1990).  Phenological shifts in response to climate change have been

475    observed in many inland fish populations (Lynch et al. 2016).  However, research on brook trout

476    suggests that the rate of climate change can outpace compensatory responses and lead to a

477    decline in population abundances (Bassar et al. 2016).  More work is needed to understand the

478    limits of adaptation to climate change by river herring.

479    *Comparing presence/absence and abundance data for spawning phenology metrics* The use of

480    presence/absence data at multiple stations to measure changes in phenology is a novel method

481    that required validation.  The established approach to measuring timing of anadromous fishes is

482    percent-of-run abundance percentiles using count data at stationary locations.  Our predictions

483    using presence/absence data were within $\pm 7$ days (average $\pm 3.5$) of those using abundance data

484    in a nearby system.  These results show that presence/absence data, which are much less labor

485    intensive and more readily accessible than abundance data, are a viable proxy for abundance data

486    when estimating measures of phenology.  We encourage further examination of other long-term

487    datasets for signals in shifting phenology using presence/absence data when abundance data are

488    unavailable.

489    *Implications* There has been increased interest in the incorporation of climate change effects (e.g.

490    changes in phenology) into fisheries management strategies (Haak and Williams 2012; Peer and

491    Miller 2014; Hare et al. 2016; Paukert et al. 2017).  Management strategies for river herring so

492    far have focused on the effects of increased fishing efforts and have attempted to mitigate

493    historical overfishing through moratoria (but see Hare et al. 2016).  While moratoria provide a

494    significant reduction in fishing mortality, it may not be sufficient to return stocks to historical

495    levels of abundance in the face of warming waters and changing climate, particularly in the

496    species' southern range (Tommasi et al. 2015).  Current river herring stocks in North Carolina

497    (White et al. 2017) and other Atlantic states (ASMFC 2017) remain in a depleted state.

498        Spawning phenologies of river herring in the ASW and recruitment should continue to be

499    monitored.  In the event that the fishery is re-opened, information on spawning migrations could

500    be used in an adaptive management strategy framework (Peer and Miller 2014).  It is important

501    to note the differences between alewife and blueback herring spawning migration behaviors and

502    apparent responses to increased vernal warming rate.  Examining the shape of the phenology

503    model curves provides insight into such differences (Fig. 2).  Alewife have a much broader

504    spawning migration season with evident pulses in migration, which appear as humps in the GAM

505    (GAMs don't assume any particular shape).  Comparatively, blueback herring spawning

506    migrations follow a more unimodal distribution, despite also migrating upstream in pulses.  The

507    same patterns and contrasts in migration behavior have been seen in the Choptank River, MD by

508    Ogburn et al. (2017) when using DIDSON to monitor spawning runs.  The shift in spawning

509    migration phenology for alewife has resulted in an 11 day truncation of the spawning season

510    over four decades (Table 1), however considerable changes in ingress and egress timing have

511    both occurred simultaneously (16 and 27 days).  This is in strong contrast to blueback herring,

512    which have maintained ingress timing (5 day change over three decades) but have egressed

513    substantially earlier over time (23 days earlier over three decades).  The variation in phenological

514    changes may be due to different conditions encountered in preferred spawning habitat, as stream

515    temperatures and water quality can vary widely throughout a watershed (Isaak et al. 2014).

516    Generally, alewife prefer more lentic habitats compared to blueback herring (Loesch and Lund

517   1977).  However, river herring in the ASW have a high-degree of overlap in spawning habitat

518   use, due in part to the slow flowing tributaries (Walsh et al. 2005; Personal observation), which

519   makes spatial separation an unlikely driver of phenological variation.  Physiological differences

520   in thermal tolerances are most likely to influence spawning migration (Mullen et al. 1986).

521        The 30% reduction in spawning season length for blueback herring is concerning,

522   considering their already depressed abundance in this region.  The most recent stock assessment

523   of blueback herring estimated the ASW population of age 3+ (sexually mature) fish to be 7.5

524   million fish in 2014; just six percent of the 127 million fish in 1976 (White et al. 2017).  The

525   truncation of time spent on the spawning grounds may have ramifications for recruitment

526   through effects on adult spawning (i.e., reduced chances for optimal spawning conditions) or

527   trophic or habitat mismatches for larvae and juveniles (Wright and Trippel 2009; Ohlberger et al.

528   2014).  Tommasi et al. (2015) found that increased temperatures in June were associated with

529   lower abundance levels of juvenile blueback herring in the Chowan River, NC (a tributary of

530   ASW); they hypothesized the decreased recruitment was due to temperatures exceeding an

531   optimal temperature and predicted that future warming would lead to reduced recruitment in

532   southern populations of river herring.  In addition to temperatures experienced by juveniles, we

533   recommend future research test for a relationship between spawning phenology and recruitment

534   in river herring.

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1

**Tables**

Table 1.  Logistic GAM-derived migration metrics for alewife and blueback herring spawning in the Albemarle Sound, NC watershed. Metrics are ordinal date of ingress (5% probability of presence on left hand side of the distribution), egress (5% probability on right hand side), peak (maximum presence probability in a unimodal curve or mean day of maximum presence probabilities in bimodal/plateaued curve), and season length estimations (difference between ordinal dates of ingress and egress). The 95% confidence intervals for ingress, egress and peak are given in parentheses. Some estimates of ingress and egress are extrapolated predictions and are denoted with an asterisk (*).  For migration metrics estimated by extrapolation, we also provide estimates of ingress and egress based upon first presence and last presence in brackets.

**Alewife**

| Decade | Ingress | Egress | Peak | Season Length |
|---|---|---|---|---|
| 1970 | 43 (37-48) | 129 (124-138) | 82 | 86 |
| 1980 | 48 [≤55]* | 122 (113-127) | 81 | 74 [≥67] |
| 2000 | 24 [≤34]* | 107 (104-110) | 70 (67-73) | 83 [≥73] |
| 2010 | 27 (22-31) | 102 (100-104) | 70 (67-73) | 75 |

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

**Blueback Herring**

| Decade | Ingress | Egress | Peak | Season Length |
|---|---|---|---|---|
| 1970 | 76 (73-79) | >150 [≥128]* | 117 (105-145) | >74 [≥52] |
| 1980 | 79 (76-82) | 138 [≥126]* | 108 (99-118) | 59 [≥47] |
| 2000 | 71 (70-73) | 117 (116-119) | 95 (88-102) | 46 |
| 2010 | 74 (73-75) | 115 (114-116) | 95 (90-101) | 41 |

| | Ingress Diff | Egress Diff | Peak Diff | Season Diff |
|---|---|---|---|---|
| 1980s vs 2010s | -5 | -23 [≤-9] | -13 | -18 [≤-6] |
| Per Decade | -1.66 | -7.66 [≤-3] | -4.33 | -6 [≤-2] |

**List of Figures**

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

Fig 2. Logistic GAM-derived predictions of (a) alewife and (b) blueback herring presence probability. Probabilities were modeled using ordinal day, decade, distance proportion, and ordinal day * decade for samples collected in the North Carolina Division of Marine Fisheries river herring spawning habitat survey throughout the Albemarle Sound, NC watershed. Solid curves are model predictions over dates sampled while dotted curves are extrapolated predictions; points represent the raw presence proportions for all nets set on each day of the decade. Predicted presence probabilities are shown as a function of ordinal day while holding other covariates at mean values. Black horizontal line at 5% for estimates of ingress and egress.

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

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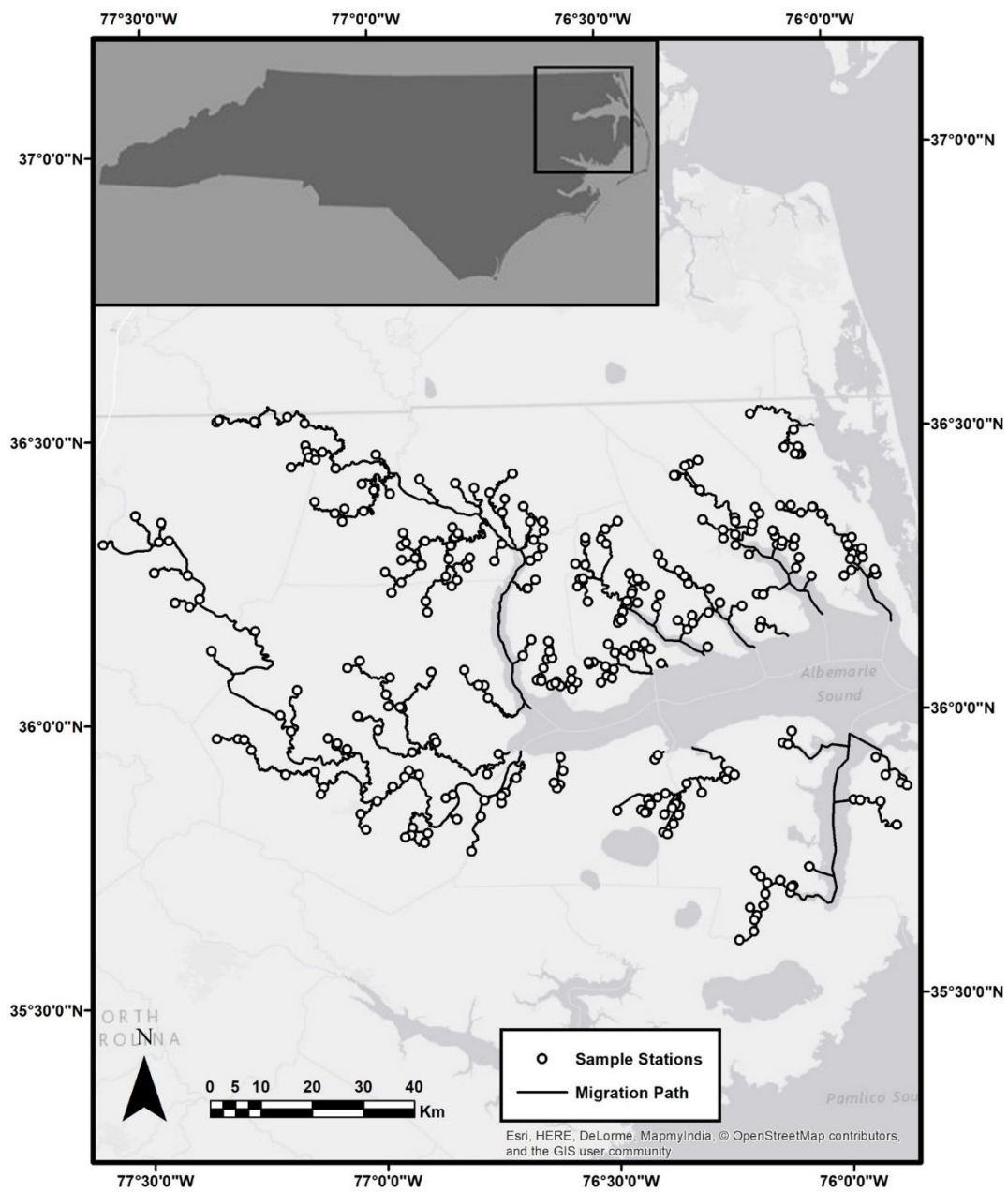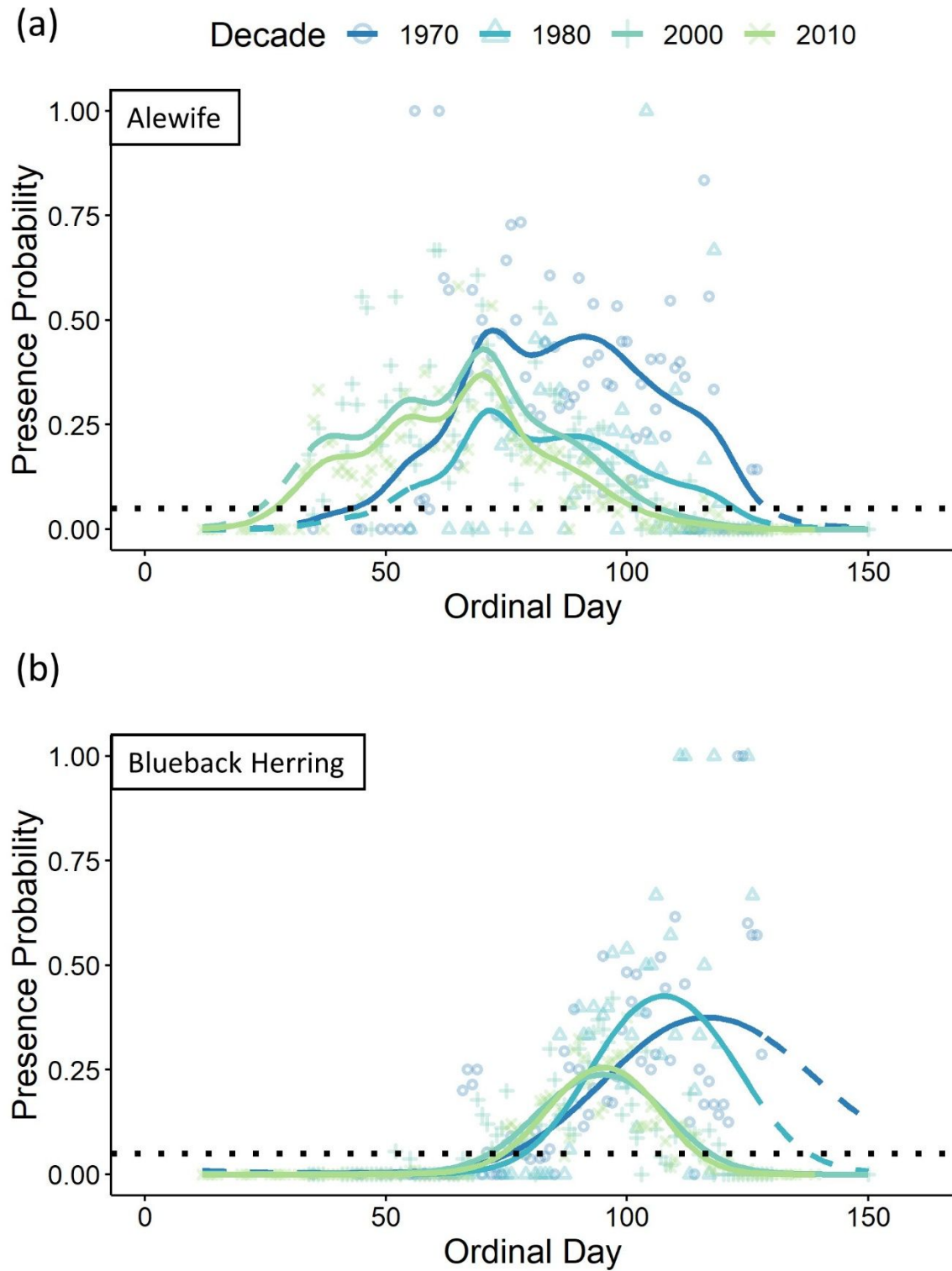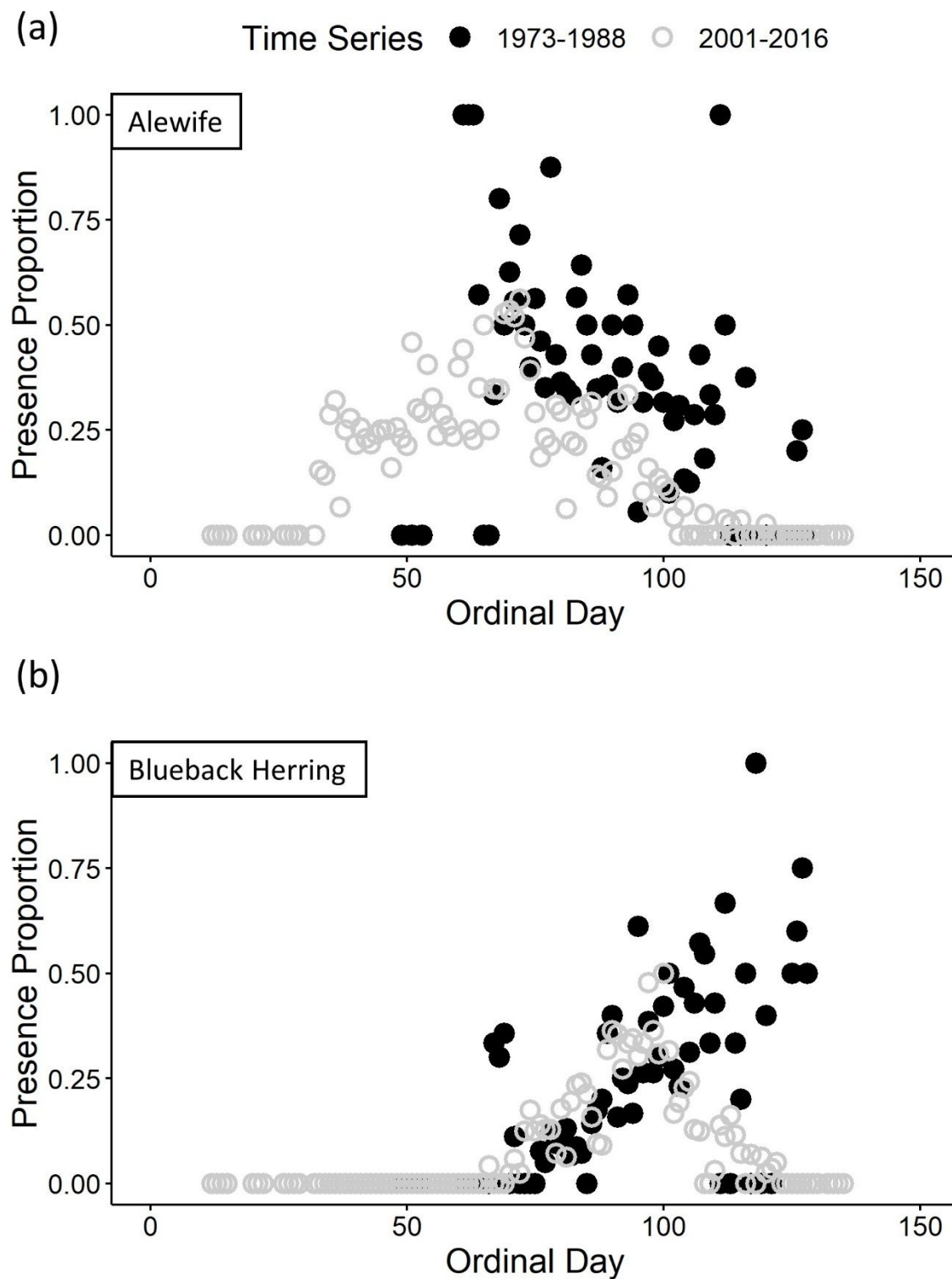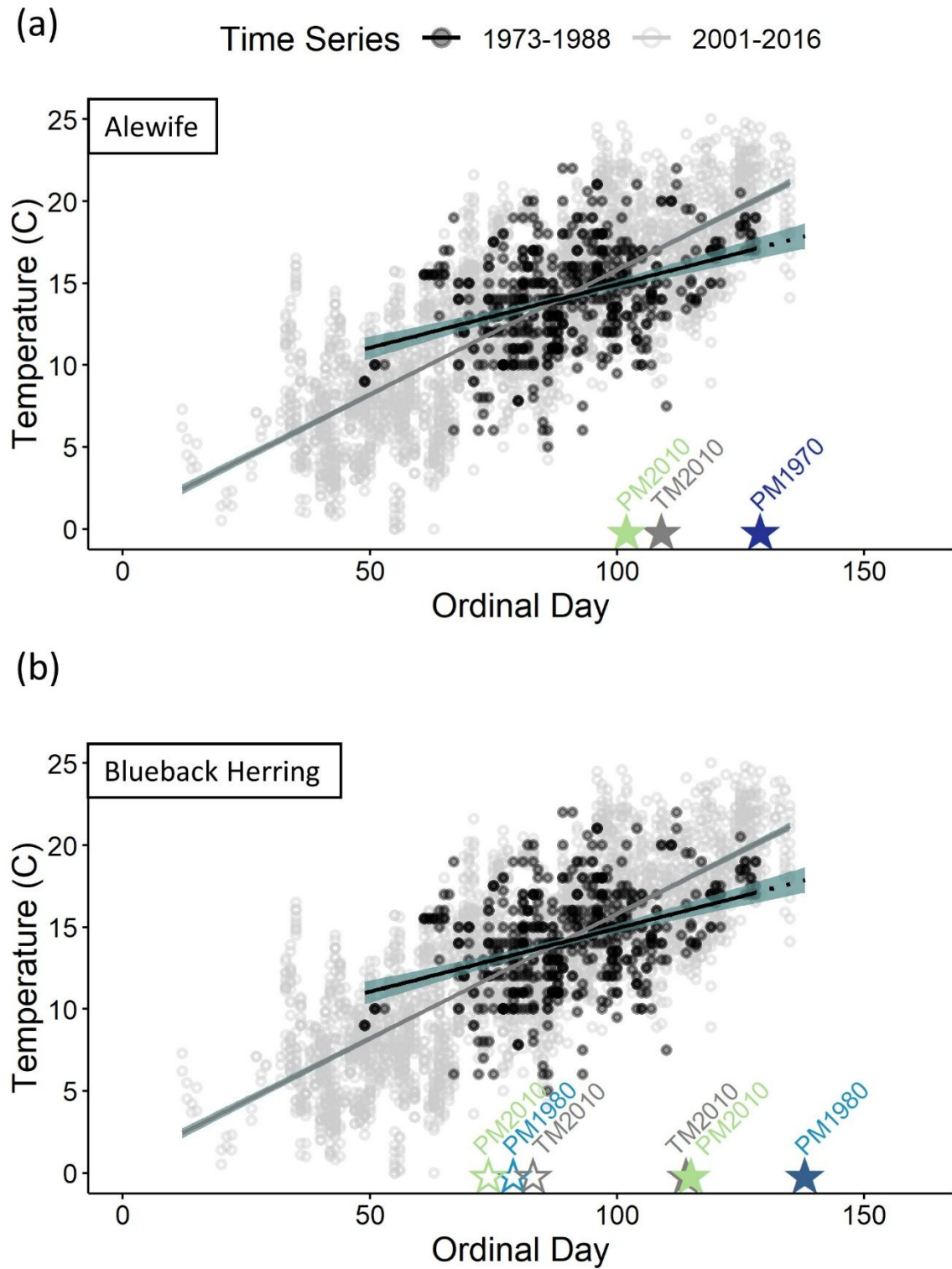
**Figures**



Figure 1

Figure 2

Figure 3

Figure 4