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NOTE

Evidence of Life Cycle Diversity of River Herring in the Penobscot River Estuary, Maine

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Abstract
Alewife *Alosa pseudoharengus* and Blueback Herring *A. aestivalis*—collectively referred to as river herring—exhibit complex life histories, exploiting freshwater and marine biomes to complete their life cycles. We investigated distribution patterns of river herring in the Penobscot River estuary, Maine, USA, from April through September in 2012 and 2013 and found both species in relatively low-salinity portions of the estuary in all months sampled. River herring made up the majority of samples in terms of abundance and biomass for most months. We developed age–length keys for monthly catches and found consistent presence of age-1 and age-2 river herring, especially during spring. We found seasonal patterns in age distribution with age-1 fish and older most abundant in spring and summer and age-0 fish only occurring in late summer through fall. These observations provide direct evidence of life cycle diversity for juvenile river herring, complementing other recent observations in other parts of their native range. Lastly, our findings suggest further consideration should be given to the importance of connectivity between marine, estuarine, and freshwater habitats for age-1 and age-2 river herring and to the more complex ecological roles of age-1 and age-2 river herring given their intermediate trophic level and presence in relatively fresh components of the Penobscot River estuary.

Life cycle diversity enables diadromous fish to use a wide array of resources in both freshwater and saltwater environments (McDowall 2009) and allows subsets of individuals to enhance their fitness by exploiting different, often ephemeral, pools of resources. For example, Cunjak (1992) reported that growth of Atlantic Salmon *Salmo salar* parr using estuaries as rearing habitat was faster than growth of those in riverine areas because of greater feeding opportunities in estuarine areas. Life cycle diversity also appears to be an important bet-hedging strategy that allows

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some segments of a population to persist through times of unfavorable environmental conditions (Ellner and Hairston 1994; Hilborn et al. 2003). The importance of life cycle diversity and plasticity is well established for a wide array of salmonid fishes (Quinn 1993; Klemetsen et al. 2003), but it is not nearly as well established in alosine fishes (Pess et al. 2014). A recent review by Waldman et al. (2016) suggests that contemporary declines in life cycle diversity (and loss of habitat diversity that often leads to life cycle diversity) may be limiting restoration of alosine fishes and other diadromous species.

River herring, the collective name for Alewife *Alosa pseudoharengus* and Blueback Herring *A. aestivalis*, are described as anadromous alosine fishes with a range from Florida, USA to Labrador, Canada (Schmidt et al. 2003). River herring fisheries have existed in many forms including commercial, recreational, and cultural sustenance; these fisheries have been tremendously valuable to humans for centuries (Watts 2012). River herring are also an important component of the ecosystems that they inhabit, providing a wide array of ecological services in freshwater (Durbin et al. 1979; Walters et al. 2009), estuaries (Hartman 2003), and the marine environment (Hall et al. 2012). Indeed, Ray (2005) concluded that river herring are key components of the coastal–estuary ecosystem in a manner similar to Pacific salmonids, known to provide a suite of ecological services to human and nonhuman components of the ecosystems they inhabit.

Contemporary abundance levels of river herring are greatly diminished when compared to historic levels (Limburg and Waldman 2009; NMFS 2013). Overfishing, dams (and other obstructions), and pollution are among the factors that led to the dramatic declines observed in abundance from historical levels (Limburg and Waldman 2009). In 2011, the National Marine Fisheries Service (NMFS) received a petition to list river herring as threatened species under the Endangered Species Act, but thus far has not determined listing to be warranted (USOFR 2019). Following completion of the most recent status review in 2019, NMFS (2019) affirmed that both species warrant greater attention in terms of conservation (e.g., fish passage improvements) and research (life history patterns, genetic stock structure, etc.).

River herring life history is well described (see Greene et al. 2009 for review), with most descriptions following a “classical” pattern of anadromy (Myers 1949), whereby freshwater habitats are used as spawning and age-0 nursery areas (Colette and Klein-MacPhee 2002; Limburg and Turner 2016). It is widely accepted that age-0 fish emigrate from freshwater habitats toward estuarine and marine environments from mid-summer through late fall (Fay et al. 1983). Cues for migrations of age-0 river herring include precipitation or river discharge (Richkus 1975; O'Leary and Kynard 1986), lunar cycle (Marcy 1969; O'Leary and Kynard 1986; Yako et al. 2002), food availability (Richkus 1975; Yako et al. 2002), and attainment of a size threshold (Iafrate and Oliveira 2008; Gahagan et al. 2010). After migration, age-0 fish are widely distributed from inshore to outer continental shelf habitats across their marine range (Stone and Jessop 1992; Colette and Klein-MacPhee 2002). Life history of age-1 to age-3 river herring is mostly described as marine with a coastal shelf distribution that varies seasonally and with a general shift south to the Mid-Atlantic in the fall and north to the Gulf of Maine and Nova Scotia in summer (Colette and Klein-MacPhee 2002). Some evidence of age-1 to age-3 river herring inhabiting higher-salinity components of estuaries (i.e., the “saltwater” zone described by Jury et al. 1994) also exists for the Bay of Fundy (Stone and Daborn 1987), Chesapeake Bay (Buchheister et al. 2013), the mid-Atlantic region (Milstein 1981), and Long Island Sound (Gottschall et al. 2000).

Recent evidence using novel technology suggests that considerable diversity in these life history patterns may exist and that life cycle diversity may be an underexamined aspect of the ecology and management of river herring. For example, studies using otolith microchemistry suggest that some age-0 fish may remain in lower-salinity waters over their first winter (Limburg 1998; Gahagan et al. 2012; Payne Wynne et al. 2015; Turner and Limburg 2016). Further, Limburg and Turner (2016) recently observed age-1 Blueback Herring in the Hudson River estuary during the spawning season and concluded that these “nontextbook” migrations may be quite common in Hudson River populations. However, direct evidence of age-1 and age-2 river herring using relatively “fresh” components of estuaries (i.e., the “mixing zone” described by Jury et al. 1994) remains relatively scarce.

In the following sections of this article, we (1) examine the relative abundance and biomass of Alewives and Blueback Herring captured during trawling of the Penobscot River estuary, Maine from April to September 2012 and 2013, (2) examine the size and age structure to develop monthly age–length keys for Alewives and Blueback Herring, (3) use the age–length keys to derive monthly catch at age of Alewives and Blueback Herring in this system, and (4) discuss some implications of our findings for management and estuarine ecology.

METHODS

Study site.— The Penobscot River watershed (Figure 1) is one of the largest in New England, draining over 22,000 km^2 of the state of Maine into the Atlantic Ocean’s Gulf of Maine with an annual average discharge of 400 m^3/s. The Penobscot River is home to over 35 freshwater and 11 diadromous fish species including Alewife and Blueback Herring (Kiraly et. al 2015). The Penobscot River

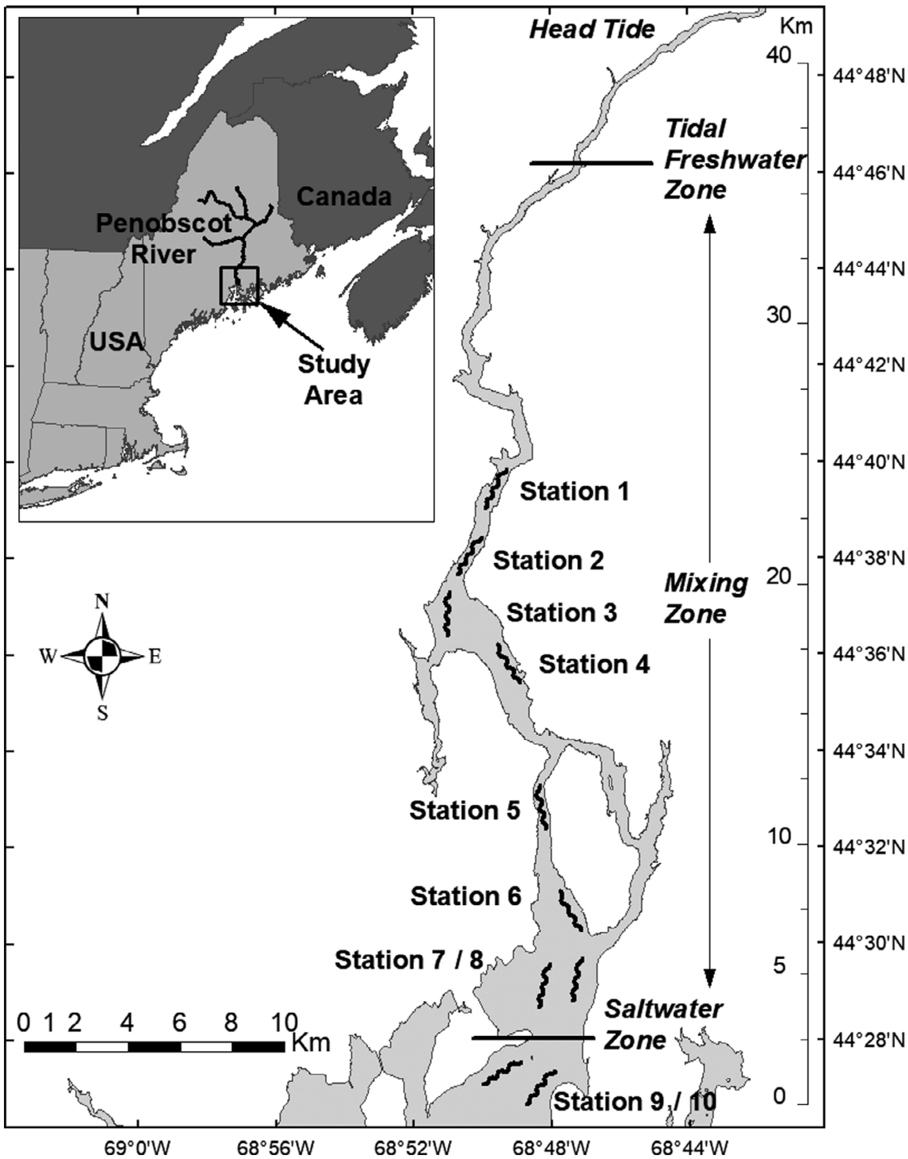

FIGURE 1. The spatial extent of the study area in the Penobscot River estuary with representative trawl sampling stations (wavy lines) and the regional location within the Gulf of Maine (inset). Salinity zones were adapted from Jury et al. (1994) to represent general conditions of the estuary relative to our sampling stations.

estuary extends from head of tide in Bangor, Maine approximately 150 km to the seaward end of Penobscot Bay in Rockland, Maine (NOAA SEAB 1985). Area tides range from 3 to 4 m, and high river discharge results in a salt-wedge type estuary (Geyer and Ralston 2018). Jury et al. (1994) delineated the tidal freshwater zone (0–1‰) from head of tide downstream approximately 20 km to the start of the mixing zone (2–25‰; 44°46’N, 68°48’E); this zone extends seaward approximately 40 km to the entrance of Penobscot Bay (44°28’N, 68°48’E; Figure 1).

The river herring runs in the Penobscot River basin are recovering but remain well below historic abundance levels. Like other major rivers in the northeastern United States, dam construction in the Penobscot (along with other perturbations) had substantially reduced river herring runs by the 1800s (Smith 1899), though the Penobscot remained one of the major populations on the east coast—even after decades of impact from dams (Atkins 1887). There have been dams spanning the main-stem Penobscot River since the early 1820s; however, many did not maintain specific structures for fish passage until the mid-20th century (Cutting 1963). Historical significance, production potential (Trinko Lake et al. 2012), and relatively low degree of fragmentation (Martin and Apse 2011) have fostered focused restoration including the Penobscot River Restoration Project. This project improved connectivity in the watershed by removing the

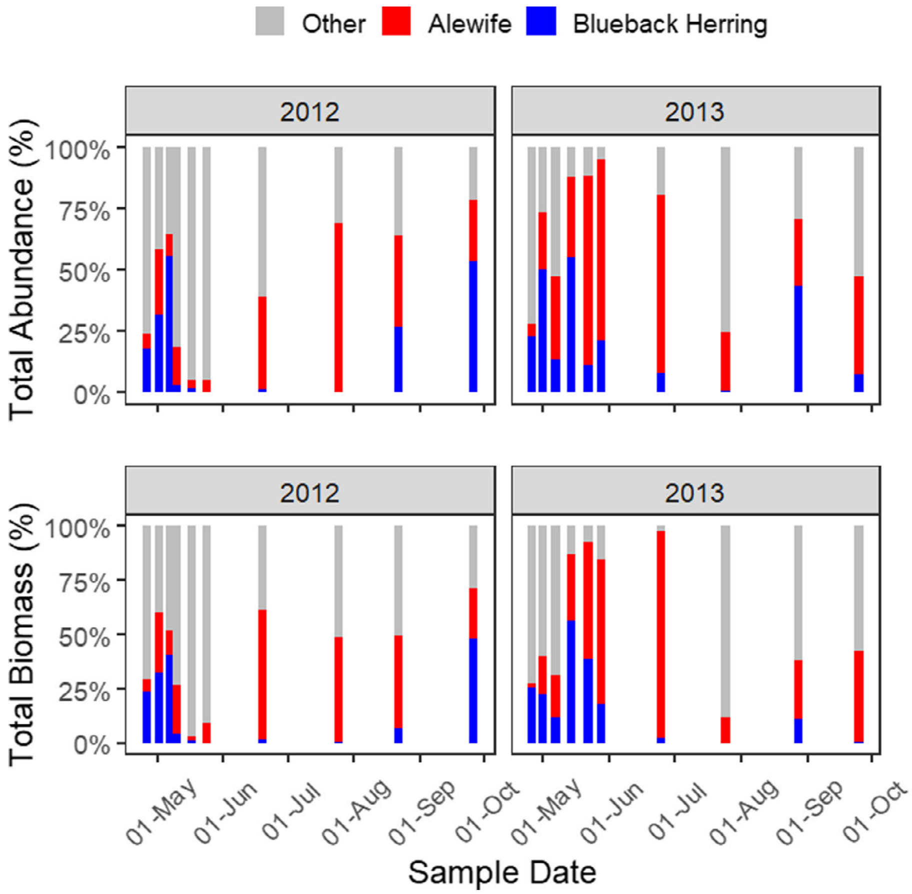

FIGURE 2. Percentage of Alewife (red), Blueback Herring (blue), and other species (gray) abundance (top) and biomass (bottom) captured in trawl samples in the Penobscot River estuary in 2012 and 2013. Note that the *x*-axis is scaled by sample date to visualize the weekly sampling in April and May and monthly sampling in June through September.

lowermost two main-stem dams and providing improved fish passage at additional upstream facilities. This project alone provided access to roughly 70% of historical habitat for Blueback Herring and 31% of historical habitat for Alewives (Trinko Lake et al. 2012). Since completion of the Penobscot River Restoration Project in 2016, annual runs of river herring have increased to over 2 million and they also occupy newly accessible habitat throughout the watershed (Watson et al. 2018).

Sampling design.— We conducted a pelagic fish trawl survey from late April through September in both 2012 and 2013. We sampled weekly in April and May and monthly from June through September. Sampling was conducted weekly in May to better characterize the period of diadromous fish migration. We trawled at ten fixed locations each sampling day in 2012 and the northernmost eight stations in 2013 (Figure 1). Prior to the start of each tow, we measured salinity 0.5 m below the water surface using a YSI 650 multiparameter meter (YSI, Yellow Springs, Ohio). Tows were conducted on a flood tide while travelling upstream during daylight hours. We sampled each station at approximately similar tidal period. To optimize net performance (i.e., spread and height), we varied vessel speed from 3.7 to 7.4 km/h depending on current (which varied substantially with river discharge and tide). To maximize capture efficiency, we towed the net to the right or left of the vessel wake. The tows ranged from 0.3 to 3.6 km in length (5 to 20 min) depending on current velocity and bathymetry. Tow distance was determined using a GPS enabled computer recording position every 1 s and using ESRI ArcGIS Desktop Release 10 (Environmental Systems Research Institute, Redlands, California) to compute the length (nearest 0.001 km) of the line intersecting all the points.

We used a two-seam shrimp trawl constructed of two 19-mm diamond stretch mesh panels of high-density polyethylene (“Mamou Trawl,” Innovative Net Systems, Milton, Louisiana). The 19-m-long net was towed with an 11-m commercial lobster vessel. The cod end was made of 6.35-mm nylon mesh and was fitted with a rigid aquarium which was a two-thirds-scale version of the aquarium described by Sheehan et al. (2011) to reduce mortality of catch. The aquarium was constructed of aluminum plate stock and had a circular opening with a diameter of 0.36 m and interior dimensions of 0.34 m in height, 0.55 m in width, and 1.3 m in length. We attached rigid, low-drag buoys (15.2 × 33.0 cm) capable of 3.9 kg of buoyancy to each corner of the aquarium, giving the aquarium buoyancy while towed. The headrope was 9.8 m long with oblong floats placed every 0.3 m. The footrope was 10.4 m with an attached 6.35-mm galvanized chain. The side net height was 3.7 m for a maximum opening of 6 m measured from the middle of the footrope to middle of the headrope out of the water. We monitored the net with depth loggers (Onset, Bourne, Massachusetts; Model U20-001-02-Ti) at the mid-point of the headrope and footrope to determine whether the net was properly opened during each tow. Tows where net height (difference from top to bottom rope) was less than 1 m were discarded from our analysis. A set of buoyant trawl doors (106.7 × 50.8 cm) spread the net while allowing the net to fish at the surface. The net was bridled to the doors with 27 m of 12.7-mm braided line. The doors were attached to 9.5-mm cable and 91.4 m of cable tow warp was deployed.

Biological sampling.— We developed a sampling plan to account for the inability to count, measure, or sacrifice every individual captured in the trawl net due to time and permit limitations. The overall sampling goal was to maximize spatial coverage while working within the temporal limits of the tidal cycle (~6 h). In addition, sampling procedures were influenced by state and federal permitting meant to protect federally endangered species and NMFS species of concern including Alewife and Blueback Herring such that lethal sampling for river herring was not permitted in 2012 and was limited in 2013.

We identified all species caught using external morphological traits found in Colette and Klein-MacPhee (2002). For species other than Alewife and Blueback Herring, we counted, measured, and weighed each individual unless there were more than 30 captured in a tow. In instances where catch of individual species was greater than 30, we haphazardly sampled 30 from each species. For Alewife and Blueback Herring identification, we used morphological traits of relative eye diameter and body depth (Mullen et al. 1986; Loesch 1987). For each tow we visually grouped catches of Alewives and Blueback Herring by size; in June, July, and August we observed three groups, in other months only two. We measured TL of each individual in these groups unless there were more than 30. For groups with more than 30 individuals, we measured a random sample of 30 from each group. We counted each individual unless practical considerations (time limitations, potential for high mortality, etc.) limited our ability to do so when catches were too large (greater than ~500). In these instances (97/327 or 30% of grouped catches), we extracted a sample of 30, then weighed the total catch and released the individuals. We measured the weight (g) of each sample. When total count was not recorded, we divided sample weight by the number of individuals in a sample to derive an estimate of the average weight of an individual. We then extrapolated the total count by dividing total weight by the average weight of an individual.

We retained any dead Alewives and Blueback Herring specimens for otolith extractions in 2012. In 2013, when targeted sample sizes (roughly 10 individuals per 50-mm size bin) were insufficient using incidental mortalities alone, we lethally sampled specimens with an overdose of buffered tricaine methanesulfonate (MS-222) solution. All specimens were immediately frozen. Retained specimens were subsequently thawed, measured for TL (mm) and individually weighed. Identification to species of deceased individuals was accomplished by examination of peritoneum color, with pink to gray assumed to be Alewife and black assumed to be Blueback Herring (Loesch 1987).

For each sacrificed fish, sagittal otoliths were removed, dried, and placed in an individual sample container. Aging was accomplished by enumerating the number of annuli (dark bands) on the whole otolith as described by Casselman (1987) via examination through a binocular dissecting microscope under 30–40× magnifications and a

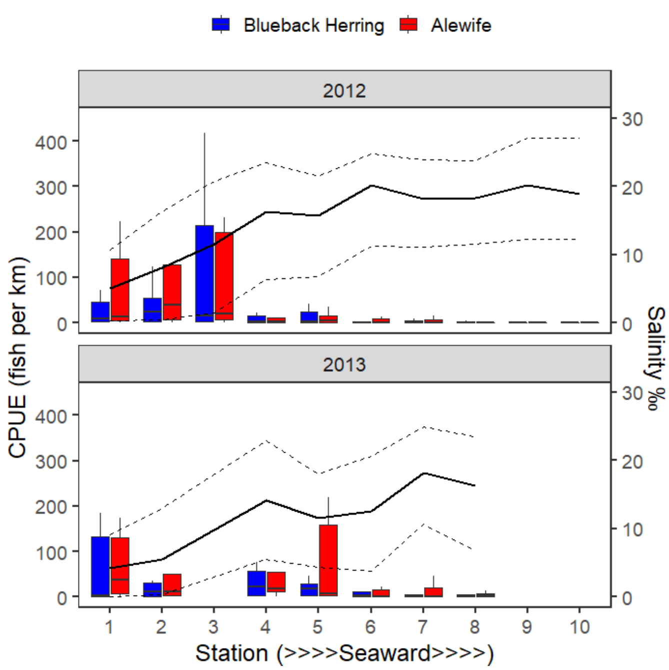

FIGURE 3. Boxplot of CPUE in (fish per km) for 2012 and 2013 surveys for Blueback Herring (blue) and Alewife (red) at trawl stations in the Penobscot River estuary. Boxes represent the interquartile range (from 25th to 75th quartile), horizontal lines represent the median, and the whisker length corresponds to ±1.5× the interquartile range. Values beyond the interquartile range are not displayed for clarity. The second *y*-axis depicts the mean (bold line), maximum, and minimum (dashed lines) surface salinity in parts per thousand (‰) taken at each station.

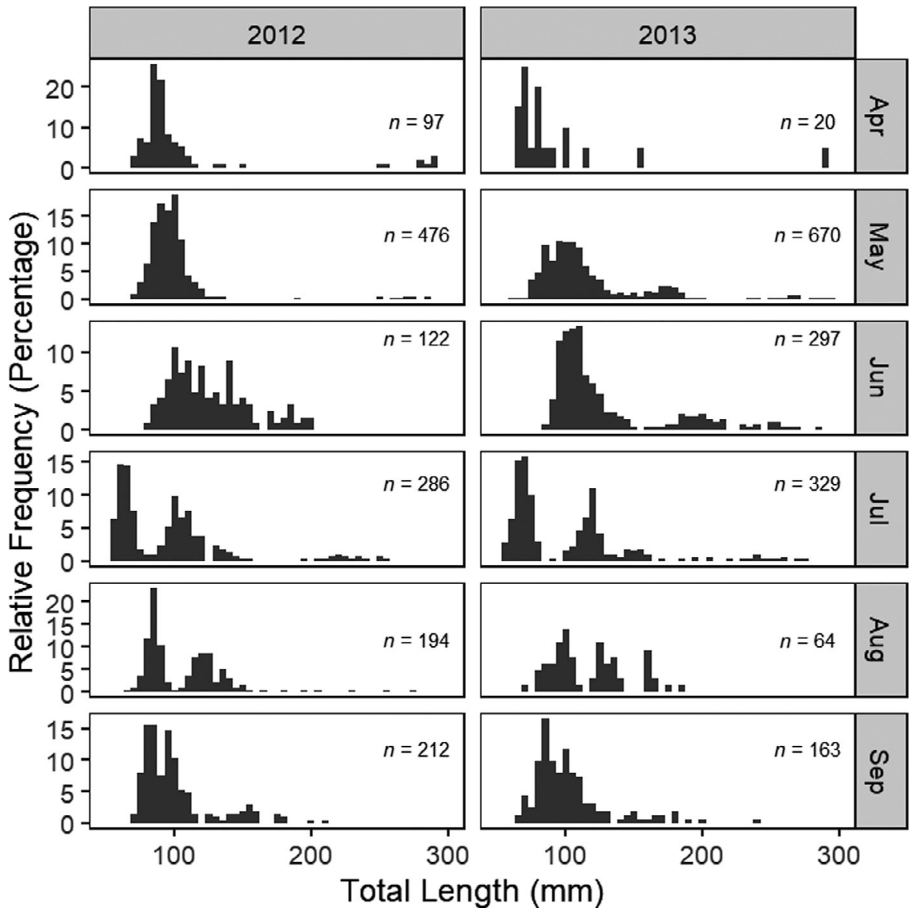

FIGURE 4. Relative length-frequency distributions and sample sizes using 10-mm bins for Alewives captured in 2012 and 2013 Penobscot River estuary trawl samples.

reflected light source. Ages were designated such that otoliths observed with no annulus were designated age 0, one annulus as age 1, and so on. The exception was for fish captured in April to June with no annulus observed. These were designated as age 1 because these species generally are not hatched until June in Maine and were assumed to be age 1 after January 1 capture (Havey 1961).

Data analysis.— We computed CPUE for each species as the number (counted or estimated) of fish caught per km towed for each station. We summarized abundance by summing the CPUE for Alewives, Blueback Herring, and all other species for all stations in a day. Because all fish captured were not weighed, we computed species biomass by performing a linear regression to predict mean weight from mean length (both log transformed) using 393 samples mostly from Alewives, Blueback Herring, Rainbow Smelt *Osmerus mordax*, and Atlantic Herring *Clupea harengus*. We used these parameters to convert the mean length to weight for species, size-class and station for all samples ($n = 1{,}223$) and multiplied this mean weight by the CPUE.

We developed length-frequency distributions by extrapolating the sample's length frequency to the total catch by 10-mm size bins. To accomplish this, we applied the scaling factor of the subsample proportion to total catch (count) for each species and size-class. This scaling factor was then applied to the length-frequency count (by species and size-class) to determine the number of each in 10-mm size bins in the catch.

We derived age–length keys for Alewives and Blueback Herring for each month in 2012 and 2013 in order to determine the proportion of catch at age using R with the package "FSA" (Ogle 2016). Specifically, we combined the length and age data in a multinomial logistic regression model to generate smoothed age–length keys and compute error for the age–length levels (age 0, age 1, etc.) for each month. When the model would not fit due to inadequate age data, we used the observed age–length key for 10-mm size bins. We applied smoothed probabilities of age or observed age for each 10-mm length bin to the trawl length frequency samples for each month and year

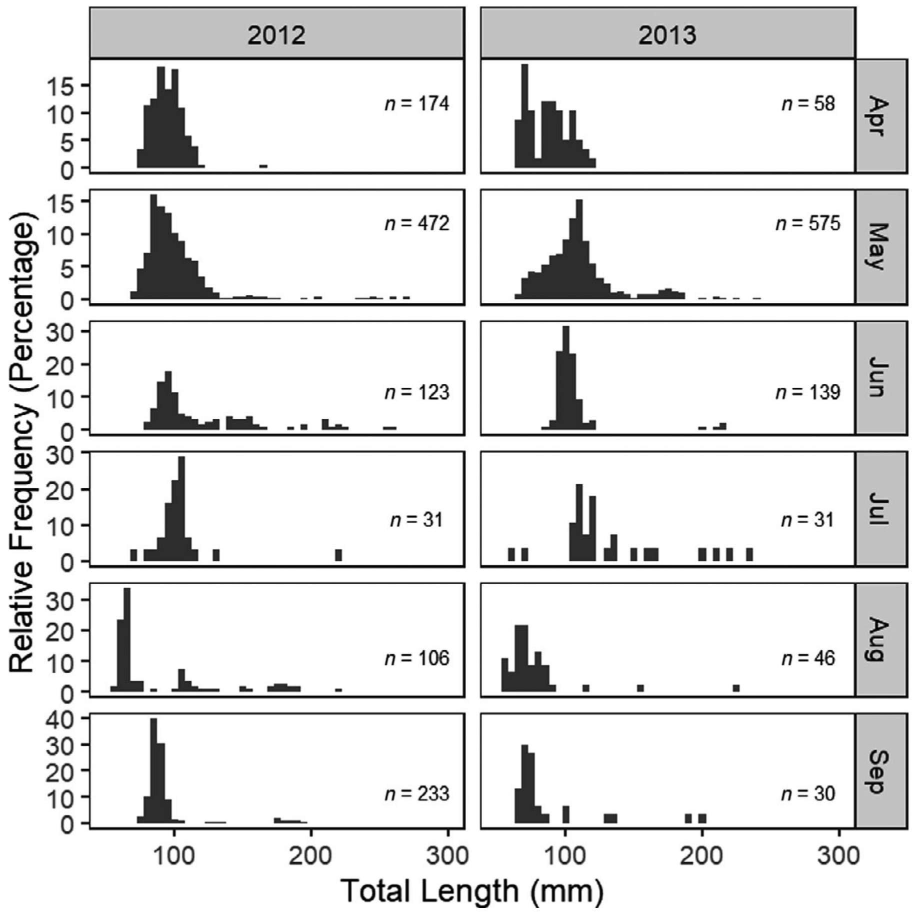

FIGURE 5. Relative length-frequency distributions and sample sizes using 10-mm bins for Blueback Herring captured in 2012 and 2013 Penobscot River estuary trawl samples.

for each species to generate age-proportioned length frequencies as described by Ogle (2016). We computed the proportion of catch at age for each month and species in 2012 and 2013 by applying these age–length frequencies to the trawl catch data.

All statistical and graphical analyses were conducted in RStudio version 1.0.15, R version 3.5.1 (R Foundation for Statistical Computing, Vienna).

RESULTS

Species Determination

A total of 504 specimens were preserved for otolith extraction in the laboratory. These specimens were vouchered with a label of date, tow, and species identified by morphology allowing for the comparison. We identified 347 Alewives using morphology and 342 using peritoneum with 7 (2%) misidentifications. We identified 157 Blueback Herring using morphology and 162 using peritoneum with 2 (1%) misidentifications.

Abundance and Biomass

Alewives and Blueback Herring were common in trawl catches for both years. We caught Alewives in 60 of 95 (63%) trawls in 2012 and 65 of 81 (80%) trawls in 2013. We caught Blueback Herring in 69 of 95 (73%) trawls in 2012 and 67 of 81 (83%) trawls in 2013. Alewives and Blueback Herring were prominent species in trawl catches for both years but varied seasonally and by species. In 2012, Alewives and Blueback Herring combined represented 36% of the roughly 49,000 fish captured in 2012 and 51% of the roughly 40,000 in 2013. We also captured 12 other species, mainly Atlantic Herring and Rainbow Smelt (summarized by Lipsky et al. 2019).

In 2012, we identified 62% of river herring as Alewives and the remaining 38% as Blueback Herring. In 2013, we identified 66% of river herring as Alewives and the remaining 34% as Blueback Herring. The proportion of river herring in the daily catch varied by sample day from 4% to 80% in 2012 and from 3% to 95% in 2013. The proportion of Alewives in the daily river herring catch was 19% to 96% per day in 2012 and 17% to 98% in 2013

(Figure 2). In both years, the catch of Alewives was greater than Blueback Herring in late May, June, and July with Blueback Herring more frequently caught in April, early May, August, and September catches.

Alewife CPUE ranged from 0 to 6,241 in 2012 and 0 to 10,646 in 2013 (Figure 3). Blueback Herring CPUE varied from 0 to 2,277 in 2012 and 0 to 7,371 in 2013. We observed variable surface salinity within and among trawl stations. Generally, salinity increased from upstream to downstream in the study area with the northernmost station ranging 0‰ to 11‰ and the southernmost station ranged from 13‰ to 27‰ (Figure 3). The greatest CPUE of Alewives and Blueback Herring were found at salinities less than 12‰.

The linear regression analysis found mean length (log transformed) was a significant predictor of mean weight (log transformed; ANOVA: $F = 5018$; df = 391; $P < 0.001$; $R^2 = 0.928$). Estimated parameters (from equation form $y = bx + a$) of $b = 3.140$ (SE = 0.044) and $a = -5.431$ (SE = 0.090) were used for calculating total biomass per tow.

Alewives and Blueback Herring were a large component of total biomass in both years but varied seasonally and by species. Alewives and Blueback Herring comprised 43% of the total biomass measured in 2012 and 65% in 2013. The proportion of river herring biomass by sample day ranged from 8% to 65% in 2012 and 11% to 93% in 2013 (Figure 2). Biomass of Blueback Herring was generally lower than Alewife within sample days during both years with seasonal patterns of greater Blueback Herring biomass (compared to Alewife) in April and early May of both years and September 2012 (Figure 2).

Size Distributions

Alewives captured by trawling exhibited a wide range of lengths ranging from 51 to 300 mm TL in 2012 and 50 to 320 mm TL in 2013 (Figure 4). Lengths of Blueback Herring ranged from 57 to 270 mm TL in 2012 and 45 to 240 mm TL in 2013 (Figure 5). The monthly length-frequency distributions were multimodal for both species in most months, although lower frequency modes were difficult to visualize for Blueback Herring and in April, May, and September for Alewives. Both species exhibited a mode near 100 mm TL in April, May, and June. A mode of smaller fish became evident in July for Alewives and in August for Blueback Herring.

Length and Catch at Age

We used sagittal otoliths to determine the age for 79 Alewives and 30 Blueback Herring in 2012 and 245 Alewives and 108 Blueback Herring in 2013 (Figure 6). We developed monthly age–length keys for each species in 2012 and 2013 except for July 2012 due to insufficient age

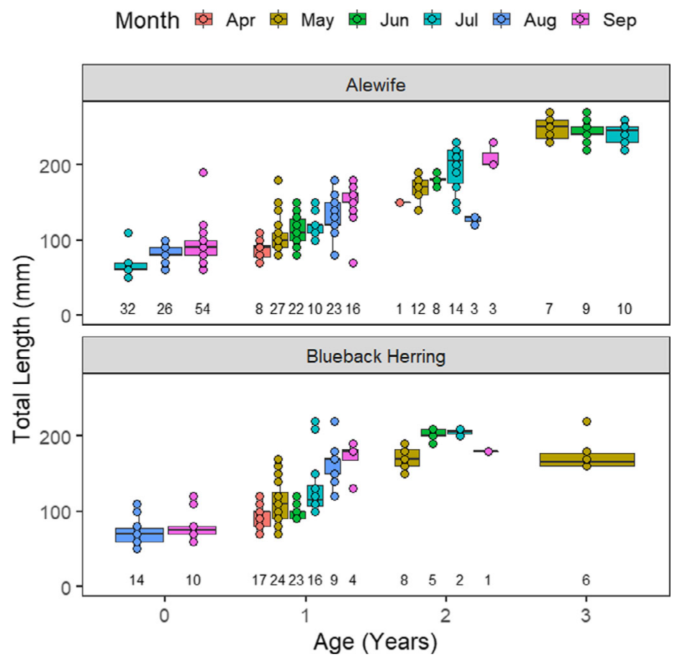

FIGURE 6. Boxplot and values of lengths and ages of Alewives (top) and Blueback Herring (bottom) used in this study for building age–length keys and estimating proportions of catch at age in monthly Penobscot River estuary trawl sampling. Note that plots include data for 2012 and 2013 combined for visualization but were used separately in determining age–length keys; sample sizes are denoted for each age-month on the *x*-axis.

samples (Figures 7, 8). Alewife samples were predominately age 1 in April, May, and June in 2012 and 2013. Alewife samples were predominately age 0 in August 2012 and July and August 2013. Age-2 and older Alewives were less than 20% of the age samples in all months and years. The oldest Alewives were age 6 captured in May 2013, and the oldest Blueback Herring were age 3 captured in May 2013.

Alewives in April through June less than 140 mm TL were age 1 in both years (Figure 7). Alewives between 140 and 190 mm TL were age 1 and age 2 with all individuals over 190 mm TL age 2 or older. Alewives in July through September less than 70 mm TL were age 0. In July through September, there was overlap in length for age-0, age-1 and age-2 Alewives between 100 and 130 mm TL, Alewives 130–190 mm TL were age 1 or age 2, and all Alewives over 190 mm TL were age 2 or older.

All Blueback Herring in April through June less than 150 mm TL were age 1 in both years (Figure 8). Blueback Herring between 150 and 190 mm TL were age 1, age 2 and age 3 with all individuals over 190 mm TL age 2 or older. In August and September, Blueback Herring less than 120 mm TL were age 0; age-0 and age-1 fish only overlapped for 120–130 mm TL. Blueback Herring 130 to 180 mm TL were age 1 with fish over 180 mm TL classified as age 1 and age 2.

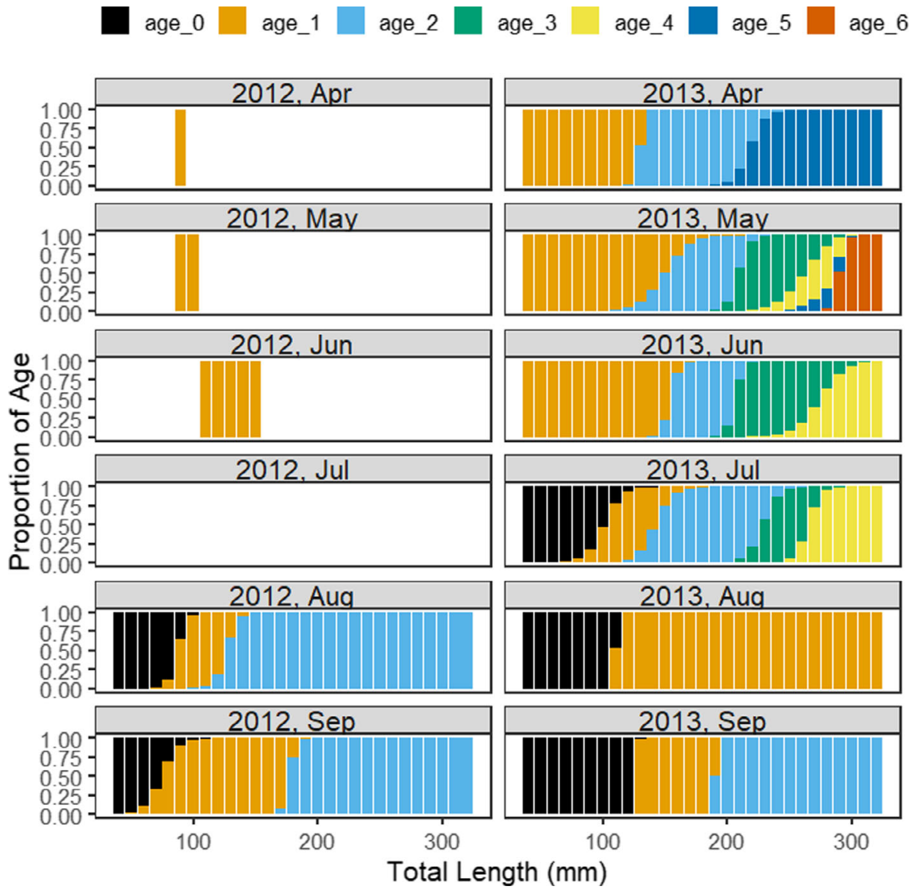

FIGURE 7. Colored bars represent proportion of age-classes for 10-mm TL bins derived from multinomial regression (August and September 2012 and all months of 2013) and observed April, May, June, and 2012) length-at-age data from Alewife otolith samples collected from the Penobscot River estuary.

Some otoliths we examined did not have any clear annuli (suggesting age 0) although they were caught in the spring and prior to the spawning season and were the same size (<150 mm TL) of other individuals identified as age 1. This was seen only for Blueback Herring and occurred for 2 of 8 (25%) individuals in 2012 and 10 of 25 (40%) individuals in 2013.

We applied the proportion of monthly age–length keys to the catch for each month and species in 2012 and 2013. Age-1 Alewives and Blueback Herring were the majority (>95%) of catch in April, May, and June of 2012 and 2013 but were found in each month and year sampled (Figure 9). The age distribution shifted to mainly age 0 in July for Alewives and August for Blueback Herring in both years, however age-1 fish of both species were present in all months.

DISCUSSION

Our results demonstrate that age-1 and age-2 river herring used relatively fresh components of the Penobscot River estuary from April through September in both years of our study. Indeed, age-1 river herring were a consistent component (and often the majority proportion) of the abundance and biomass of all fishes captured in trawl surveys. The somewhat surprising prevalence of age-1 and age-2 river herring in our study may result from emigration occurring over a range of ages and seasons, a form of semi-anadromy, migration from the ocean, or some other mechanism. Either way, these results provide direct evidence of life cycle diversity in river herring populations in this system. Life cycle diversity is increasingly recognized as providing a key buffer against environmental stochasticity in many diadromous species (McDowall 2009; Secor and Kerr 2009).

Our direct observations of life cycle diversity of river herring complement studies that similarly demonstrated life cycle diversity including prolonged and recurrent use of freshwater inferred from otolith microchemistry for age-0 river herring (e.g., Gahagan et al. 2012; Payne Wynne et al. 2015) and repeated migrations of adult Alewives during a single spawning season (McCartin et al. 2019).

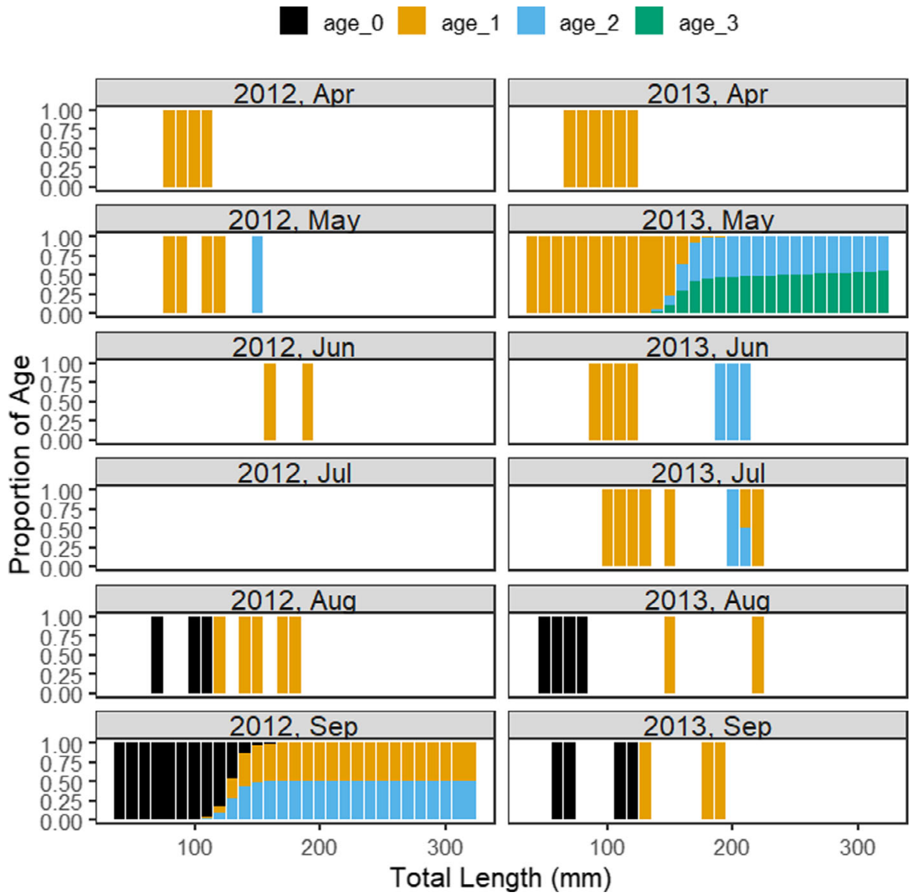

FIGURE 8. Colored bars represent proportion of age-classes for 10-mm TL bins derived from multinomial regression (September 2012 and May 2013) and observed (remaining months) length-at-age data from Blueback Herring otolith samples collected from the Penobscot River estuary.

Several forms of life cycle diversity in river herring require connectivity among freshwater, estuarine, and marine environments. Limburg and Turner (2016) refer to these as "nontextbook" migrations, inferring that they do not follow the expected pattern described in textbooks. The "classical" pattern is for river herring to emigrate at age 0 from a river to an estuary during summer and then to migrate to the ocean by the end of the summer (Fay et al. 1983). It is presently unknown how widespread nontextbook migrations are or how widespread they might be if barriers to migration (i.e., dams) did not constrain them. In our example, upstream migration of age-1 and age-2 river herring would be curtailed by a dam at the head of tide. Further work to assess the extent of freshwater migration by subadult river herring would be valuable to begin to evaluate the importance of this component of their life cycle diversity in the Penobscot River.

Our results also suggest that the roles that river herring play at the freshwater–marine interface may be even more important and extensive than previously thought. Our findings are suggestive of prolonged use of estuarine mixing zones by age-1 and age-2 river herring where they are presumably consuming nekton and providing forage for estuarine piscivores, among other ecological services. In freshwater environments, river herring are reasonably well established as keystone species with adult life stages serving as sources of marine-derived nutrients to freshwater systems (MacAvoy et al. 2009; Walters et al. 2009) and age-0 fish acting as nutrient exporters (West et al. 2010). In the marine environment, the ecological role of river herring as forage for commercially important species (McDermott et al. 2015) including cod (Ames 2004) and Striped Bass *Morone saxatilis* (Walter and Austin 2003) is also well established. However, further investigation into the degree that age-1 and age-2 river herring provide similar ecological services in mixing zones of estuaries seems warranted. Diet studies suggest that food items for juvenile river herring are pelagic and benthic zooplankton in estuaries (e.g., Stone and Daborn 1987). Applying those data into ecosystem energetics modeling (e.g., Ecopath analysis) would be informative research on the ecosystem services that juvenile river herring provide for estuaries.

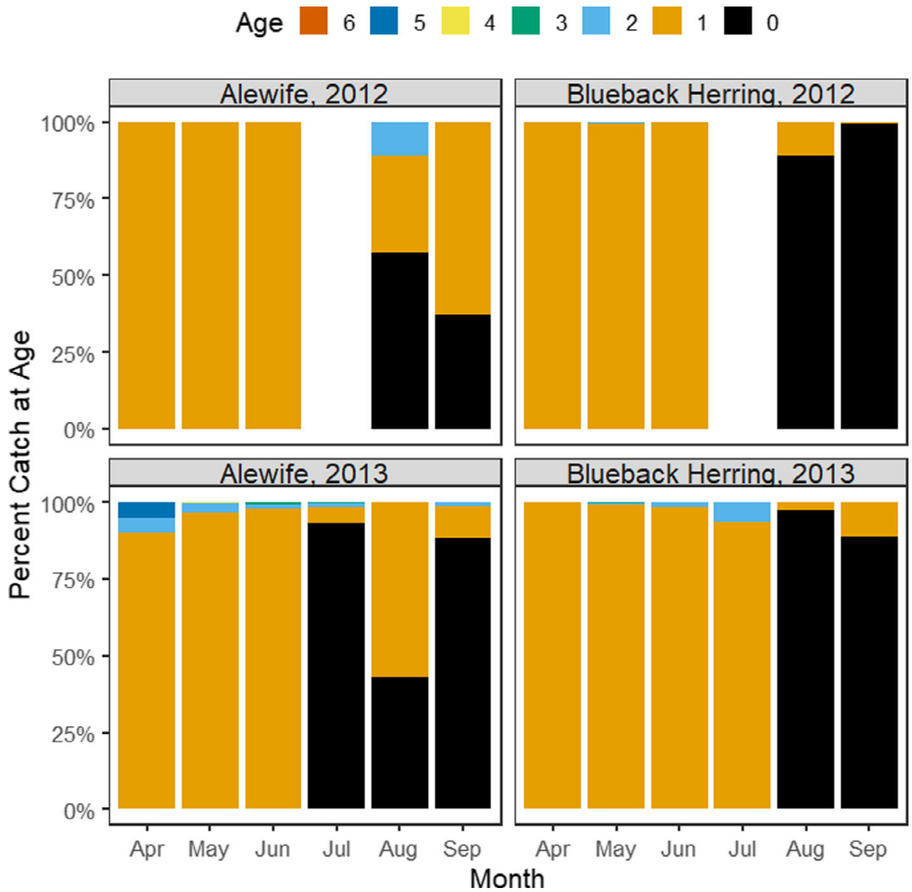

FIGURE 9. Percentage of catch by age and by month for Alewives and Blueback Herring captured in 2012 and 2013 Penobscot River estuary trawl samples. Note that no proportions were calculated for July 2012 due to lack of age data. Blueback Herring ages ranged from age 0 to age 3, and Alewives ranged from age 0 to age 6.

Our results address some research needs identified by the Atlantic States Marine Fisheries Commission and NMFS including the accuracy of nonlethal species identification methods, and the size, age, growth, and spatial distribution of juveniles (ASMFC 2012; NMFS 2019). First, we were able to estimate ages of juvenile Alewives and Blueback Herring as age 1 and age 2 using otoliths. There are currently no validated methods to estimate age and growth for Alewives and Blueback Herring, and we acknowledge that more research into aging juvenile and adult river herring using otoliths is essential for confirming the accuracy of ages (Campana 2001). Although aging river herring adults can have high discrepancy, otoliths are the preferred aging structure over scales (ASMFC 2014). The Atlantic States Marine Fisheries Commission (2014) found that bias and precision may be higher in older fish but suggested more work on aging younger fish is needed to ensure consistency across researchers and managing agencies. We acknowledge that small samples were collected for some age-classes in some months; however, permitting limitations and low catches prevented collecting more samples. Given both precision uncertainty and sample size limitations, we have limited the interpretation of our results to the observation that age-1 and age-2 river herring are present in hopes that this will shed light upon research gaps and highlight the need for continued research. The second research gap our study sought to address was species identification using external morphology. We correctly classified each river herring species 98% of the time using external morphology. Although our results indicate that external morphology can be a reliable methodology, we recommend continued diligence in sampling procedures to ensure that the rates and patterns of species misidentification can be estimated. Further, monitoring for occurrence of hybridization through more variable peritoneal coloration may be necessary in sympatric populations (Berlinsky et al. 2015; Kan et al. 2017).

Our findings also provide insight into juvenile growth patterns of both species. We observed an apparent seasonal increase in length-frequency modes for both species in both years. Estimated median lengths of age-1 Blueback Herring suggested considerable growth over the summer, with median size increasing from 94 mm TL in April to 184 mm TL in September (Figure 6). Similarly, age-1 Alewife median lengths changed from 100 mm TL in April to 154 mm TL in September (Figure 6). Age-0 fish were 80 mm TL (Blueback Herring) and 97 mm TL (Alewife) in September of each year, suggesting that little growth occurred during the fall and winter period for these fish. However, sampling during the winter is needed to validate this pattern. Growth parameters are rare in literature as most studies focus on adult migration (e.g., Walton 1983). Our findings roughly correlate with trawl surveys by NMFS and the state of Maine that indicate age-1 Blueback Herring and Alewives are approximately 100 mm TL in spring in offshore and inshore Gulf of Maine marine habitats (Munroe 2000; ASMFC 2012; Sherman et al. 2015).

Some of our findings were somewhat surprising, and we suggest that they may offer several opportunities for future research. First, our catch rates of juvenile Alewives and Blueback Herring were consistently high even though we used surface-oriented trawl gear during daylight in the Penobscot River estuary. This is somewhat contradictory to the limited literature on the diel and vertical distribution of juvenile river herring (e.g., Stone and Jessop 1994). However, Stone and Daborn (1987) successfully collected river herring via drift gill net in the daytime in a turbid estuary in Canada. If river herring in our study were negatively phototropic as suggested in other studies, it is possible that catch rates in the Penobscot River estuary may be even higher at night. In addition, catch rates of age-1 and age-2 river herring were surprisingly high, but our sampling regime was limited temporally to April through September, leaving the question of habitat use in winter unanswered. Finally, our results contribute to the growing understanding of life cycle diversity in river herring, but do not directly address the length of time that any individual spends in the estuary. Answers to these questions will require the application of novel technologies (stable isotopes, microchemical analysis, etc.) in the future.

In conclusion, our results clearly demonstrate that age-1 and age-2 river herring were using the Penobscot River estuary from April to September. This supports the building volume of evidence that Alewives and Blueback Herring exhibit substantial life cycle diversity and such nontextbook migrations appear to be more common than previously thought (Limburg and Turner 2016), potentially contributing to their resilience (Waldman et al. 2016). Further, their role in the ecology of the coastal estuary ecosystem may be more complex than previously thought using traditional life history descriptions. Given the challenges to conserve these species and their habitats across their range, it seems prudent to consider revising the "textbook" to expand our understanding and better appreciate the ecological and evolutionary processes of these imperiled species.

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