



**Abstract**—Annual life history events, such as migration and spawning in fish, are often timed to match seasonal fluctuations in environmental conditions. Understanding phenological patterns and their drivers is needed to conserve vulnerable fish populations, particularly as climate change is disrupting seasonal transitions. In this study, we examined the phenology of spring spawning migrations of river herring, the alewife (*Alosa pseudoharengus*) and the blueback herring (*A. aestivalis*), in 4 rivers of Chesapeake Bay over 7 years (2013–2019). We used imaging sonar and weekly biological samples to estimate species-specific hourly fish counts in the Choptank River, Deer Creek (a tributary of Susquehanna River), Marshyhope Creek (a tributary of Nanticoke River), and the Patapsco River. Our results indicate that patterns of water temperature in spring drive spawning migrations at seasonal, daily, and hourly scales. The relationship between fish counts and other environmental factors, such as streamflow, lunar phase, turbidity, wind stress, and tides, were annually inconsistent, and their influences on migrations may be river specific. For both species, distinct diel patterns in movement were observed. Migrations were diurnal in the Choptank River and Marshyhope Creek but nocturnal in Deer Creek and the Patapsco River. Observed interannual and inter-river variation in phenology and the influence of non-temperature factors on migrations highlight the need for long-term, multi-river monitoring of river herring in Chesapeake Bay.

Manuscript submitted 4 January 2023.  
Manuscript accepted 24 July 2023  
Fish. Bull. 121:96–111 (2023).  
Online publication date: 24 August 2023.  
doi: 10.7755/FB.121.3.4

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

## Timing and environmental drivers of spawning migrations of alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) in rivers of Chesapeake Bay

Henry D. Legett (contact author)

Robert Aguilar

Keira Heggie

Kimberly D. Richie

Matthew B. Ogburn

Email address for contact author: [legetth@si.edu](mailto:legetth@si.edu)

Smithsonian Environmental Research Center  
647 Contees Wharf Road  
Edgewater, Maryland 21037

The life history strategies of many plants and animals depend on specific environmental conditions and resource levels that fluctuate with seasons (Forrest and Miller-Rushing, 2010). Annual migration events, for example, are often timed to match spatiotemporal shifts in resources. However, species across taxa are altering the timing of their life history events in response to climate change (Root et al., 2003), disrupting such phenological linkages (e.g., Staudinger et al., 2019). As species respond differently to changes in environmental regimes and seasonal transitions, asynchrony in biotic interactions can result in extirpations and extinctions (Parmesan, 2007; Bellard et al., 2012). Therefore, understanding phenology and how environmental conditions drive life history events is critical for the conservation of vulnerable populations and development of climate adaptation management strategies.

*River herring*, which is the collective term for the alewife (*Alosa pseudoharengus*) and the blueback herring (*A. aestivalis*), are anadromous fish species that range along the Atlantic coast of North

America. Adult river herring annually migrate between marine and freshwater habitats, spending most of their adult lives at sea and returning to freshwater systems in spring to spawn. These migrations connect different aquatic ecosystems by moving energy and nutrients among ocean, estuarine, and freshwater food webs and support a diverse community of higher trophic level fishes, birds, and mammals (MacAvoy et al., 2009; Dias et al., 2019). In addition, the predictable timing of these migrations historically made river herring a valuable resource for coastal human communities (Hall et al., 2012). Through the 19th and 20th centuries, however, severe declines in abundance of river herring occurred across the range of these taxa, and by the 2010s commercial harvests had decreased to <2% of their historical peaks (ASMFC, 2017). These declines were driven by overfishing, bycatch in other fisheries, the destruction and degradation of freshwater spawning habitats, and the damming of waterways that obstruct spawning migrations (Atkins and Foster, 1868; Limburg and Waldman, 2009; Hall et al., 2012; Hasselman et al., 2016).

Although restoration efforts, such as fishing moratoria and dam removals, have resulted in increasing abundance of river herring in some rivers (e.g., Wippelhauser, 2021), many populations remain at historic lows. Furthermore, these low abundances make river herring vulnerable to the detrimental effects of climate change (Hare et al., 2021). Loss of suitable spawning habitat, northward shifts in distributions, and temporal shifts in migration and spawning patterns due to warming temperatures have already been documented for river herring and other diadromous fishes (Nye et al., 2009; Peer and Miller, 2014; Lynch et al., 2015; Lombardo et al., 2019; Nack et al., 2019; Staudinger et al., 2019).

The sensitivity of river herring to climate change is, in part, due to a link between their life cycles and water temperature. The results of previous behavioral experiments and counts of adults migrating upstream indicate that changes in water temperature drive their spring spawning migrations at both seasonal and daily scales (Collins, 1952; Saila et al., 1972; Richkus, 1974; Ogburn et al., 2017a; Rosset et al., 2017; Lombardo et al., 2019; Legett et al., 2021). Taken in aggregate, river herring begin migrating into freshwater systems when water temperatures reach 9–10°C and stop at temperatures around 20–21°C (Kissil, 1974; Loesch, 1987; Ellis and Vokoun, 2009; Ogburn et al., 2017a; Rosset et al., 2017). Within this thermal threshold, alewife typically migrate earlier in the spring in colder water (approximately 9–16°C) (Greene et al., 2009; ASMFC, 2017). Alewife are also more abundant than blueback herring in the northern extent of their range in the Labrador Sea and Gulf of Maine. Blueback herring, in comparison, migrate later in the spring in warmer water (approximately 15–21°C) and range farther south into Georgia and northern Florida.

The link between migration and water temperature also results in latitudinal variation in the annual timings of migrations that correspond with the seasonal transitions to spring and summer. In the southern extent of the range of river herring, migrations span from January through April, and in the more northern extent of their range, migrations typically span from March through June (ASMFC, 2017). As climate change is causing the transitions between seasons to occur earlier in the year (Friedland et al., 2015; Henderson et al., 2017), migrations of river herring also have begun to occur earlier (Huntington et al., 2003; Ellis and Vokoun, 2009; Lombardo et al., 2019; Cobb, 2020). More concerning, is that climate change may be shortening the window of time (i.e., phenophase) during which temperatures are suitable for migration and spawning. This compression of the thermal window for migration (a threshold of 9–21°C) has already been observed in long-term studies in some regions, for example, in southern New England (Ellis and Vokoun, 2009) and in Albemarle Sound, North Carolina (Lombardo et al., 2019). Therefore, the increasing rate at which temperatures change throughout the spring can temporally restrict reproduction of river herring. In addition, if thermal shifts are not uniform across that window, alewife and blueback herring may be affected differently.

Although there is a growing body of literature on the phenology of the spawning migrations of river herring (e.g., Huntington et al., 2003; Ellis and Vokoun, 2009; Rosset et al., 2017; Lombardo et al., 2019; Cobb, 2020; Legett et al., 2021; Dalton et al., 2022), the timing of migrations in many regions and rivers is not well known (ASMFC, 2012, 2017). Furthermore, the environmental drivers of migration and spawning other than water temperature, such as streamflow and lunar cycle, can be inconsistent among rivers in a region (Rosset et al., 2017; Legett et al., 2021; Bi et al., 2021). Given the threat of climate change to river herring, understanding the timing and environmental drivers of their spawning migrations has been identified as a key research need for preservation and restoration efforts (Nelson et al., 2020; Hare et al., 2021). This need is especially high in regions like Chesapeake Bay, where air and water temperatures are warming faster than global averages (IPCC, 2013; Hinson et al., 2022) and where some of the most severe declines in populations of alewife and blueback herring have occurred (Palkovacs et al., 2014).

In the early 20th century, the fishery targeting river herring (alewife and blueback herring combined) was the largest fishery by quantity in Chesapeake Bay, with an estimated annual catch of over 10,000 metric tons (over 22 million pounds) (Hildebrand and Schroeder, 1928). Because of subsequent declines in abundance, a moratorium was imposed in 2012 on the commercial and recreational fisheries of river herring in Maryland and Virginia to prevent the extirpation of these species (ASMFC, 2017). In 2013, a fisheries-independent monitoring program was established by the Smithsonian Environmental Research Center (SERC) to assess the stock status, population dynamics, and ecology of river herring in the Upper and Middle Chesapeake Bay regions. In an initial analysis of spawning run counts from this monitoring effort, runs from a single year in a single river were examined (Choptank River in 2014; Ogburn et al., 2017a).

In this study, we examined the phenology of spawning migrations of alewife and blueback herring in Chesapeake Bay, expanding on initial analyses of the SERC monitoring program (Ogburn et al., 2017a) by analyzing multi-year, multi-river fish counts. From 2013 through 2019, hourly counts of upstream migrations were collected by using imaging sonar in the Choptank River (over 4 years); Deer Creek, a tributary of the Susquehanna River (over 1 year); Marshyhope Creek, a tributary of the Nanticoke River (over 2 years); and the Patapsco River (over 4 years) to characterize spatial and interannual variability in spawning runs. We assessed migration timing and environmental drivers at 3 temporal scales: seasonal, daily, and hourly.

At a seasonal scale, we examined the start and end dates of the runs and how those metrics align with previously observed temperature thresholds (9–21°C; Ogburn et al., 2017a). We predicted that the timing of migrations of river herring would match the time when these temperatures occurred across river systems, with runs starting and ending earlier in warmer years and later in cooler

years. At a daily scale, we examined the relationship between migration and environmental factors that fluctuate daily throughout the spring, including water temperature, streamflow (also referred to as *discharge*), lunar phase, turbidity, and wind stress. Given that daily changes in water temperature are a consistent predictor of daily movements of river herring in other regions (Legett et al., 2021), we predicted that temperature would be the primary driver of upstream migrations in the rivers of Chesapeake Bay. At an hourly scale, we compared the diel cycles of migrations of river herring in each river and examined the relationship between migration and environmental factors with diel patterns, including water temperature, tides, and solar elevation. Because migrations of river herring often fluctuate on a 24-h cycle (Saila et al., 1972; Richkus, 1974; Ogburn et al., 2017a), we predicted solar elevation to be a primary driver of hourly movement. Herein, we discuss our results in the context of monitoring and management of river herring in Chesapeake Bay.

## Materials and methods

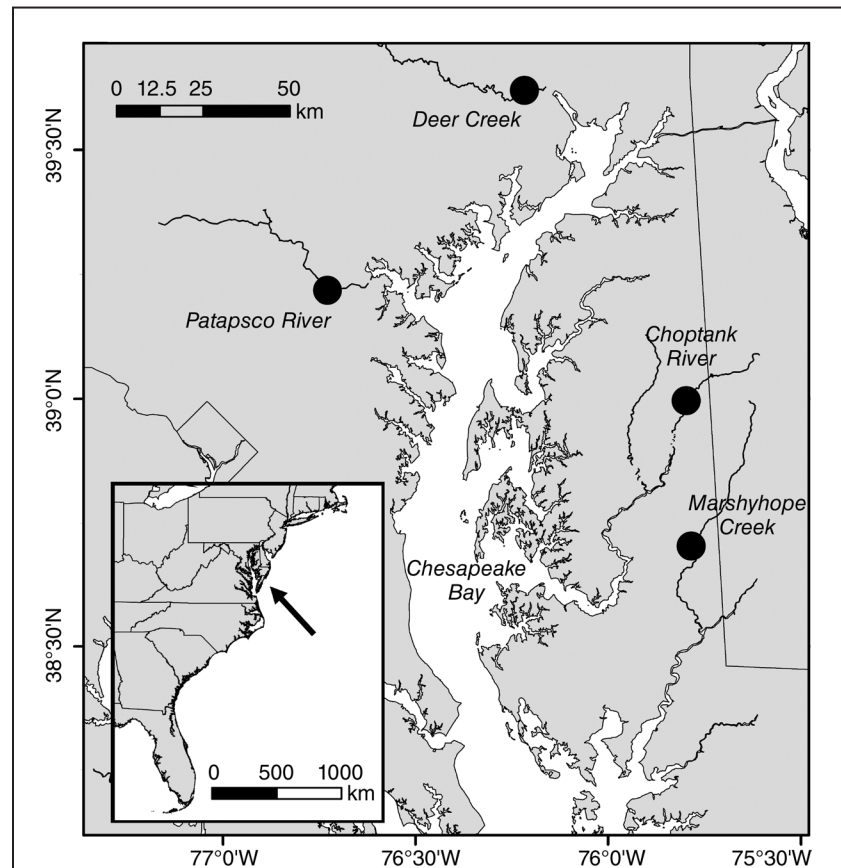
### Fish counts

We collected counts of adult river herring during their spawning migrations in the Choptank River (during 2014–2017), Deer Creek (in 2015), Marshyhope Creek (in 2013 and 2014), and the Patapsco River (during 2016–2019) (Fig. 1). The study sites were located just upstream of the tidal influence in each river system. Fish were counted for the duration of the spawning runs, from March through late May or early June (Suppl. Table 1), by using a dual-frequency identification sonar unit (DIDSON<sup>1</sup> unit with DIDSON V5.25.52 software, Sound Metrics Corp., Bellevue, WA). Imaging sonar video recordings were collected and processed following established protocols (Ogburn et al., 2017a). The sonar unit was set to a high resolution (1.8 mHz) to record a 10-m field of view. Construction fencing was used to block fish from swimming outside the field of view on the near and far side of the stream during normal and low flow conditions. Sonar video recordings were collected for 10-min segments every hour, with a randomized hourly start time. A sampling effort at the rate of 10 min/h is common for estimating the passage of

anadromous fish during their migrations and can result in low variation (coefficient of variation: ~5.5%) between estimated fish counts and real passage (Xie and Martens, 2014).

We used these counting protocols consistently across the time period of this study in the Choptank River, Deer Creek, and the Patapsco River. In Marshyhope Creek, hourly recordings were collected and analyzed for 1 month during the spawning season in 2013 (27 March–2 May). For the rest of the season in 2013 (14 March–26 March and 3 May–30 May) in Marshyhope Creek, and for the entire season in 2014 (11 April–27 May), sonar video recordings were analyzed every other hour each day from 0600 to 1800 GMT as opposed to every hour.

Individual fish moving upstream were manually counted from playbacks of the sonar video recordings by using DIDSON V5.25.52 software. Fish were digitally measured in the recordings by using a straight line, and only fish in the size range of adult river herring (200–350 mm in total length [TL]) were counted (Ogburn et al., 2017a). For each river, 1–7 observers counted fish; each observer was trained by using a standard set of files. For quality



**Figure 1**

Map of Chesapeake Bay in Maryland showing the locations of the 4 sites where counts of adult alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) were collected from 2013 through 2019. The geographic coordinates for each site can be found in [Supplementary Table 1](#).

<sup>1</sup> Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.



assurance, multiple observers reviewed at least 20 files from each river and year. Results from a previous study on observer variability indicate that there is no significant difference among trained observers counting fish during migrations in recordings made by using imaging sonar (Petreman et al., 2014; but see Keefer et al., 2017). To generate hourly estimates, counts from the 10-min recordings were multiplied by a factor of 6.

During this study, high flow events in the rivers sometimes disrupted the sonar or changed the field of view of the recordings such that fish could not be counted. In several instances, when an extreme event such as a large storm was expected, equipment was preemptively removed from the river to prevent its loss. These disruptions and removals created gaps in the counts of fish during spawning runs and was a particular problem in the Patapsco River, which had extreme flooding during the study period (Doheny and Nealen<sup>2</sup>).

### Species-specific estimates

The 2 species of river herring, alewife and blueback herring, and similarly sized individuals of other species cannot be differentiated in the sonar video recordings. To measure the relative abundance of each species and estimate species-specific counts, weekly biological samples were collected by using backpack or boat electrofishing (in the Choptank River, Marshyhope Creek, and the Patapsco River) or fyke nets (in Deer Creek) within 500 m of the sonar sites. These collections were approved by the Maryland Department of Natural Resources (MDNR) and the SERC Institutional Animal Care and Use Committee. All fish within the size range of 200–350 mm TL were counted and identified to species. The proportions of alewife and blueback herring were calculated for each biological sample, and daily proportions for each species were calculated by using linear interpolation (Hughes and Hightower, 2015; Ogburn et al., 2017a). Daily species compositions were calculated in this way to smooth day-to-day changes in species composition rather than having sharp breaks week to week. These daily proportions were then applied to the hourly sonar counts for each date to generate species-specific hourly counts.

### Environmental factors

Hourly measurements of water temperature were collected by using either HOBO U20-001-2-Ti or HOBO U24-002-C data loggers (Onset Computer Corp., Bourne, MA). The loggers were housed in PVC pipping and anchored underwater next to the sonar unit. Measures of streamflow were obtained for U.S. Geological Survey monitoring stations from the National Water Dashboard (data available from [website](#), accessed August 2021). Stations were located

upstream of the sonar unit site in each river (Choptank River: gauge 01491000, ~0.5 km upstream; Deer Creek: gauge 01580520, ~50 m upstream; Marshyhope Creek: gauge 01488500, ~20 km upstream; Patapsco River: gauge 01589035, ~2 km upstream). Measures of turbidity were obtained from the National Water Dashboard for the monitoring station in the Patapsco River, which was the only site for which these data were available for the time frame of the study.

Lunar cycle data were obtained by using the fisheries stock assessment model MULTIFAN-CL and the associated R4MFCL scripts for use in statistical software R (Hoyle et al.<sup>3</sup>). Tidal data were obtained from water level measurements relative to mean lower low water recorded at NOAA stations (data available from [website](#), accessed August 2021). The closest NOAA station downstream to each site was used for each river. These stations were located either at the mouth of each river (Choptank River: station 8571892, ~67 km downstream; Patapsco River: station 8574680, ~14 km downstream) or in Chesapeake Bay (Deer Creek: station 8573364, ~60 km downstream; Marshyhope Creek: station 8571421, ~75 km downstream).

Hourly measures of wind speed and wind direction were also obtained for these same NOAA stations. Daily measures of wind stress ( $\tau$ ) were calculated from wind speed and wind direction at 45° intervals by using the following equation (Wilson, 1960; Large and Pond, 1981):

$$\tau = C_d \times \rho_{\text{air}} \times U^2, \quad (1)$$

where  $C_d$  = a dimensionless drag coefficient that was set at 0.0012;

$\rho_{\text{air}}$  = 1.2 kg/m<sup>3</sup>, the mass density of air; and  
 $U$  = the wind magnitude.

Solar elevation (measured in degrees above the horizon) was obtained from the solar geometry calculator of the NOAA Earth System Research Laboratories (data available from [website](#), accessed August 2021), with angles corrected for atmospheric refraction. All data were set to the standardized time of GMT.

### Statistical analyses

Counts of alewife and blueback herring were analyzed at seasonal, daily, and hourly scales by using R, vers. 4.0.3 (R Core Team, 2020). The estimated hourly counts for each species were used to calculate the mean daily rate of upstream migration (number of fish per hour) and the overall annual counts. At a seasonal scale, run initiation and end dates were calculated as the days when the estimated counts exceeded 5% and 95% of the total run (Ellis and Vokoun, 2009). The duration of each run was the number of days between the initiation and end

<sup>2</sup> Doheny, E. J., and C. W. Nealen. 2021. Storms and floods of July 30, 2016, and May 27, 2018, in Ellicott City, Howard County, Maryland. U.S. Geol. Surv., Fact Sheet 2021-3025, 6 p. [Available from [website](#).]

<sup>3</sup> Hoyle, S., D. Fournier, P. Kleiber, J. Hampton, F. Bouyé, N. Davies, and S. Harley. 2009. Update of recent developments in MULTIFAN-CL and related software for stock assessment. West. Cent. Pac. Fish. Comm., WCPFC-SC5-2009/SA-IP-07, 16 p. [Available from [website](#).]

dates. For the run initiation and end dates, we calculated the daily average and maximum water temperature for each species, river, and year. We also calculated the 7-day average water temperature for each initiation and end date (average of the 7 days leading up to the date). The thermal transition dates for the combined migrations of both species of river herring each year were calculated as the first days the average temperature exceeded 9°C and 21°C, and the thermal season length was the number of days between these dates.

At a daily scale, the relationship between counts of river herring and daily changes in environmental factors was assessed by using cross-correlation analysis at lags of  $\pm 4$  days with 95% confidence intervals (CIs) (Ogburn et al., 2017a); CIs were calculated following Brockwell and Davis (2002). For this analysis,  $\log_{10}+1$  of the mean daily rate of upstream migration (number of fish per hour per day) was compared to the change in daily mean water temperature, mean streamflow, lunar phase, and mean wind stress. Mean daily turbidity was also assessed for the Patapsco River. Because temperature generally increases day to day throughout the spring, water temperature data needed to be detrended to separate daily from seasonal changes (Wu et al., 2007). A weighted index of change in mean daily water temperature, therefore, was used for this analysis and was calculated by using this equation (following Ogburn et al., 2017a):

$$\Delta T = [(T_0 - T_1) \times 3 + (T_1 - T_2) \times 2 + (T_2 - T_3)] / 6, \quad (2)$$

where  $T_0$  = the mean daily temperature, and

$T_{1-3}$  = the mean temperatures 1–3 days earlier.

By considering changes in temperatures up to 3 days earlier, this index both detrends temperature on a seasonal scale and reflects multiday warming and cooling trends.

Hourly patterns in migrations of river herring were analyzed by using the R package *circular* (vers. 0.4-95; Agostinelli and Lund, 2022). The parameters of the von Mises distribution, mean ( $\mu$ ) and dispersion ( $\kappa$ ), of estimated counts for each species were calculated from maximum-likelihood estimates. A Rayleigh test of uniformity was used to test the null hypothesis that counts were randomly distributed by hour (Humphreys and Ruxton, 2017). Cyclical patterns at an hourly scale were additionally assessed by using wavelet analyses in the R package *WaveletComp* (vers. 1.1; Rösch and Schmidbauer<sup>4</sup>), with 95% CIs used to identify period lengths associated with hourly variability in the fish counts (Torrence and Compo, 1998). The relationships between counts of river herring and hourly changes in environmental factors were assessed by using cross-correlation analysis at lags up to  $\pm 4$  h with 95% CIs. For this analysis, the  $\log_{10}+1$  of estimated hourly counts (number of fish) were compared with hourly measures of water temperature, tide, and solar elevation. Hourly patterns in Marshyhope Creek were analyzed for only the time period in the 2013 season

when 24-h counts were available (27 March 27–2 May). Data supporting this study are publicly available on Figshare at [website](#).

## Results

### Species composition of biological samples

A total of 5451 fish within the size range of 200–350 mm TL, representing 24 species, were collected by using boat electrofishing or fyke nets. River herring were the dominant species in these samples and typically composed >80% of the collection during the peaks of the runs. Overall, 34% of the total samples were alewife, and 39% were blueback herring. Other abundant species included white perch (*Morone americana*) (9%), gizzard shad (*Dorosoma cepedianum*) (5%), yellow perch (*Perca flavescens*) (3%), hickory shad (*A. mediocris*) (2%), striped bass (*Morone saxatilis*) (2%), and white sucker (*Catostomus commersonii*) (2%). In Deer Creek, all sampled fish within the required size range were alewife.

### Estimated sonar counts of river herring

A total of 1.35 million fish within the required size range were counted in 10-min sonar video recordings. After multiplying these counts by a factor of 6 to generate hourly estimates and adjusting for daily species composition, an estimated 2.69 million alewife and 3.06 million blueback herring migrated upstream across the 4 rivers and 7 years of this study (Table 1). Species-specific estimates ranged from 800,000 of each species in the Choptank River in 2015 to less than 10,000 of each species in the Patapsco River in 2019. Although low counts in the Patapsco River can be partially attributed to inconsistent collection efforts caused by weather related disruptions, the counts were notably lower in this river in 2016 when efforts to collect recordings were consistent.

### Seasonal patterns in migrations

Alewife began migrating approximately 22 d (standard deviation [SD] 12) earlier in the season compared with the timing of migration by blueback herring (day of year: 52–105 versus 91–121; Table 1). Alewife also stopped migrating 22 d (SD 7) earlier than blueback herring (day of year: 105–132 versus 126–144). The earlier migrations of alewife occurred in colder waters, starting at the average daily water temperature of 11.2°C (SD 1.1), compared with the temperature at which migrations of blueback herring started, 15.2°C (SD 0.9) (Suppl. Table 2). The migrations ended at an average daily water temperature of 15.4°C (SD 1.2) for alewife and 18.9°C (SD 1.1) for blueback herring. Overall, the migrations of both species generally occurred within the thermal window of 9–21°C, and the durations of the migrations roughly corresponded with the duration of this thermal window (Table 1, Fig. 2). Migrations occurred earlier

<sup>4</sup> Rösch, A., and H. Schmidbauer. 2018. *WaveletComp 1.1: a guided tour through the R package*, 58 p. [Available at [website](#).]

**Table 1**

Seasonal phenology of spawning runs of alewife (AW) (*Alosa pseudoharengus*) and blueback herring (BBH) (*A. aestivalis*) from 2013 through 2019 in 4 rivers of Chesapeake Bay in Maryland. Start day (first 5% of the run), end day (95% of the run), and total counts of fish were calculated from the estimated hourly upstream counts (the symbol > or < indicates that counting either started after the run had begun or ended before the run ended). The thermal window range (i.e., the thermal thresholds in which river herring migrations typically occur) is the first day that the average water temperature exceeded 9°C and the first day that it exceeded 21°C (the symbol < indicates that counting began after temperatures crossed the threshold).

River	Year	Species	Total count (000s)	Start date (day of year)	End date (day of year)	Run duration (d)	Thermal window range (days of year)
Choptank River	2014	AW	552	79	115	37	71–133
		BBH	757	104	135	32	
	2015	AW	796	89	112	24	76–129
		BBH	793	106	132	27	
	2016	AW	232	<60	105	>46	55–147
		BBH	477	91	>138	>48	
2017 <sup>1</sup>	AW	326	<52	111	>59	50–119	
	BBH	259	96	>140	>45		
Deer Creek	2015 <sup>1</sup>	AW	418	107	122	16	92–131
		BBH	–	–	–	–	
Marshyhope Creek <sup>2</sup>	2013 <sup>1</sup>	AW	255	<87	107	>20	79–142
		BBH	321	103	126	24	
	2014 <sup>1</sup>	AW	60	<102	116	>15	<101–133
		BBH	303	<107	>133	>27	
Patapsco River	2016	AW	17	87	132	46	<70–147
		BBH	50	121	144	24	
	2017 <sup>1</sup>	AW	12	88	117	30	67–119
		BBH	18	112	137	26	
	2018 <sup>1</sup>	AW	11	105	118	14	88–124
		BBH	71	115	133	19	
2019 <sup>1</sup>	AW	5	89	106	18	74–140	
		BBH	9	103	138	36	

<sup>1</sup> Counts were not collected, or were inconsistently collected, for large portions of the season. Total upstream counts for both river herring species are underestimated.

<sup>2</sup> In Marshyhope Creek, hourly sonar video recordings were collected and analyzed for 1 month during the season in 2013 (27 March–2 May). For the rest of the season in 2013 and for the season in 2014, recordings were collected and analyzed every other hour each day from 0600 to 1800 GMT.

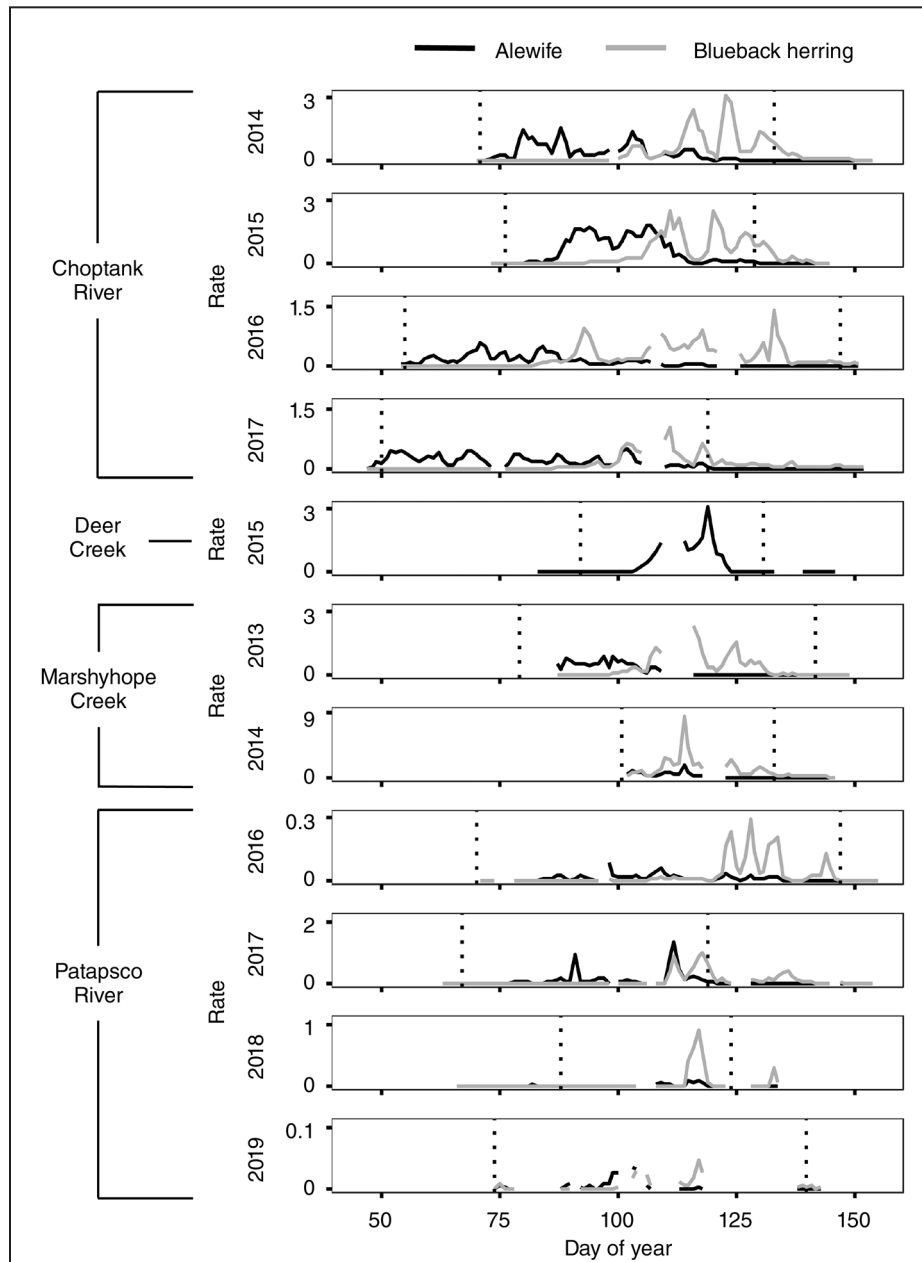
in years when spring water temperatures reached 9°C earlier, and migrations ended later in years when water temperatures reached 21°C later.

There were inter-river differences in water temperatures at the start of migrations of alewife, particularly between the Choptank River and the other 3 systems (Suppl. Table 2). Alewife began migrating in colder water (8.6°C [SD 1.1]) in the Choptank River compared with the average water temperatures in Deer Creek (15.7°C [SD 1.2]), Marshyhope Creek (12.7°C [SD 1.0]), and the Patapsco River (12.2°C [SD 1.3]). Temperatures at which migrations of alewife ended were more similar among all the rivers (Choptank River: 15.6°C [SD 0.8]; Deer Creek: 14.5°C [SD 1.6]; Marshyhope Creek: 16.9°C [SD 1.2]; Patapsco River: 14.8°C [SD 1.4]). The migration of alewife in Deer Creek in 2015 (the only year during which river herring were monitored in this river) was unique in that it started and ended at around the same temperature. Water temperatures during migrations of blueback

herring were similar among the rivers at their starts (Choptank River: 16.5°C [SD 1.1]; Marshyhope Creek: 14.3°C [SD 0.8]; Patapsco River: 14.5°C [SD 0.6]) and endings (Choptank River: 19.3°C [SD 0.8]; Marshyhope Creek: 17.7°C [SD 0.5]; Patapsco River: 18.9°C [SD 1.6]).

#### Daily patterns in migrations

Increases in the daily rates of migration for both alewife and blueback herring were consistently associated with increases in weighted mean change in water temperature (Suppl. Tables 3–6). This relationship occurred most often between lags from –1 to 0 d, such that days with peaks in upstream migration rates occurred on days, or followed days, with increased water temperatures. In an exception to this trend, daily migration of alewife in the Patapsco River in 2018 was strongly negatively correlated with changing water temperature (correlation <–0.80) –1 to 0 d before peaks in counts (Suppl. Table 6).



**Figure 2**

Daily mean estimated rates of upstream migration (number of fish per hour in thousands) of alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) in each year from 2013 through 2019 in 4 rivers of Chesapeake Bay in Maryland. Vertical dotted lines indicate the thermal window, with the first line at the first day the mean water temperature reached 9°C and the second line at the first day the mean temperature reached 21°C. Gaps in plots are days on which counts were not collected. Note the differences in scales among plots.

Streamflow, lunar phase, and turbidity were also often associated with daily migration patterns. However, these associations and the direction of the relationship were more inconsistent than they were for water temperature.

In the Choptank River, streamflow was significantly negatively correlated with migrations of alewife in 2015

and with migrations of both alewife and blueback herring in 2017 (lags from -2 to 2 d; [Suppl. Table 3](#)). In Deer Creek, streamflow was negatively correlated with migrations of alewife (lag of 3 d; [Suppl. Table 4](#)). In Marshyhope Creek, streamflow was positively correlated with migrations of alewife in 2013 (lag of -2 d) but negatively correlated with



migrations of blueback herring in 2013 and alewife in 2014 (lags from -1 to 1 d) (Suppl. Table 5). In the Patapsco River, streamflow was positively correlated with migrations of blueback herring in 2016 and 2018 (lags from -2 to 0 d) but negatively correlated with migrations of blueback herring in 2017 (lags from 1 to 4 d) and with migrations of both alewife and blueback herring in 2019 (lags from -4 to -2 d) (Suppl. Table 6).

Lunar phase in the Choptank River was positively correlated with migrations of alewife and blueback herring in 2016 (lags from -4 to 4 d) but negatively correlated with migrations of blueback herring in 2017 (lags from 1 to 4 d) (Suppl. Table 3). In Deer Creek, lunar phase was positively correlated with migrations of alewife (lags from 1 to 3 d; Suppl. Table 4). In Marshyhope Creek, lunar phase was negatively correlated with migrations of blueback herring in 2014 (lags from 0 to 4 d; Suppl. Table 5). In the Patapsco River, lunar phase was negatively correlated with migrations of alewife in 2017 and blueback herring in 2016, 2017, and 2019 (lags from -3 to 4 d) but positively correlated with migrations of alewife in 2016 and 2019 and blueback herring in 2018 (lags from -1 to 4 d) (Suppl. Table 6).

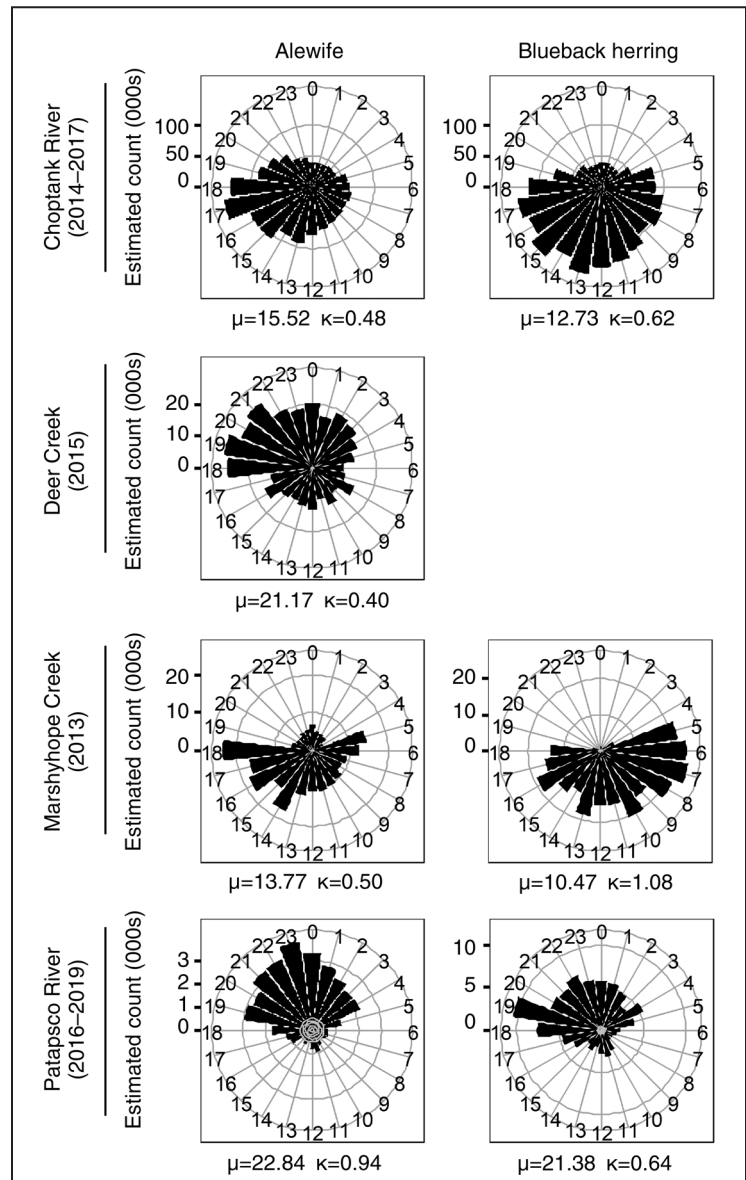
Turbidity in the Patapsco River was positively correlated with migrations of alewife in 2016 and 2019 and migrations of blueback herring in 2016 and 2018 (lags from -3 to 0 d). In this river, turbidity was negatively correlated with migrations of alewife in 2016 and blueback herring in 2017 (lags from 1 to 3 d).

Wind stress also had a variable relationship with daily migration patterns among rivers and years (Suppl. Figs. 1–4). In the Choptank River, wind stress from the southwest was strongly positively correlated with migrations of alewife and blueback herring in 2014 at lags from -3 to 0 d before peaks in counts, but it was strongly negatively correlated with migrations of blueback herring in 2018 at the same lags (Suppl. Fig. 1). The only consistent trend related to wind stress was observed in the Patapsco River. There, wind stress originating from the south was negatively associated with migrations of alewife in all 4 years of this study (2016–2019) and with migrations of blueback herring in 2016 (lag of 0 d) but positively associated with migrations of alewife and blueback herring from -4 to -2 d before peaks in counts (Suppl. Fig. 4).

**Hourly patterns in migrations**

Distinct diel patterns in migrations of both alewife and blueback herring were observed in each river (Rayleigh test of uniformity:  $P < 0.001$  in all cases). In the Choptank River during 2014–2017, counts were diurnal and most concentrated in the afternoons, with alewife moving slightly later in

the day ( $\mu = 15.52$ ,  $\kappa = 0.48$ ) compared with blueback herring ( $\mu = 12.73$ ,  $\kappa = 0.62$ ; Fig. 3). In Deer Creek in 2015, most of the alewife migration occurred at night ( $\mu = 21.17$ ,  $\kappa = 0.40$ ; Fig. 3). In Marshyhope Creek in 2013, counts were diurnal, with alewife most concentrated in the early afternoon ( $\mu = 13.77$ ,  $\kappa = 0.50$ ) and blueback herring most concentrated in the later morning ( $\mu = 10.47$ ,  $\kappa = 1.08$ ) (Fig. 3). In the



**Figure 3**

Circular histograms representing estimated fish counts (number of fish per hour in thousands) by time of day for alewife (*A. pseudoharengus*) and blueback herring (*A. aestivalis*) in 4 rivers of Chesapeake Bay in Maryland: the Choptank River in 2014–2017, Deer Creek in 2015, Marshyhope Creek in 2013, and the Patapsco River in 2016–2019. Note the differences in scales among histograms. The mean ( $\mu$ ) and dispersion ( $\kappa$ ) values for the von Mises distribution are given below each histogram. Only alewife were detected in the Choptank and Patapsco Rivers can be found in Supplementary Figures 5 and 6.



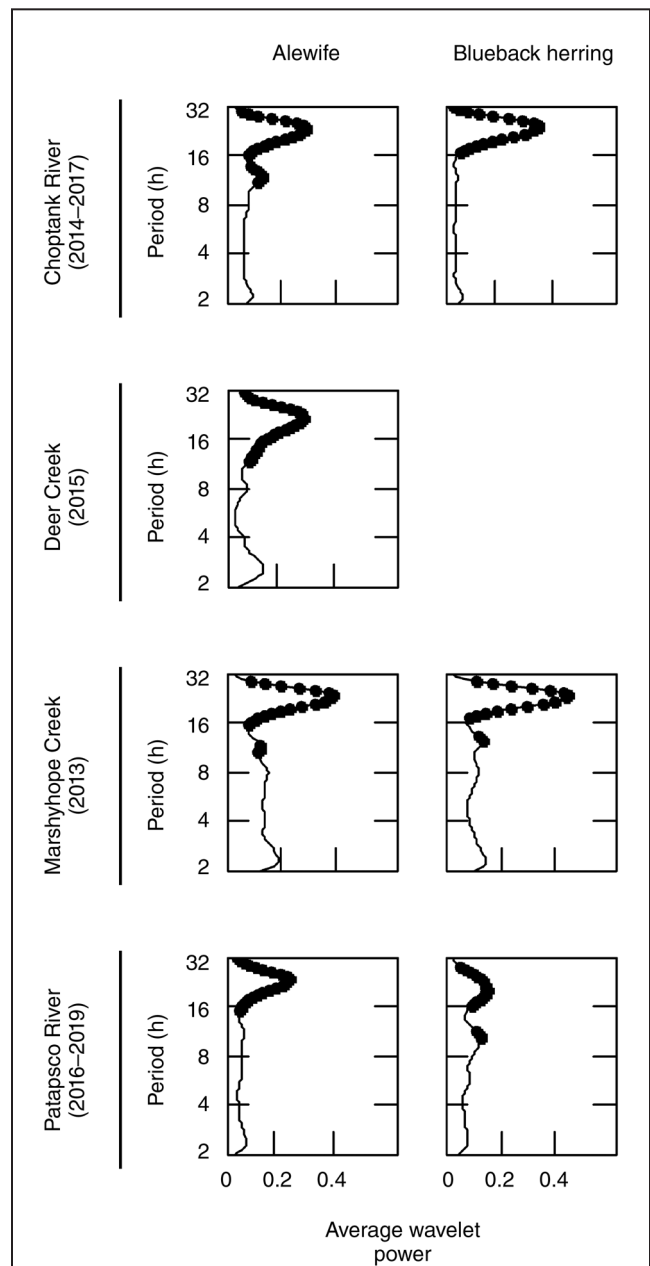
Patapsco River during 2016–2019, migrations occurred at night for both alewife ( $\mu=22.84$ ,  $\kappa=0.94$ ) and blueback herring ( $\mu=21.38$ ,  $\kappa=0.64$ ) (Fig. 3). Migrations in Marshyhope Creek and the Patapsco River were generally more concentrated than in the other 2 river systems, with a greater majority of counts restricted almost exclusively to daytime hours (Marshyhope Creek) or nighttime hours (Patapsco River). Circular histograms representing the time of day of estimated upstream migrations for each year in the Choptank and Patapsco Rivers can be found in [Supplementary Figures 5 and 6](#).

Corresponding to these diel patterns, hourly increases in estimated counts were consistently correlated with solar elevation at all measured lags (from –4 to 4 h) across rivers and years ([Suppl. Tables 7–10](#)). This relationship with solar elevation was positive in the Choptank River and Marshyhope Creek, where the migrations were diurnal, but the relationship was negative in Deer Creek and the Patapsco River, where the majority of the migrations were nocturnal.

Generally, there was a positive correlation between hourly counts and water temperature. Exceptions to this trend include a negative correlation between temperature and counts of alewife in the Choptank River in 2015 (lags from –4 to –2 h), blueback herring in the Patapsco River in 2018 and 2019 (lags from –4 to 4 h), and alewife and blueback herring in Marshyhope Creek in 2013 (lags from –4 to 1 h). In the Patapsco River, the correlation with temperature was still positive for counts of alewife in all 4 years of the study (2016–2019) and for counts of blueback herring in 2016 and 2017, despite migrations occurring at night when daily temperatures were lowest. Similarly, in Deer Creek, hourly counts were positively correlated with temperature despite nocturnal migrations.

Hourly counts were often correlated with tides; however, the direction of the relationship was not consistent. Tides in the Choptank River were positively correlated with migrations of alewife in 2017 (lags from –4 to 1 h) and blueback herring in 2015 and 2016 (lags from 0 to 4 h), but tides were negatively correlated with migrations of alewife in 2015 (lags from –4 to 4 h) and blueback herring in 2017 (lags from 3 to 4 h) ([Suppl. Table 7](#)). Tides were negatively correlated with migrations of alewife in Deer Creek (lags from –1 to 0 h; [Suppl. Table 8](#)) and with migrations of alewife and blueback herring in Marshyhope Creek (lags from 2 to 4 h; [Suppl. Table 9](#)). In the Patapsco River, counts were positively correlated with tides in migrations of alewife in 2018 (lags from 3 to 4 h) and blueback herring in 2016 and 2018 (lags from –4 to 4 h), but they were negatively correlated with migrations of alewife in 2016 (lags from –4 to 2 h) and blueback herring in 2017 and 2019 (lags from –4 to 4 h) ([Suppl. Table 10](#)).

In wavelet analyses, significant peaks in power of the global wavelet spectrum occur at a period of approximately 24 h (corresponding to diel patterns) for migrations of both alewife and blueback herring in all years and rivers (Fig. 4). An additional significant peak around 10–14 h (corresponding to the ~12-h tidal cycle) occurred in all migrations of alewife in the Choptank River in



**Figure 4**

Global spectra from wavelet analyses of hourly estimated fish counts of alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) in 4 rivers of Chesapeake Bay in Maryland: the Choptank River in 2014–2017, Deer Creek in 2015, Marshyhope Creek in 2013, and the Patapsco River in 2016–2019. Black dots represent statistically significant points that exceed the 95% confidence interval. Only alewife were detected in Deer Creek. Results from wavelet analyses for each year in the Choptank and Patapsco Rivers can be found in [Supplementary Figure 7](#).

2014–2017, in migrations of alewife and blueback herring in Marshyhope Creek in 2013, in migrations of alewife in the Patapsco River in 2016 and 2019, and in migrations of blueback herring in the Patapsco River in

2016–2018. Results of wavelet analyses for each year in the Choptank and Patapsco Rivers can be found in [Supplementary Figure 7](#).

## Discussion

### Seasonal migration patterns: correspondence with water temperature

Counts at a seasonal scale indicate that the duration of migrations of river herring in rivers of Upper and Middle Chesapeake Bay are bounded by a known temperature threshold, approximately 9–21°C. This thermal tolerance window is generally consistent across rivers in Chesapeake Bay and in other regions (Kissil, 1974; Loesch, 1987; Ellis and Vokoun, 2009; Rosset et al., 2017; Bi et al., 2021). Interspecific differences in seasonal migration patterns were also consistent across river systems and align with long-established and range-wide reports of behavior of river herring, with alewife migrating earlier in the spring in cooler water temperatures and blueback herring migrating later in warmer temperatures (ASMFC, 2017). Our results indicate some inter-river differences in this temperature threshold, specifically in the Choptank River, where alewife began migrating in slightly colder water compared with their migrations in the other 3 rivers (~8°C versus ~12°C).

In Deer Creek, our biological sampling efforts captured only alewife, and the phenology of migration at a seasonal scale was unique compared to those of the migrations in the other 3 rivers. As a tributary of the Susquehanna River, Deer Creek is one of the most northern spawning locations for river herring in Chesapeake Bay. This farther distance from the mouth of Chesapeake Bay may result in fish arriving at Deer Creek later in the year in warmer water temperatures and leaving earlier in colder temperatures compared to their behavior in other rivers in this region. Monitoring was conducted in only 1 year (2015) in this system. Blueback herring have been collected in biological samples from Deer Creek in other years (e.g., blueback herring were collected by the Maryland Department of Natural Resources in 2014; R. Aguilar, personal commun.), but additional monitoring is needed to confirm the interannual presence–absence of blueback herring in this system, to distinguish any species-specific timings of migrations, and to examine river-specific patterns in environmental drivers.

### Daily migration patterns: correspondence with water temperature

Increases in daily mean water temperature were consistently followed by increased migration rates for both species of river herring. This link between daily migration patterns and temperature has also been observed in other regions (Saila et al., 1972; Richkus, 1974; Rosset et al., 2017). For example, in long-term (8–28 years) fish counts conducted across 12 streams in Massachusetts,

water temperature was a predictor of both daily presence–absence and abundance of river herring (Legett et al., 2021). An exception to this pattern was in the Patapsco River in 2018, where the majority of the migrations of both species occurred in a single large pulse negatively correlated with water temperature, indicating that in some systems under certain conditions, other environmental factors may override the influence of water temperature.

The correlations between fish counts and streamflow and turbidity in the Patapsco River indicate that river herring may increase in abundance in this system following heavy rains. This result is further supported by our analysis of wind stress: high wind stress in the Patapsco River, indicating a storm event, may have led to a decrease in fish counts the day of the event and an increase in fish counts 2–4 d after the event. However, it is important to note that extreme flooding events in the Patapsco River during the study period (Doheny and Nealen<sup>2</sup>) disrupted counting efforts during events with some of the highest streamflow in this system. Additional years of monitoring, particularly the collection of counts during storm events, are needed to confirm the relationship between fish counts and streamflow, turbidity, and wind stress and to determine whether this relationship is specific to the Patapsco River.

Overall, across all 4 rivers, the relationships between daily migration rates of river herring and non-temperature environmental factors (streamflow, lunar phase, turbidity, and wind stress) were inconsistent, similar to the interannual and inter-river inconsistencies reported in previous fish count studies (Saila et al., 1972; Richkus, 1974; Legett et al., 2021). The influence of non-temperature factors may be river specific, as we observed with southerly wind stress in the Patapsco River.

The various ways in which individual environmental factors may influence migrations of river herring need to be considered. For example, changes in streamflow may motivate fish to migrate, but this influence may be separate from accessibility thresholds, where streamflow is so low or so high that fish are physically limited from moving upstream. The interactions between environmental factors also need to be considered. Increased wind stress from a storm event might correspond with increased streamflow from precipitation and changes in water temperature from runoff. It is possible that environmental factors are important only in how they shift water temperature. For instance, increased streamflow from stormwater runoff may have a positive or negative influence on fish migrations depending on the degree to which that runoff changes the water temperature. Therefore, further studies that consider the direct and indirect relationships between environmental factors are needed, and such examination may be achieved by using structural equation modeling (Malaeb et al., 2000; Fan et al., 2016). Such analysis requires data sets from long-term monitoring because of the degree of interannual variation in migration dynamics within and between river systems.

### Hourly migration patterns: indication of inter-river variability

We observed divergent diel patterns in migrations of river herring among rivers. Migrations of both alewife and blueback herring were diurnal in the Choptank River and Marshyhope Creek but nocturnal in Deer Creek and the Patapsco River. On the basis of previous analyses of fish counts, the following have been reported: diurnal patterns in upstream migrations (Cooper, 1961; Sails et al., 1972; Kissil, 1974; Richkus, 1974; Mullen et al., 1986; Andrews, 2014; Rillahan, et al. 2021), nocturnal patterns (McCartin et al., 2019), crepuscular patterns (Alcott et al., 2021), and bimodal peaks in movement from dawn to noon and dusk to midnight (Tyus, 1974). The cause of this diel variation is not well known.

Nocturnal activity may be a strategy to avoid diurnal predators, such as ospreys (*Pandion haliaetus*), bald eagles (*Haliaeetus leucocephalus*), and striped bass (Bendall et al., 2005; McCartin et al., 2019; Alcott et al., 2021). This hypothesis of predator avoidance is supported by differences in water clarity between the rivers in our study, as the Choptank River and Nanticoke River (downstream of Marshyhope Creek) are tannic coastal plain systems located on the Delmarva Peninsula and are typically more turbid (secchi depth <0.5 m) compared with the Susquehanna River (downstream of Deer Creek) and Patapsco River (secchi depth >0.5 m), whose watersheds are located largely on the piedmont (turbidity data used in this study are from 4 water-quality stations of the Eyes on the Bay Program, Maryland Department of Natural Resources, the Choptank River station ET5.1, Nanticoke River station XDJ9007, Susquehanna River station CB1.1, and Patapsco River station WT5.1; available from [website](#), accessed May 2022). Therefore, fish migrating in Deer Creek and the Patapsco River during the day are more visible to predators compared with fish migrating in the Choptank River and Marshyhope Creek and may migrate at night to reduce this exposure. Highlighting the predator avoidance hypothesis, large numbers of bald eagles have been observed at the sampling location in Deer Creek during the short 2-week period when alewife were present (R. Aguilar and K. Heggie, personal observ.), indicating that avian predators target river herring during their spawning migration.

Diel patterns in migrations of river herring most strongly correlated with solar elevation, but migrations were also positively correlated with water temperatures at an hourly scale. This relationship was expected for the Choptank River, where migrations are diurnal and solar elevation and temperature are colinear. However, this relationship was also present in Deer Creek and the Patapsco River, where migrations are nocturnal and consequently concentrated at times when water temperatures are at their coldest each day. This result indicates that, to some extent, hourly patterns in water temperature may drive hourly migration patterns independent of solar elevation. Exceptions to this relationship of hourly patterns, similar to the exceptions to the relationship of daily patterns in migrations and water temperatures, may indicate that the

influence of water temperature can also be overridden by other conditions at this scale.

Our results also indicate a potential influence of changing tides on hourly migration patterns, but this relationship was inconsistent within and between rivers and years. In previous studies, it has been found that tidal transitions can influence diel movement patterns of river herring in systems where higher water levels are needed for fish to pass through anthropogenic structures, such as culverts or tide gates (Rillahan et al., 2021). Tidal influence may also change throughout the season depending on streamflow and overall water levels, and as with streamflow, there is a need to separate accessibility thresholds from the general influence of tides on movement rates. This variable influence and these potential interactions between environmental factors may explain why inconsistent results have similarly been found in previous studies of the effects of tides and lunar cycles on migrations of river herring (Ogburn et al., 2017a; Legett et al., 2021). A limitation of our study is that tides were not measured near the sampling sites in each river. For the Choptank River and Patapsco River, the NOAA stations where tide data were collected were located inside the mouth of each river. For Deer Creek and Marshyhope Creek, the nearest station was located beyond the river in Chesapeake Bay. The tidal cycles immediately downstream of the tidal or non-tidal boundary nearer to the sampling sites would have lagged behind the water levels recorded at the stations.

### Inter-river variations in phenology and environmental drivers of migrations

Inter-river differences in migrations of river herring observed in our study, and in other multi-river studies (e.g., Legett et al., 2021; Dalton et al., 2022), may be due to the morphology and ecohydrological characteristics of each river. The Patapsco River, for example, is a rocky piedmont system in a narrow river valley with higher annual streamflow than the flow of coastal plain systems like the Choptank River and Marshyhope Creek (Suppl. Table 1). The comparative influence of streamflow and wind stress on daily migration patterns in the Patapsco River may be a result of these environmental differences. Inter-river differences in patterns of migration by river herring may also be a result of the specific locations where fish are monitored in each river. Because water temperature patterns can vary spatially within a watershed (e.g., Isaak et al., 2014; Steel et al., 2016), we expect the timing and dynamics of migrations of river herring to similarly vary. In the Choptank River, for example, we observed that alewife began their migrations in comparatively colder water temperatures. It is unknown if this inter-river difference in seasonal timing would persist if counts were collected from other locations in the Choptank River. Further studies in which water temperatures are monitored and river herring are tracked throughout a river, by using passive integrated transponder tags or acoustic telemetry (McCartin et al., 2019), would allow for the examination

of spatial variability in temperature and spawning migration phenology.

Finally, inter-river differences in migrations may also be species specific, as our results indicate that differences in temperature among rivers were not as great for blueback herring as they were for alewife. In other studies of migrations of river herring, in which the 2 species are not distinguished (e.g., Legett et al., 2021; Dalton et al., 2022), observed inter-river variability in phenology may similarly have been species specific. Therefore, our results highlight the need to differentiate between counts of alewife and blueback herring in studies of phenology of river herring.

### Management implications

The thermal window for migrations of river herring is a concern for the management of these species, particularly as water temperatures in Chesapeake Bay are warming faster than global averages (Hinson et al., 2022). Changes in the timing of migrations of river herring due to warmer spring temperatures have been observed in other regions, occurring at rates of 0.3–1.2 d earlier in a year (Huntington et al., 2003; Ellis and Vokoun, 2009; Lombardo et al., 2019; Cobb, 2020). Although our study was not long enough for observation of trends in the seasonal timing of migrations, we expect that similar shifts are occurring for migrations of river herring in Chesapeake Bay, threatening the persistence of these species in this region and undermining restoration efforts.

Continued monitoring is needed to identify shifts in migration timing and the rate at which the thermal window for migrations is shortening, to identify whether changes in the thermal window are uneven or uniform, and to observe how populations of alewife and blueback herring are responding to these changes. Given the critical role of water temperature for river herring, management and conservation practices that reduce seasonal water temperatures in streams and rivers may benefit these species. For example, the establishment and maintenance of riparian buffers can provide shade and prevent direct runoff from agricultural lands, potentially mitigating the warming effects of climate change in streams and providing thermal habitat for spawning (Palone and Todd, 1998; Bowler et al., 2012; Albertson et al., 2018; Timm et al., 2021). Use of thermal mitigation practices for urban stormwater runoff may also help to maintain thermal habitat (Timm et al., 2020), especially in urban systems like the Patapsco River, which flows through the Baltimore metropolitan area.

Differences in diel patterns of migrations of river herring among rivers may have implications for restocking efforts. It is unclear whether the nocturnal migrations of river herring in Deer Creek and the Patapsco River are the result of behavioral plasticity or adaptation. If a nocturnal strategy is adaptive, river herring from a population with diurnal migrations may fail when stocked in a nocturnal system because nocturnality is driven by selective pressure and because the migrations and spawning activity of restocked fish will not temporally overlap with those of the native

nocturnal population. Therefore, for restocking efforts, the respective phenologies of both the stocked and native populations may have to be considered. Furthermore, in genetic analyses of previous studies in the Upper Chesapeake Bay, genetically distinct spawning populations of river herring among rivers have been found (Ogburn et al., 2017b). Differences in diel patterns between populations may serve as a behavioral barrier limiting straying rates between rivers and preventing gene flow.

### Viability of imaging sonar for monitoring migrations

As demonstrated in this study, imaging sonar, when combined with biological sampling, can be an effective tool for monitoring migrations of specific species in unobstructed natural waterways, especially in the turbid coastal streams common in the Chesapeake Bay watershed. Other methods used to monitor anadromous fish migrations, such as electronic resistivity counters and video recordings, require narrow fish passage structures (e.g., fish ladders) that can restrict upstream migration rates. In addition, video recordings are not effective in turbid waters or at night, and electronic counters can be inaccurate when fish are abundant or migrating at high densities (Hiebert et al., 2000; Sheppard and Bednarski, 2015).

A drawback of imaging sonar is its high cost, both in terms of the equipment and the time needed to count fish. Some automatic methods, such as passive acoustic monitoring of the natural sounds fish produce while spawning, may offer a less accurate but more cost-effective way to assess phenology of river herring (Staples et al., 2023). Another drawback to the use of imaging sonar in natural waterways is that high streamflow events can disrupt sonar video recordings at times when data are most needed. In the Patapsco River, which flows through the Patapsco Valley, extreme flooding was a reoccurring challenge during this study, especially in 2018 and 2019 (Doheny and Nealen<sup>2</sup>). When heavy rainfall was expected, equipment was removed from the river to prevent its destruction or loss; as a result, the dynamics of the migration of river herring immediately prior, during, and after the high streamflow event could not be assessed. In rivers with less variability in streamflow, such as the Choptank River, this issue was not as common.

Finally, although counts of fish made with imaging sonar are useful for examining relative changes in migration at fine temporal resolutions, counts alone are an inaccurate method for estimating abundances of river herring. Individual river herring may “oscillate” in a river throughout a season, migrating upstream and downstream between estuaries and spawning grounds multiple times (McCartin et al., 2019). Upstream counts of fish, including the count data analyzed in this study, are therefore likely an overestimation of run size. Pairing counts with tracking data of individuals, such as data from passive integrated transponder tags or acoustic telemetry, can account for milling behavior and upstream–downstream oscillations and may produce more accurate estimates of run sizes (e.g., Raabe and Hightower, 2014). There is a need to monitor



how populations of river herring in specific rivers respond to restoration activities, changes in management, climate change, and other anthropogenic factors (Hare et al., 2021). By accounting for oscillations, interannual changes in behavior (i.e., number of oscillations per individual) can be separated from changes in abundance.

## Conclusions

Migrations of river herring were monitored every spring during 2013–2019 in 4 rivers of Chesapeake Bay: the Choptank River, Deer Creek, Marshyhope Creek, and the Patapsco River. Hourly estimates of fish counts, made by using imaging sonar combined with weekly biological sampling, allowed the assessment of the phenology of alewife and blueback herring. At a seasonal scale, migrations occurred within a temperature threshold (9–21°C), and annual shifts in the timing and duration of migrations corresponded to annual shifts in the timing and duration of this thermal window. Therefore, as climate change alters the shape and size of the thermal window in Chesapeake Bay, we expect migrations of river herring to be similarly altered.

At a daily scale, migration rates were positively correlated with changes in temperature, but the relationships between migration and non-temperature factors (streamflow, lunar phase, turbidity, and wind stress) were inconsistent among the rivers. Increased streamflow and turbidity following storm events may disrupt the relationship of temperature and migrations in the Patapsco River; however, long-term monitoring is needed to assess the interactions between the environmental variables and the extent to which the influence of non-temperature factors is river specific. At an hourly scale, we observed both diurnal (Marshyhope Creek and the Choptank River) and nocturnal (Deer Creek and the Patapsco River) patterns in spawning migrations. This divergence in diel patterns is potentially the result of inter-river differences in water clarity and therefore pressure from diurnal predators. In addition to solar elevation, hourly changes in counts were also correlated with water temperature and tides.

Overall, our results add to the body of literature supporting the strong link between water temperature and migrations and spawning of river herring at multiple temporal scales across their range (e.g., Collins, 1952; Saila et al., 1972; Richkus, 1974; Rosset et al., 2017; Lombardo et al., 2019; Legett et al., 2021). Therefore, although there may be some interannual and inter-river variability in the influence of non-temperature factors on the migrations of alewife and blueback herring, practices that reduce seasonal water temperatures and conserve and restore thermal habitat in rivers could be broadly applied to benefit these species.

## Resumen

Los eventos anuales del ciclo vital de los peces, como la migración y el desove, suelen coincidir con las fluctuaciones

estacionales de las condiciones ambientales. Es necesario comprender los patrones fenológicos y sus causas para conservar las poblaciones de peces vulnerables, sobre todo teniendo en cuenta que el cambio climático está alterando las transiciones estacionales. En este estudio, examinamos la fenología de las migraciones primaverales de desove del arenque de río, la pinchagua (*Alosa pseudoharengus*) y el arenque azul (*A. aestivalis*), en 4 ríos de la bahía de Chesapeake durante 7 años (2013–2019). Utilizamos un sonar de imágenes y muestras biológicas semanales para estimar los recuentos de peces de cada especie por hora en el Río Choptank, Deer Creek (un afluente del Río Susquehanna), Marshyhope Creek (un afluente del Río Nanticoke) y el Río Patapsco. Nuestros resultados indican que los patrones de temperatura del agua en primavera determinan las migraciones de desove a escala estacional diaria y por hora. La relación entre los recuentos de peces y otros factores ambientales, como el caudal, la fase lunar, la turbidez, la fuerza del viento y las mareas, fue anualmente inconsistente, y sus influencias en las migraciones pueden ser específicas de cada río. Para ambas especies se observaron distintos patrones de movimiento diurnos. Las migraciones fueron diurnas en el Río Choptank y el Arroyo Marshyhope, pero nocturnas en el Arroyo Deer y el Río Patapsco. La variación interanual e interfluvial observada en la fenología y la influencia de factores distintos de la temperatura en las migraciones, destacan la necesidad de un seguimiento a largo plazo del arenque de río en varios ríos de la bahía de Chesapeake.

## Acknowledgments

We thank Patapsco Valley State Park, Maryland Park Service, MDNR, U.S. Army Corps of Engineers, F. Wothers, and Henry's Furniture for providing access to study sites. We thank W. McBurney, M. Goodison E. Kinnebrew, M. Kramer, G. Marafino, P. Roberts, H. Soulen, and J. Spires for counting fish in sonar video recordings. Funding was provided by the National Fish and Wildlife Foundation (award nos. 34809, 40321, 45567, and 50023), Smithsonian Environmental Research Center, and MDNR.

## Literature cited

- Agostinelli, C., and U. Lund.  
2022. R package 'circular': circular statistics. Version 0.4-95. [Available from [website](#), accessed September 2022.]
- Albertson, L. K., V. Ouellet, and M. D. Daniels.  
2018. Impacts of stream riparian buffer land use on water temperature and food availability for fish. *J. Freshw. Ecol.* 33:195–210. [Crossref](#)
- Alcott, D., E. Goerig, C. Rillahan, P. He, and T. Castro-Santos.  
2021. Tide gates form physical and ecological obstacles to river herring (*Alosa* spp.) spawning migrations. *Can. J. Fish. Aquat. Sci.* 78:869–880. [Crossref](#)
- Andrews, S. N.  
2014. Fishway efficiency and passage behaviour of Alewife in three fishways on Tantramar Marsh near Amherst, Nova Scotia. M.S. thesis, 98 p. Acadia Univ., Wolfville, Canada. [Available from [website](#).]

- ASMFC (Atlantic States Marine Fisheries Commission).  
2012. River herring benchmark stock assessment, vol. 1. ASMFC, Stock Assess. Report 12-02, 207 p. [Available from [website](#).]
2017. River herring stock assessment update. Volume 2: state-specific reports, 680 p. ASMFC, Arlington, VA. [Available from [website](#).]
- Atkins C. G., and N. Foster.  
1868. First report of the commissioners of fisheries of the state of Maine, 1867, 128 p. Owen and Nash, Augusta, ME. [Available from [website](#).]
- Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp.  
2012. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15:365–377. [Crossref](#)
- Bendall, B., A. Moore, and V. Quayle.  
2005. The post-spawning movements of migratory brown trout *Salmo trutta* L. *J. Fish Biol.* 67:809–822. [Crossref](#)
- Bi, R., Y. Jiao, L. A. Weaver, B. Greenlee, G. McClair, J. Kipp, K. Wilke, C. Haas, and E. Smith.  
2021. Environmental and anthropogenic influences on spatiotemporal dynamics of *Alosa* in Chesapeake Bay tributaries. *Ecosphere* 12:e03544. [Crossref](#)
- Bowler, D. E., R. Mant, H. Orr, D. M. Hannah, and A. S. Pullin.  
2012. What are the effects of wooded riparian zones on stream temperature? *Environ. Evid.* 1, article 3. [Crossref](#)
- Brockwell, P. J., and R. A. Davis.  
2002. Introduction to time series and forecasting, 3rd ed., 425 p. Springer Nature, Cham, Switzerland.
- Cobb, C. K.  
2020. The impact of climate change on the migration phenology of New England's anadromous river herring and American Shad. Honors thesis, 32 p. Colby College, ME. [Available from [website](#).]
- Collins, G. B.  
1952. Factors influencing the orientation of migrating anadromous fishes. *Fish. Bull.* 52:375–396.
- Cooper, R. A.  
1961. Early life history and spawning migration of the alewife, *Alosa pseudoharengus*. M.S. thesis, 58 p. Univ. Rhode Island, Kingston, RI. [Available from [website](#).]
- Dalton, R. M., J. J. Sheppard, J. T. Finn, A. Jordaan, and M. D. Staudinger.  
2022. Phenological variation in spring migration timing of adult alewife in coastal Massachusetts. *Mar. Coast. Fish.* 14:e10198. [Crossref](#)
- Dias, B. S., M. G. Frisk, and A. Jordaan.  
2019. Opening the tap: increased riverine connectivity strengthens marine food web pathways. *PLoS ONE.* 14:e0217008. [Crossref](#)
- Ellis, D., and J. C. Vokoun.  
2009. Earlier spring warming of coastal streams and implications for alewife migration timing. *North Am. J. Fish. Manag.* 29:1584–1589. [Crossref](#)
- Fan, Y., J. Chen, G. Shirkey, R. John, S. R. Wu, H. Park, and C. Shao.  
2016. Applications of structural equation modeling (SEM) in ecological studies: an updated review. *Ecol. Process.* 5, article 19. [Crossref](#)
- Forrest, J., and A. J. Miller-Rushing.  
2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philos. Trans. R. Soc. B.* 365:3101–3112. [Crossref](#)
- Friedland, K. D., R. T. Leaf, J. Kane, D. Tommasi, R. G. Asch, N. Rebeck, R. Ji, S. I. Large, C. Stock, and V. S. Saba.  
2015. Spring bloom dynamics and zooplankton biomass response on the US Northeast Continental Shelf. *Cont. Shelf Res.* 102:47–61. [Crossref](#)
- Greene, K. E., J. L. Zimmerman, R. W. Laney, and J. C. Thomas-Blate.  
2009. Atlantic coast diadromous fish habitat: a review of utilization, threats, recommendations for conservation, and research needs. *Atl. States Mar. Fish. Comm., Habitat Manag. Ser.* 9, 463 p. [Available [website](#).]
- Hall, C. J., A. Jordaan, and M. G. Frisk.  
2012. Centuries of anadromous forage fish loss: consequences for ecosystem connectivity and productivity. *BioScience* 62:723–731. [Crossref](#)
- Hare, J. A., D. L. Borggaard, M. A. Alexander, M. M. Bailey, A. A. Bowden, K. Damon-Randall, J. T. Didden, D. J. Hasselman, T. Kerns, R. McCrary, et al.  
2021. A review of river herring science in support of species conservation and ecosystem restoration. *Mar. Coast. Fish.* 13:627–664. [Crossref](#)
- Hasselman, D. J., E. C. Anderson, E. E. Argo, N. D. Bethoney, S. R. Gephard, D. M. Post, B. P. Schondelmeier, T. F. Schultz, T. V. Willis, and E. P. Palkovacs.  
2016. Genetic stock composition of marine bycatch reveals disproportional impacts on depleted river herring genetic stocks. *Can. J. Fish. Aquat. Sci.* 73:951–963. [Crossref](#)
- Henderson, M. E., K. E. Mills, A. C. Thomas, A. J. Pershing, and J. A. Nye.  
2017. Effects of spring onset and summer duration on fish species distribution and biomass along the Northeast United States continental shelf. *Rev. Fish Biol. Fish.* 27:411–424. [Crossref](#)
- Hiebert, S., L. A. Helfrich, D. L. Weigmann, and C. Liston.  
2000. Anadromous salmonid passage and video image quality under infrared and visible light at Prosser Dam, Yakima River, Washington. *North Am. J. Fish. Manag.* 20:827–832. [Crossref](#)
- Hildebrand, S. F., and W. C. Schroeder.  
1928. Fishes of Chesapeake Bay. *Fish. Bull.* 43:1–366.
- Hinson, K. E., M. A. M. Friedrichs, P. St-Laurent, F. Da, and R. G. Najjar.  
2022. Extent and causes of Chesapeake Bay warming. *J. Am. Water Resour. Assoc.* 58:805–825. [Crossref](#)
- Hughes, J. B., and J. E. Hightower.  
2015. Combining split-beam and dual-frequency identification sonars to estimate abundance of anadromous fishes in the Roanoke River, North Carolina. *North Am. J. Fish. Manag.* 35:229–240. [Crossref](#)
- Humphreys, R. K., and G. D. Ruxton.  
2017. Consequences of grouped data for testing for departure from circular uniformity. *Behav. Ecol. Sociobiol.* 71, article 167. [Crossref](#)
- Huntington, T. G., G. A. Hodgkins, and R. W. Dudley.  
2003. Historical trend in river ice thickness and coherence in hydroclimatological trends in Maine. *Clim. Change* 61:217–236. [Crossref](#)
- IPCC (Intergovernmental Panel on Climate Change).  
2013. Climate change 2013: the physical science basis. Contribution of working group 1 to the fifth assessment report of the Intergovernmental Panel on Climate Change, 1535 p. (T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P.M. Midgley, eds.) Cambridge Univ. Press, Cambridge, UK. [Available from [website](#).]
- Isaak, D. J., E. E. Peterson, J. M. Ver Hoef, S. J. Wenger, J. A. Falke, C. E. Torgersen, C. Sowder, E. A. Steel, M.-J. Fortin, C. E. Jordan, et al.  
2014. Applications of spatial statistical network models to stream data. *Wiley Interdiscip. Rev. Water* 1:277–294. [Crossref](#)

- Keefer, M. L., C. C. Caudill, E. L. Johnson, T. S. Clabough, C. T. Boggs, P. N. Johnson, and W. T. Nagy.  
2017. Inter-observer bias in fish classification and enumeration using dual-frequency identification sonar (DIDSON): a Pacific lamprey case study. *Northwest Sci.* 91:41–53. [Crossref](#)
- Kissil, G. W.  
1974. Spawning of the anadromous alewife, *Alosa pseudoharengus*, in Bride Lake, Connecticut. *Trans. Am. Fish. Soc.* 103:312–317. [Crossref](#)
- Large, W. G., and S. Pond.  
1981. Open ocean momentum flux measurements in moderate to strong winds. *J. Phys. Oceanogr.* 11:324–336. [Crossref](#)
- Legett, H. D., A. Jordaan, A. H. Roy, J. J. Sheppard, M. Somos-Valenzuela, and M. D. Staudinger.  
2021. Daily patterns of river herring (*Alosa* spp.) spawning migrations: environmental drivers and variation among coastal streams in Massachusetts. *Trans. Am. Fish. Soc.* 150:501–513. [Crossref](#)
- Limburg, K. E., and J. R. Waldman.  
2009. Dramatic declines in North Atlantic diadromous fishes. *BioScience* 59:955–965. [Crossref](#)
- Loesch, J. G.  
1987. Overview of life history aspects of anadromous alewife and blueback herring in freshwater habitats. *Am. Fish. Soc. Symp.* 1:89–103.
- Lombardo, S. M., J. A. Buckel, E. F. Hain, E. H. Griffith, and H. White.  
2019. Evidence for temperature-dependent shifts in spawning times of anadromous alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*). *Can. J. Fish. Aquat. Sci.* 77:741–751. [Crossref](#)
- Lynch, P. D., J. A. Nye, J. A. Hare, C. A. Stock, M. A. Alexander, J. D. Scott, K. L. Curti, and K. Drew.  
2015. Projected ocean warming creates a conservation challenge for river herring populations. *ICES J. Mar. Sci.* 72:374–387. [Crossref](#)
- MacAvoy, S. E., G. C. Garman, and S. A. Macko.  
2009. Anadromous fish as marine nutrient vectors. *Fish. Bull.* 107:165–174.
- Malaeb, Z. A., J. K. Summers and B. H. Pugsek.  
2000. Using structural equation modeling to investigate relationships among ecological variables. *Environ. Ecol. Stat.* 7:93–111. [Crossref](#)
- McCartin, K., A. Jordaan, M. Sclafani, R. Cerrato, and M. G. Frisk.  
2019. A new paradigm in Alewife migration: oscillations between spawning grounds and estuarine habitats. *Trans. Am. Fish. Soc.* 148:605–619. [Crossref](#)
- Mullen, D. M., C. W. Fay, and J. R. Moring.  
1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic)—alewife/blueback herring. *U.S. Fish Wildl. Serv. Biol. Rep.* 82 (11.56), 21 p. U.S. Army Corps Eng. TR EL-82-4. [Available from [website](#).]
- Nack, C. C., D. P. Swaney, and K. E. Limburg.  
2019. Historical and projected changes in spawning phenologies of American Shad and Striped Bass in the Hudson River estuary. *Mar. Coast. Fish.* 11:271–284. [Crossref](#)
- Nelson, G. A., B. I. Gahagan, M. P. Armstrong, A. Jordaan, and A. Bowden.  
2020. A life cycle simulation model for exploring causes of population change in Alewife (*Alosa pseudoharengus*). *Ecol. Model.* 422:109004. [Crossref](#)
- Nye, J. A., J. S. Link, J. A. Hare, and W. J. Overholtz.  
2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Mar. Ecol. Prog. Ser.* 393:111–129. [Crossref](#)
- Ogburn, M. B., J. Spires, R. Aguilar, M. R. Goodison, K. Heggie, E. Kinnebrew, W. McBurney, K. D. Richie, P. M. Roberts, and A. H. Hines.  
2017a. Assessment of river herring spawning runs in a Chesapeake Bay coastal plain stream using imaging sonar. *Trans. Am. Fish. Soc.* 146:22–35. [Crossref](#)
- Ogburn, M. B., D. J. Hasselman, T. F. Schultz, and E. P. Palkovacs.  
2017b. Genetics and juvenile abundance dynamics show congruent patterns of population structure for depleted river herring populations in the upper Chesapeake Bay. *North Am. J. Fish. Manag.* 37:1083–1092. [Crossref](#)
- Palkovacs, E. P., D. J. Hasselman, E. E. Argo, S. R. Gephard, K. E. Limburg, D. M. Post, T. F. Schultz, and T. V. Willis.  
2014. Combining genetic and demographic information to prioritize conservation efforts for anadromous alewife and blueback herring. *Evol. Appl.* 7:212–226. [Crossref](#)
- Palone, R. S., and A. H. Todd (eds.).  
1998. Chesapeake Bay riparian handbook: a guide for establishing and maintaining riparian forest buffers. USDA Forest Service NA-TP-02-97, rev., 48 p. [Available from [website](#).]
- Parmesan, C.  
2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biol.* 13:1860–1872. [Crossref](#)
- Peer, A. C., and T. J. Miller.  
2014. Climate change, migration phenology, and fisheries management interact with unanticipated consequences. *North Am. J. Fish. Manag.* 34:94–110. [Crossref](#)
- Petreman, I. C., N. E. Jones, and S. W. Milne.  
2014. Observer bias and subsampling efficiencies for estimating the number of migrating fish in rivers using Dual-frequency Identification SONar (DIDSON). *Fish. Res.* 155:160–167. [Crossref](#)
- R Core Team.  
2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from [website](#), accessed October 2020.]
- Raabe, J. K., and J. E. Hightower.  
2014. Assessing distribution of migratory fishes and connectivity following complete and partial dam removals in a North Carolina river. *North Am. J. Fish. Manag.* 34:955–969. [Crossref](#)
- Richkus, W. A.  
1974. Factors influencing the seasonal and daily patterns of alewife (*Alosa pseudoharengus*) migration in a Rhode Island river. *J. Fish. Res. Board Can.* 31:1485–1497. [Crossref](#)
- Rillahan, C. B., D. Alcott, T. Castro-Santos, and P. He.  
2021. Activity patterns of anadromous fish below a tide gate: observations from high-resolution imaging sonar. *Mar. Coast. Fish.* 13:200–212. [Crossref](#)
- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds.  
2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60. [Crossref](#)
- Rosset, J., A. H. Roy, B. I. Gahagan, A. R. Whiteley, M. P. Armstrong, J. J. Sheppard, and A. Jordaan.  
2017. Temporal patterns of migration and spawning of river herring in coastal Massachusetts. *Trans. Am. Fish. Soc.* 146:1101–1114. [Crossref](#)
- Saila, S. B., T. T. Polgar, D. J. Sheehy, and J. M. Flowers.  
1972. Correlations between alewife activity and environmental variables at a fishway. *Trans. Am. Fish. Soc.* 101:583–594. [Crossref](#)

- Sheppard, J. J., and M. S. Bednarski.  
2015. Utility of single-channel electronic resistivity counters for monitoring river herring populations. *North Am. J. Fish. Manag.* 35:1144–1151. [Crossref](#)
- Staples, A., H. D. Legett, J. L. Deichmann, K. Heggie, M. B. Ogburn.  
2023. Automated acoustic detection of river herring (Alewife and Blueback Herring) spawning activity. *North Am. J. Fish. Manag.* 43:869–881. [Crossref](#)
- Staudinger, M. D., K. E. Mills, K. Stamieszkin, N. R. Record, C. A. Hudak, A. Allyn, A. Diamond, K. D. Friedland, W. Golet, M. E. Henderson, et al.  
2019. It's about time: a synthesis of changing phenology in the Gulf of Maine ecosystem. *Fish. Oceanogr.* 28:532–566. [Crossref](#)
- Steel, A. E., C. Sowder, and E. E. Peterson.  
2016. Spatial and temporal variation of water temperature regimes on the Snoqualmie River network. *J. Am. Water Resour. Assoc.* 52:769–787. [Crossref](#)
- Timm, A., V. Ouellet, and M. Daniels.  
2020. Swimming through the urban heat island: can thermal mitigation practices reduce the stress? *River Res. Appl.* 36:1973–1984. [Crossref](#)
2021. Riparian land cover, water temperature variability, and thermal stress for aquatic species in urban streams. *Water* 13:2732. [Crossref](#)
- Torrence, C., and G. P. Compo.  
1998. A practical guide to wavelet analysis. *Bull. Am. Meteorol. Soc.* 79:61–78. [Crossref](#)
- Tyus, H. M.  
1974. Movements and spawning of anadromous alewives, *Alosa pseudoharengus* (Wilson) at Lake Mattamuskeet, North Carolina. *Trans. Am. Fish. Soc.* 103:392–396. [Crossref](#)
- Wilson, B. W.  
1960. Note on surface wind stress over water at low and high wind speeds. *J. Geophys. Res. Atmos.* 65:3377–3382. [Crossref](#)
- Wippelhauser, G.  
2021. Recovery of diadromous fishes: a Kennebec River case study. *Trans. Am. Fish. Soc.* 150:277–290. [Crossref](#)
- Wu, Z., N. E. Huang, S. R. Long, and C.-K. Peng.  
2007. On the trend, detrending, and variability of nonlinear and nonstationary time series. *Proc. Natl. Acad. Sci. U.S.A.* 104:14889–14894. [Crossref](#)
- Xie, Y., and F. J. Martens.  
2014. An empirical approach for estimating the precision of hydroacoustic fish counts by systematic hourly sampling. *North Am. J. Fish. Manag.* 34:535–545. [Crossref](#)