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ARTICLE

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Abstract

The timing of life history events in many plants and animals depends on the seasonal fluctuations of specific environmental conditions. Climate change is altering environmental regimes and disrupting natural cycles and patterns across communities. Anadromous fishes that migrate between marine and freshwater habitats to spawn are particularly sensitive to shifting environmental conditions and thus are vulnerable to the effects of climate change. However, for many anadromous fish species the specific environmental mechanisms driving migration and spawning patterns are

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not well understood. In this study, we investigated the upstream spawning migrations of river herring *Alosa* spp. in 12 coastal Massachusetts streams. By analyzing long-term data sets (8–28 years) of daily fish counts, we determined the local influence of environmental factors on daily migration patterns and compared seasonal run dynamics and environmental regimes among streams. Our results suggest that water temperature was the most consistent predictor of both daily river herring presence–absence and abundance during migration. We found inconsistent effects of streamflow and lunar phase, likely due to the anthropogenic manipulation of flow and connectivity in different systems. Geographic patterns in run dynamics and thermal regimes suggest that the more northerly runs in this region are relatively vulnerable to climate change due to migration occurring later in the spring season, at warmer water temperatures that approach thermal maxima, and during a narrower temporal window compared to southern runs. The phenology of river herring and their reliance on seasonal temperature patterns indicate that populations of these species may benefit from management practices that reduce within-stream anthropogenic water temperature manipulations and maintain coolwater thermal refugia.

In many plants and animals, the timing of cyclical life history events is driven by environmental conditions that fluctuate within and across seasons (Forrest and Miller-Rushing 2010). Annual patterns of migration and reproduction, for example, are often timed to match periods of resource availability. However, shifts in environmental regimes due to climate change are disrupting the timing of natural cycles across communities (Parmesan and Yohe 2003; Staudinger et al. 2019). Asynchrony in biotic interactions and the resulting breakdown of trophic linkages constitute one of the primary ways in which climate change is contributing to biodiversity loss (Bellard et al. 2012). Thus, it is critical to understand the environmental drivers of phenological patterns to assess the potential impact of climate change on natural populations and to develop relevant adaptation strategies.

There is mounting evidence that climate change is altering the timing of migration and spawning cycles of anadromous fishes by shifting distributions, restricting suitable habitat, or shortening the window of time (i.e., phenophase) in which ideal conditions for those activities take place (Nye et al. 2009; Peer and Miller 2014; Lynch et al. 2015; Lombardo et al. 2019; Nack et al. 2019; Staudinger et al. 2019). In addition, many anadromous fishes are subjected to overfishing, bycatch in marine fisheries, degradation and destruction of freshwater spawning habitat by human activities, and the obstruction of spawning migration by dams and culverts (Hall et al. 2012; ASMFC 2017). For these reasons, anadromous fish species have been identified as being highly vulnerable to the cumulative effects of climate change (Hare et al. 2016) and other direct anthropogenic pressures. This is especially true for regional populations of river herring *Alosa* spp., which are at historically low abundances across their range along the Atlantic coast of North America. River herring is the collective name for two anadromous fish species: the Alewife *A. pseudoharengus* and Blueback Herring *A. aestivalis*. In the spring, adult river herring annually migrate from marine environments up coastal streams to freshwater lakes to spawn. The specific timing of migration can vary throughout the river herrings' range, mirroring latitudinal differences in the onset of

spring. In the New England and Gulf of Maine regions, migrations typically span from March to June. Historically, these spring migrations were initiated when rivers reached around 10°C and ended at 20°C (Kissil 1974; Loesch 1987; Ellis and Vokoun 2009; Rosset et al. 2017). In recent decades, climate change has resulted in water temperatures reaching these thresholds earlier in the year (Friedland et al. 2015; Henderson et al. 2017). Thus, warming temperatures could help to explain river herring migrations starting earlier in the spring as well as the considerable interannual variation in migration patterns (Huntington et al. 2003; Ellis and Vokoun 2009; Lombardo et al. 2019). For example, river herring migrations in the Albemarle Sound watershed, North Carolina, started 16 d earlier in the 2010s compared to the 1970s (Lombardo et al. 2019).

Within-season, intra-annual movement dynamics may also be vulnerable to shifts in environmental regimes due to climate change. Understanding changes in fine-scale, within-season movement patterns is important because they can reveal more nuanced responses to altered environmental conditions and can provide insights into whether a species or population has the flexibility to adjust its behavior accordingly, thus adapting in place (Parmesan 2007; Beever et al. 2016). However, unlike interannual migration patterns, the environmental drivers of within-season patterns are less clear. Fluctuations in the rate of seasonal warming and daily variability in temperature and precipitation are becoming increasingly variable in many systems (USGCRP 2018; Lombardo et al. 2019). This could affect the dynamics of upstream pulses of movement exhibited by adult river herring, which are characterized by peaks and troughs of high and low abundance throughout the season (Nelson et al. 2020).

Among different anadromous fish species, temperature, river flow, lunar cycle (which also corresponds with tidal cycle), and the relative abundance of conspecifics have varying influences on daily movement patterns (Leggett 1977; for recent examples, see Keefer et al. 2008; Bizzotto et al. 2009; Snook et al. 2016; Berdahl et al. 2017; Giri et al. 2019). In some cases, daily fluctuations in run strength occur without obvious environmental triggers

(Berdahl et al. 2017). For river herring, previous behavioral experiments (Collins 1952) and counts of adults migrating upstream (Saila et al. 1972; Richkus 1974; Ogburn et al. 2017; Rosset et al. 2017) suggested a correlation between daily movement and water temperature but found conflicting or inconclusive results for the influence of river flow and lunar cycle. Given the interannual and interpopulation variability in environmental regimes and run dynamics (Ogburn et al. 2017; Rosset et al. 2017; Lombardo et al. 2019), a multi-year, regional examination of river herring migration patterns is needed to disentangle the variety of possible drivers of river herring migrations and aid in optimizing monitoring efforts, population models, and management strategies. Understanding the interannual drivers of spawning migrations has been useful for the management of other anadromous fish stocks in setting seasonal closures and time-of-year restrictions (Keefer et al. 2008; Peer and Miller 2014). Understanding within-season movements may help to explain when large pulses of fish move to their spawning grounds and what environmental drivers best predict these events. This information may be useful for guiding river herring management in terms of needed adjustments to water withdrawals and other activities that could interrupt major migrations upstream.

To address these information needs, we investigated the spawning migration of river herring (Alewife and Blueback Herring in aggregate) across 12 coastal streams in Massachusetts using long-term data sets (8–28 years) of daily fish counts. As a primary aim, we examined the relative influence of water temperature and streamflow variability as well as lunar phase on two metrics of daily river herring movement within each stream: fish presence–absence and abundance. Because previous

behavioral experiments indicated a link between water temperature and upstream migrations in river herring (e.g., Ogburn et al. 2017; Rosset et al. 2017), we expected temperature to be a consistent predictor of daily movement. In addition, we compared the long-term characteristics of the 12 streams, including environmental regimes and seasonal run dynamics, to identify any stream-specific or geographic patterns in river herring runs. We discuss our results in the context of climate change and potential management decisions.

METHODS

Daily fish counts.— We compiled data sets of daily river herring counts during upstream migration from 12 coastal streams in Massachusetts between 1990 and 2017, which resulted in 8–28 years of data per stream (Table 1; Figure 1). The data were collected as part of a long-term monitoring program based on a collaborative effort between the Massachusetts Division of Marine Fisheries (MA DMF) and associated stakeholders, including municipalities, watershed associations, and citizen scientists (Nelson et al. 2011). The counts were collected primarily by using visual counting methods, but video monitoring systems and electronic counting systems were used at a subset of locations. Collection methods were consistent within each stream over the course of the time period evaluated except for the Parker River, where visual counts (1997–2012), an electronic counter (2013), and video monitoring (2014–2017) were used. The counting method was always consistent within a given season at each site.

Visual counts were conducted in eight streams using a two-way stratified random design according to

TABLE 1. Number of years of data and river herring run size (mean ± SE) for each study stream, ordered from north to south along the Massachusetts coast. Annual runs size data was provided by the Massachusetts Division of Marine Fisheries and compiled by R. M. Dalton, Duke University. The Monument River is located on the Cape Cod Canal and can be accessed from either the north or south side of the peninsula.

| Stream name	Abbreviation	Total years	Years for models (n)	Annual run size (number of fish)
Parker River	PAR	19	18	11,709 ± 3,797
Ipswich River	IPS	19	7	873 ± 196
Little River	LIT	15	9	1,890 ± 373
Jones River	JON	13	7	2,784 ± 458
Town Brook	TOW	8	7	153,907 ± 10,206
Monument River	MON	28	26	174,175 ± 20,451
Stony Brook	STO	11	10	89,657 ± 28,338
Herring (Harwich) River	HER	9	8	80,572 ± 25,499
Marstons Mills River	MAM	12	5	27,338 ± 6,729
Acushnet River	ACU	13	12	3,555 ± 865
Agawam River	AGA	12	11	41,203 ± 6,810
Nemasket River	NEM	20	18	571,239 ± 62,746
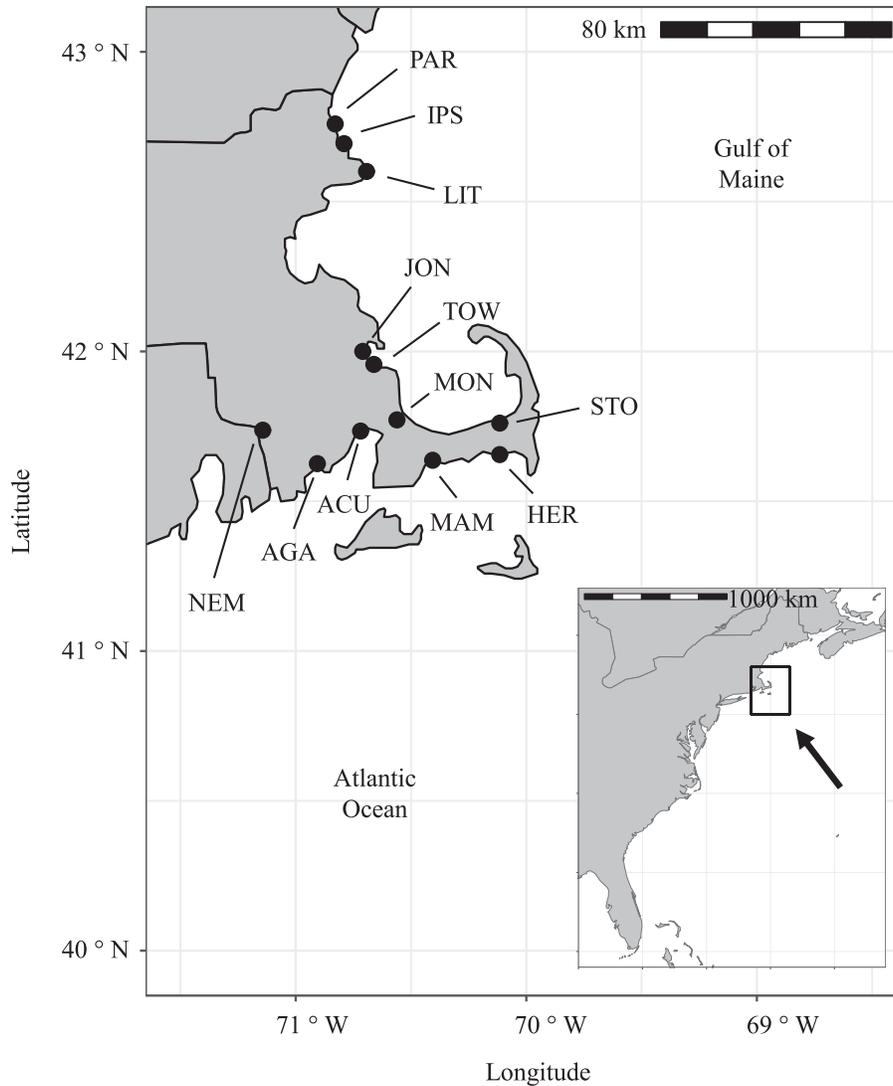
FIGURE 1. Locations of the 12 streams in Massachusetts where daily river herring counts and stream temperatures were taken. Stream abbreviations are defined in Table 1.

methodologies described by Nelson (2006). In this design, counts were randomly collected every day from three 4-h periods (strata). Estimates of total daily passage were calculated from these counts (following the statistical procedures of Nelson 2006). The eight streams were selected based on a minimum time series of counts (>5 years) and a high probability to detect year-to-year changes in abundance and trends using the power analysis procedures described by Gerrodette (1987).

The MA DMF monitored one stream by using a video monitoring system and three streams by using electronic resistivity counters (Smith-Root Models 1101 and 1601). Evaluation of these counting methods by Sheppard and Bednarski (2015) determined that their accuracy decreases as the passage rate increases. To correct for this decreased accuracy, visual counts were additionally conducted at

random periods in these systems to calculate a correction factor for the estimates of daily passage. Information for each stream, including a map, counting method, and location of the count, is included in the online Supplement (Figures S1–S12).

Environmental factors.— Mean daily water temperatures (°C) for each stream were synthesized from measurements made using HOBO ProV2 temperature loggers or mercury thermometers at the locations where the fish counts were taken. Values associated with the lunar cycle, daily moon phase, were adapted from the MULTIFAN-CL fisheries stock assessment model using code in R (R Core Team 2018) from the R4MFCL project (Hoyle et al. 2009). Years and streams with fish counts but no corresponding environmental data or with inconsistent data were not included in the analyses.

Mean daily streamflow (m³/s), also referred to as stream discharge, was estimated using Weather Research and Forecasting Hydro (WRF-Hydro) to predict hydrological conditions in the river herring spawning runs (Gochis et al. 2015). The WRF-Hydro modeling system couples hydrological model components to atmospheric models and other Earth System modeling architectures (Gochis et al. 2015). We ran WRF-Hydro in uncoupled mode using the Noah-MP model (Niu et al. 2011; Yang et al. 2011). For the forcing data, we used eight climate variables: incoming shortwave radiation (W/m²), incoming longwave radiation (W/m²), specific humidity (kg/kg), air temperature (K), surface pressure (Pa), near-surface wind north–south (m/s), near surface wind east–west (m/s), and precipitation rates (mm/s). We accessed hourly climate variables from the North American Land Data Assimilation System project that matched to the years of the present study (Xia et al. 2012). The resolution of the WRF-Hydro model is 1 km, and the terrain routing resolution is 250 m. The model was calibrated using direct flow observations made by the U.S. Geological Survey from neighboring gauged streams (streamflow observations from Geospatial Attributes of Gages for Evaluating Streamflow II; Falcone 2011). See Somos-Valenzuela and Palmer (2018) for a full description of the flow models used in this study, including model performance and limitations.

Statistical analyses.— Analyses of daily river herring counts were conducted in R version 3.5.2 (R Core Team 2018) using generalized linear mixed-effect models (GLMMs) in the glmmTMB package (Brooks et al. 2017). A hurdle model framework (Mullahy 1986) was used to examine the environmental drivers of both daily run presence–absence and abundance in each stream. Changes in presence–absence were analyzed using logistic regressions and GLMMs with binomial error structures and logit link functions. Changes in abundance were analyzed using GLMMs with truncated negative binomial (II) error structures and log link functions and included only data from days with fish counts greater than zero. All models included the main effects and interactions of water temperature, flow, and lunar cycle as fixed factors, with year as a random factor. Model fit was evaluated using diagnostic tools and residual plots (Zuur and Ieno 2016) in the DHARMa package version 0.3.2.0. For these analyses, both stream temperature and streamflow were detrended (Wu et al. 2007), as temperature generally increased linearly and flow decreased exponentially throughout the spawning period. By detrending these data, day-to-day changes in environmental factors (i.e., variation relative to the mean) could be separated from the overall seasonal patterns.

River herring run dynamics (i.e., start and end dates and duration) and environmental regimes were compared among streams by using linear mixed-effect models, with stream as a fixed factor and year included as a random factor. Least-squares mean estimates and post hoc pairwise comparisons were calculated using the R package emmeans version 1.4.8 (Searle et al. 1980). Run start and end dates were defined as 10% and 90% of the total spawning run count, respectively. Run duration was calculated as the differences between the run end (90th quantile) and start (10th quantile) dates. These conservative metrics of run start and end are hypothesized to better capture the main pulse of population movements at each site compared to absolute first and last occurrences (Ferreira et al. 2014; Staudinger et al. 2019). Environmental conditions included water temperature and flow at the start date and end date of each run, mean temperature during the run, rate of temperature increase throughout the run, and spring thermal transition date. The spring thermal transition date, or spring onset, for each stream was calculated as the first day of the year following eight consecutive days with stream temperatures at or above 10°C (following Friedland et al. 2015; Henderson et al. 2017). This thermal threshold also roughly represents the temperature at which the river herring spawning migration is initiated (e.g., Loesch 1987). In addition to the pairwise comparisons among the streams, geographic trends for each run dynamic and environmental factor were assessed using a two-tailed Kendall's tau correlation analysis. This nonparametric analysis tests for significant ranking of the streams, where streams were ordered from north to south based on their location along the coast.

RESULTS

Water temperature variation was a significant predictor ($P < 0.05$) of daily river herring presence in 11 out of 12 coastal streams (Figure 2A) and a significant predictor of abundance in 7 of the 12 streams (Figure 2B). Variation in streamflow was not a significant predictor of fish presence or absence in any stream (Figure 2C); furthermore, streamflow was only found to be a significant predictor of abundance in two streams (Figure 2D), with one being negatively influenced (Monument River: estimate $\pm$ SE = -1.38 ± 0.44, $z_{972} = -3.16$, $P = 0.002$) and the other being positively influenced (Agawam River: estimate = 1.20 ± 0.30, $z_{660} = 4.02$, $P < 0.001$). Lunar cycle (Figure 2E) was a significant predictor of fish presence in two streams (Nemasket River: estimate = 1.13 ± 0.45, $z_{910} = 2.54$, $P = 0.011$; Stony Brook: estimate = 1.36 ± 0.45, $z_{452} = 3.00$, $P = 0.003$) and a significant predictor of daily fish abundance in only one stream (Marstons Mills River: estimate = 0.92 ± 0.27, $z_{180} = 3.42$, $P < 0.001$; Figure 2F). For daily fish abundance, the effect sizes of water temperature were smaller (|estimate| < 0.5) than those of flow (|estimate| > 1.0). Interactions among water temperature, flow, and lunar cycle were significant in three streams for daily fish
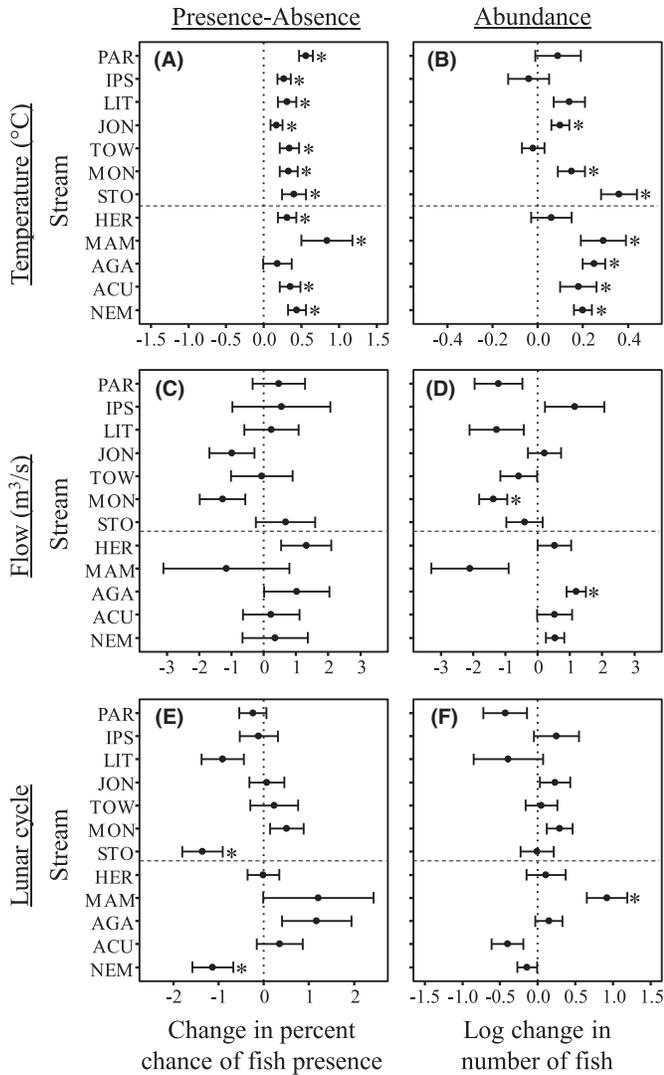
FIGURE 2. Coefficients from the river herring presence–absence models (left column) and abundance models (right column), showing the predicted daily percentage change of counting more than zero fish or daily changes in fish abundance for a 1-unit increase in **(A)**, **(B)** water temperature; **(C)**, **(D)** flow; and **(E)**, **(F)** lunar cycle. Streams with significant effects for each model are indicated with an asterisk. Note the differences in scales among plots. Streams are ordered based on geographic position from north to south along the Massachusetts coast. Stream abbreviations are defined in Table 1. The horizontal dotted lines indicate the ordinal location of the easternmost extent of Cape Cod (i.e., the division between northern and southern streams).

presence–absence (Marstons Mills River, Parker River, and Town Brook) and in four streams for daily fish abundance (Ipswich River, Monument River, Stony Brook, and Town Brook). In the cases of the Ipswich River and Town Brook, only interactions (i.e., no main effects) were significant for abundance. A full list of GLMM results for both the presence–absence and abundance models for each stream is included in the online Supplement (Table S1).

There was a high degree of variability in river herring run dynamics and environmental regimes among streams (Table 2), with a north-to-south trend along the coast. Run start and end dates were weakly correlated with geographic position (start date: Kendall's $\tau = 0.370$, $z = 6.78$, $P < 0.001$; end date: Kendall's $\tau = 0.352$, $z = 6.59$, $P < 0.001$). The more southerly runs (Acushnet, Agawam, and Nemasket rivers) started (~day 90–100) and ended (~day 115–125) earlier in the year compared to the northernmost runs (Ipswich and Parker rivers) and the runs on the Cape Cod peninsula (Herring River, Monument River, and Stony Brook), which started on approximately day 111–115 and ended on approximately day 134–140 (Figure 3A). The more southerly runs were also longer in duration, lasting about 57–80 d compared to the more northerly runs, which lasted approximately 45–53 d (run duration: Kendall's $\tau = -0.217$, $z = -4.08$, $P < 0.001$). In addition, the range of temperatures at which runs occurred were correlated with geographic position (start temperature: Kendall's $\tau = 0.330$, $z = 5.29$, $P < 0.001$; end temperature: Kendall's $\tau = 0.125$, $z = 2.04$, $P = 0.041$; mean temperature: Kendall's $\tau = 0.271$, $z = 4.65$, $P < 0.001$). The southern runs started and ended in colder water (start temperature was ~8–12°C; end temperature was ~13–16°C) compared to the northern and Cape Cod runs (start temperature was ~13–14°C; end temperature was ~16–17°C; Figure 3B). Estimates of streamflow rates were significantly higher on average (pairwise comparisons: $P < 0.05$) in the Ipswich and Nemasket rivers (>3.0 m³/s) compared to any of the other streams (<1.0 m³/s; Figure 3C). In addition, the Ipswich River was the only system where flow increased on average throughout the season.

The spring thermal transition date in the northernmost stream (Parker River) occurred later in the year (day of year $= 121 \pm 9$) compared to the southernmost streams (Acushnet, Agawam, and Nemasket rivers; mean < day 112; pairwise comparisons: $P < 0.05$; Figure 3D). Spring thermal transition was weakly positively correlated with geographic position (Kendall's $\tau = 0.185$, $z = 2.90$, $P = 0.004$). A full list of pairwise comparisons for the general run dynamics and environmental characteristics among the streams can be found at the U.S. Geological Survey's digital repository, ScienceBase (https://doi.org/10.21429/cr80-fy95).

DISCUSSION

Environmental conditions can have varying effects on the timing of anadromous fish migrations, making the primary drivers of within-system movements difficult to identify over different time scales. Indeed, in the literature there has been much debate on whether temperature or flow is the master variable affecting anadromous fish

TABLE 2. River herring run (migration) timing and environmental characteristics (mean ± SE) associated with the run period for each study stream, ordered from north to south along the Massachusetts coast. Stream abbreviations are defined in Table 1.

Stream	Run start (day of year)	Run end (day of year)	Duration (d)	Spring transition date (day of year)	Mean temperature (°C)	Mean flow (m³/s)
PAR	115 ± 2	133 ± 2	45 ± 4	121 ± 2	14.7 ± 0.7	0.95 ± 0.1
IPS	112 ± 2	135 ± 2	53 ± 3	114 ± 4	14.1 ± 0.7	8.65 ± 0.9
LIT	104 ± 3	127 ± 2	53 ± 1	113 ± 3	13.5 ± 0.5	0.02 ± <0.1
JON	107 ± 1	134 ± 2	58 ± 2	115 ± 2	13.0 ± 0.5	0.84 ± 0.1
TOW	106 ± 2	131 ± 1	63 ± 3	118 ± 4	11.7 ± 0.7	0.35 ± 0.1
MON	115 ± 1	131 ± 1	77 ± 1	117 ± 5	13.9 ± 0.2	0.36 ± <0.1
STO	116 ± 1	136 ± 2	57 ± 2	111 ± 2	15.2 ± 0.5	0.16 ± <0.1
HER	111 ± 1	140 ± 2	58 ± 2	117 ± 3	13.9 ± 0.3	0.31 ± 0.1
MAM	105 ± 2	124 ± 2	39 ± 3	111 ± 1	13.3 ± 0.3	0.51 ± 0.1
ACU	103 ± 1	125 ± 1	74 ± 3	110 ± 3	13.5 ± 0.2	0.27 ± <0.1
AGA	95 ± 2	118 ± 3	80 ± 3	110 ± 3	11.8 ± 0.6	0.57 ± 0.1
NEM	90 ± 2	116 ± 1	57 ± 3	112 ± 2	10.3 ± 0.5	3.61 ± 0.5

movements (e.g., Keefer et al. 2008; Bizzotto et al. 2009; Snook et al. 2016; Berdahl et al. 2017; Giri et al. 2019). Across 12 stream systems in Massachusetts, water temperature was found to be the most common predictor of daily river herring movement during spawning migrations. In a majority of the streams, a day-to-day increase in temperature above the estimated mean corresponded with an increase in both of our metrics (river herring presence–absence and river herring abundance). This result supports previous behavioral experiments (Collins 1952) and single-year fish count studies (Saila et al. 1972; Richkus 1974; Ogburn et al. 2017) that also suggest a correlation between temperature and daily movements. Thus, both overall timing of seasonal river herring migrations (e.g., Ellis and Vokoun 2009; Lombardo et al. 2019) and daily movement patterns of river herring are primarily driven by temperature regimes.

Streamflow and lunar cycle had variable or inconclusive effects on within-season fish migrations. Streamflow was only a predictor of river herring run abundance in 2 of the 12 coastal streams (Agawam and Monument rivers). Interestingly, while higher flow positively influenced run size in the Agawam River, it negatively influenced run size in the Monument River. Flow and related factors, such as channel depth and width, can impact accessibility, where fish physically cannot move upstream (or downstream as juveniles) due to too little or too much flow. However, beyond these extreme limitations the effects of increasing flow remain inconclusive. Lunar cycle was a predictor of river herring presence–absence in two streams (Nemasket River and Stony Brook) and run abundance in only one stream (Marstons Mills River). Lunar effects were considered a proxy for tidal cycles and, similar to flow, may interfere with accessibility if lower tides physically prevent fish from moving upstream. Overall, our results for flow and lunar cycle

are consistent with previous studies in other systems, which found no definitive association between these factors and river herring movement (Kissil 1974; Ogburn et al. 2017).

Geographic patterns in both seasonal run dynamics and environmental regimes suggest that some runs may be more vulnerable to warming temperatures due to climate change. The more northerly runs (Ipswich, Little, and Parker rivers) and the runs on the Cape Cod peninsula (Marstons Mills River, Monument River, and Stony Brook) started and ended later in the season and in overall warmer conditions compared to the southern runs. This is consistent with known latitudinal trends in phenology that progress seasonally from south to north (Greene et al. 2009; Staudinger et al. 2019). The runs that started later were also shorter in duration and occurred in a narrower range of temperatures, closer to the historical thermal maximum at which river herring migrations have been observed (~20°C; Kissil 1974; Loesch 1987; Ellis and Vokoun 2009; Rosset et al. 2017). Thus, increases to within-season rates of warming may constrict run duration in these streams. This is concerning, as the runs start and end within a window of about 3°C, which corresponds to the projected amount of warming expected in the northeastern U.S. region in the next 10–20 years (Karmalkar and Bradley 2017). In contrast to the northern runs, the more southerly runs (Acushnet, Agawam, and Nemasket rivers) have a broader thermal range to respond and adapt to warming temperatures, suggesting higher resilience to climate change. Previous analyses of run counts in these same 12 coastal streams found that river herring run durations have not shifted substantially over recent decades (R. M. Dalton, Duke University and M. D. Staudinger, U.S. Geological Survey, unpublished data). In those analyses, run initiation was best predicted by a combination of winter variables prior to the spring run, while the median and end
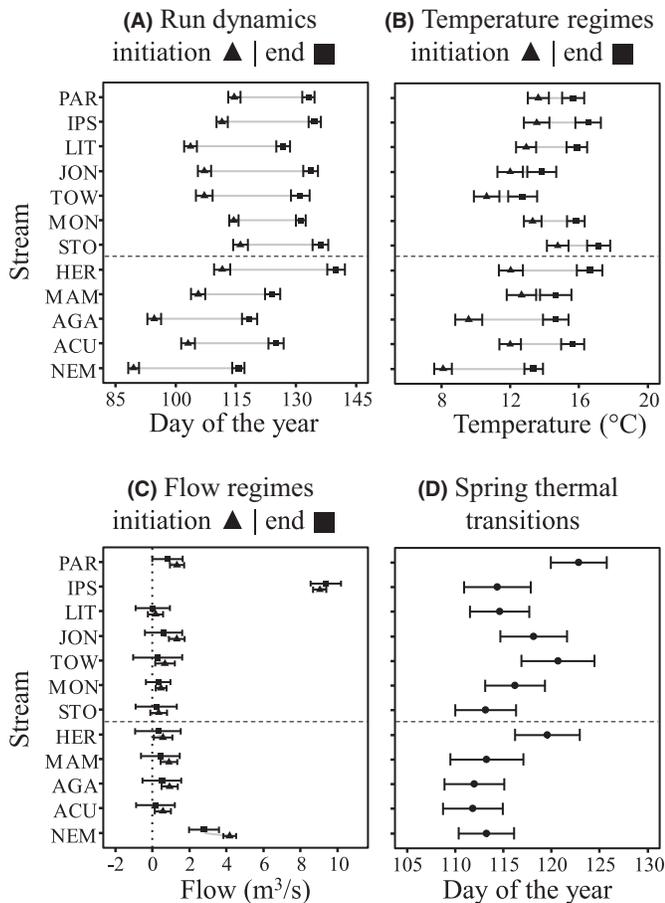
FIGURE 3. Averages, SEs, and ranges for river herring run dynamics and environmental characteristics in each stream, including **(A)** the start and end day of the run, **(B)** water temperature at the start and end of each run, **(C)** streamflow at the start and end of each run, and **(D)** the spring thermal transition date. The spring transition date was calculated as the first day of the year following eight consecutive days with water temperatures at or above 10°C for each stream. Streams are ordered based on geographic position from north to south along the Massachusetts coast. Stream abbreviations are defined in Table 1. The horizontal dotted lines indicate the ordinal location of the easternmost extent of Cape Cod (i.e., the division between northern and southern streams).

of run timing were more affected by within-season (spring) conditions (Dalton and Staudinger, unpublished data). In other systems, however, such as the Albemarle Sound watershed in North Carolina, decreases in river herring run durations were observed due to increasing within-season warming rates (Lombardo et al. 2019).

Population- and Community-Level Effects of Warming Temperatures

As the seasonal rate of warming and daily variability in temperatures increase (USGCRP 2018; Lombardo et al. 2019), shifts in river herring migration dynamics may have broader population- and community-level impacts. At the population level, changes in within-season migration timing may correspondingly affect other aspects of the river herring life cycle, such as when spawning occurs and when juveniles out-migrate, thus affecting spawning rates and juvenile growth and survival (ASMFC 2012; Tommasi et al. 2015; Rosset et al. 2017). In addition, individuals can migrate upstream and downstream multiple times within a single season (McCartin et al. 2019), and individuals that initially migrate earlier in a season are more likely to have multiple successful mating events (Marjadi et al. 2019). If the window of time during which runs occur is constricted due to increases in within-season warming rates, then upstream spawning migration and mating could be limited to a single event per individual. Narrower phenophases could also make these systems increasingly vulnerable to extreme events (e.g., storms) by reducing the windows available for successful migrations into spawning grounds. Overall, however, the specific consequences of a reduced migration window on spawning success represent an area that requires more research, as the link between the timing of spawning migrations and eventual juvenile output is not well understood.

Changes in river herring abundance and phenology can also have broader ecological consequences. River herring and other anadromous forage fishes are keystone species and play a critical role in sustaining coastal ecosystems (Willson and Halupka 1995; Dias et al. 2019). Their migrations connect riverine and oceanic habitats and provide an influx of marine nutrients to freshwater food webs (Walters et al. 2009). In addition, river herring support a diverse community of higher-trophic-level predators, including raptors and important recreational freshwater fish (e.g., Largemouth Bass *Micropterus salmoides*; Yako and Mather 2000; Mattocks et al. 2017), economically valuable marine species (e.g., Atlantic Cod *Gadus morhua*), and species of conservation concern (e.g., whales, pinnipeds, sharks, and seabirds; Dias et al. 2019). Thus, a loss of river herring or shifts in their phenology may result in trophic mismatches and cascading effects in freshwater and marine communities (Cushing 1990; Edwards and Richardson 2004).

Anthropogenic Influences and Other Confounding Factors

All 12 streams in this study contain anthropogenic structures and obstructions (e.g., dams and culverts) that may create unique conditions that affect flow rates, fish passage, and within-season movement patterns. Furthermore, water withdrawals from river herring spawning habitats are conducted for municipal uses (in the Jones, Little, and Nemasket rivers) or for use as irrigation sources for agriculture (in the Acushnet, Agawam, Herring, and Marstons Mills rivers; Brady et al. 2005; Reback

et al. 2004a, 2004b, 2004c). Withdrawals are regulated through issuing permits that set daily and annual withdrawal limits in accordance with the Massachusetts Water Management Act (1986), through operation and management plans for fishway operations (Massachusetts General Law chapter 130, section 19), or voluntarily through best management practices to maintain adequate levels of flow to allow river herring passage during critical migratory periods. These hindrances to fish passage and manipulations of streamflow limit our ability to accurately assess the effects of environmental drivers on river herring movement. In addition, no streams in this study were directly monitored for flow during the time period of our analyses. Our streamflow models were calibrated using observations from neighboring gauged streams and represent the natural hydrological characteristics of our 12 study sites. However, the models do not account for water withdrawals within a season (Somos-Valenzuela and Palmer 2018), potentially resulting in a disconnect between our estimates of flow and the actual flow in our target systems. Thus, our inconclusive results regarding the effects of streamflow on daily fish migrations may be explained by anthropogenic manipulation of flow. To clearly understand the influence of flow and potential interactive effects of water withdrawals on river herring migrations, future studies are needed that include direct monitoring of streamflow (e.g., the installation of streamflow gauges) in the systems that contain migratory fish populations.

The effects of lunar cycle on river herring migration timing may also be confounded by anthropogenic manipulations of flow. If lunar influence on fish migration is related to tidal cycles, then the manipulation of water levels and connectivity may dampen that tidal effect. However, given the variety of water level manipulations across streams, parsing out the influence of specific anthropogenic factors on river herring migration dynamics is a challenge. Information for each stream, including the area and location of available spawning habitat, obstructions to connectivity, and restoration efforts, is included in the online Supplement (Figures S1–S12).

The methods for counting fish and collecting environmental data may also limit the interpretations of our results. The location within each stream where fish counts were taken varied in terms of distance from the ocean and anthropogenic barriers. In addition, temperature measurements were only taken at a single location within each stream. Both temperature and the movement of fish are temporally and spatially variable throughout a river network over the course of a day. River herring likely take advantage of the thermal corridors and refugia that are dispersed throughout each system rather than relying on conditions at any given point. Recently developed modeling techniques that consider systemwide environmental conditions (Mazza and Steel 2017) may assist investigations of how thermal regimes and fine-scale river herring movements shift within river networks.

Finally, species-specific differences in migration timing may be confounding our results. In this study, we did not differentiate between the two species of river herring. Alewife migrate upstream earlier in the spring (March–June), while Blueback Herring typically migrate later (late April to June; Saunders et al. 2006). Given the window of time in which daily fish counts were collected, it is likely that most of the river herring counted in this study were Alewife. This assumption is further supported by weekly biological sampling of several of these streams during the spring spawning season (MA DMF, unpublished data). However, Alewife and Blueback Herring runs are known to temporally overlap (Saunders et al. 2006), and co-occurrences of these two species have previously been observed in at least three of the streams included in our study (Monument River, Parker River, and Stony Brook; Rosset et al. 2017). Alewife and Blueback Herring are also known to hybridize in the systems of the current study (Marjadi et al. 2019). Thus, although it could be assumed that the majority of the fish counted were Alewife, the presence of Blueback Herring in some systems may affect late-season run counts. New studies and tools (e.g., Plough et al. 2018) that sample throughout the migration season and that can separate counts of Alewife and Blueback Herring are needed to differentiate the environmental drivers of movements in each species.

Management Implications

River herring and other anadromous fishes in the northwest Atlantic have been identified as species that are highly vulnerable to climate change (Nye et al. 2009; Lynch et al. 2015; Hare et al. 2016). Our results support this threat assessment, as we found a connection between within-season temperature patterns and river herring phenology. In addition, our results confirm the previously identified thermal threshold for river herring upstream movement (Kissil 1974; Loesch 1987; Ellis and Vokoun 2009; Rosset et al. 2017), as the mean water temperature for the start and end of the spawning runs in all 12 streams was less than 20°C. Given their sensitivity to warming temperature regimes, river herring may benefit from protections that maintain thermal refugia. This may be particularly pertinent in the more northerly systems, where fish are migrating near their thermal maximum within a narrower temporal window and where the 20°C thermal threshold is projected to be crossed in the next two decades (Karmalkar and Bradley 2017). In Massachusetts, waterbodies (streams, rivers, or tributaries) that are used by reproducing "coldwater" fish are protected as Coldwater Fish Resources (CFRs; Division of Fisheries and Wildlife 2014). Designation as a CFR is meant to maintain the coldwater thermal refugia for species of

interest by regulating and minimizing the impacts of water withdrawals. Coldwater fishes under the CFR classification include native species, such as Brook Trout *Salvelinus fontinalis* and Rainbow Smelt *Osmerus mordax*, and non-native species, such as Brown Trout *Salmo trutta* and Rainbow Trout *Oncorhynchus mykiss*, many of which are sympatric with river herring. Some of the streams in this study, namely Marstons Mills River and tributaries of the Jones and Nemasket rivers, are already designated as CFRs. However, while river herring upstream migration occurs in waters less than 20°C, spawning is not as thermally restricted and can occur in warmer waters. Furthermore, the timing and duration of spawning in river herring may not be linked to the timing and duration of migration (Rosset et al. 2017). Thus, thermal restrictions to migration may not have a proportionate impact on spawning success and recruitment. To understand how maintaining thermal refugia might benefit river herring populations, future studies could examine how shifts in migration dynamics impact other life stages.

Although we found inconclusive evidence of the effects of streamflow on river herring migrations, low flows caused by water withdrawals may be affecting movements. In the two streams where flow was a significant predictor of daily movement (Agawam and Monument rivers), our results also suggested that flow had a greater effect on daily fish abundance than water temperature. Thus, in some systems flow may be a more influential driver of river herring migration patterns, possibly outweighing the influence of temperature. Stream management practices that better maintain flow and control for water withdrawals during the spawning season may benefit river herring populations by improving passage and increasing resilience to shifting thermal regimes due to climate change.

Conclusion

Temperature has long been suspected as the driving variable affecting within-season river herring migration patterns (e.g., Collins 1952; Saila et al. 1972; Richkus 1974; Huntington et al. 2003; Ogburn et al. 2017; Rosset et al. 2017). Previous studies, however, lacked the long-term data sets of daily measurements needed to examine day-to-day spawning run dynamics in river herring—a known gap in the literature (Nelson et al. 2020). Our results confirm the assumption that temperature is the primary driver of within-season migration dynamics and suggest widespread influence of daily temperature on fish migration among 12 coastal Massachusetts streams. In addition, among-stream variation in run dynamics suggests a geographic trend in phenology and that the more southerly runs in the study region may be more resilient to climate change. Overall, given the vulnerability of river herring to warming temperatures (Hare et al. 2016), increased protections that maintain thermal refugia may benefit populations of river herring. Finally, there are several remaining research questions that warrant further investigation following this study. If the southern runs in Massachusetts occur over longer durations in colder water compared to the northern runs, are there (1) genetic or physiological differences in these populations or (2) differences in condition between fish that spawn in the northern versus southern runs? The effects of streamflow and lunar cycle on fish movement were inconclusive in this study. However, it remains unclear how anthropogenic manipulations of streams, such as obstructions and water withdrawals, influence the environmental factors that affect fish movement. Correspondingly, how would stream restoration efforts and better management of streamflow during river herring runs affect within-season fish migrations? Finally, can river herring adapt to changing thermal regimes in these systems, and how do shifts in migration dynamics impact other life history events? Addressing these questions will allow for a clearer understanding of river herring phenology and is necessary to guide more climate-adaptive management and habitat restoration efforts.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.