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Acoustic telemetry captures the full annual migration of alewife between Chesapeake Bay and the Gulf of Maine

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ABSTRACT: Anadromous fish are declining at a global scale, and a more holistic approach to management is needed that addresses threats across their freshwater, estuarine, and ocean habitats. In this study, we used acoustic telemetry to track adult alewife *Alosa pseudoharengus* in Chesapeake Bay, USA, to evaluate, for the first time, habitat use throughout the entire annual migration cycle. Fifty adult alewife were tagged in the Choptank River, Maryland, in spring 2022, and detection data were obtained via collaborative acoustic telemetry networks along the Eastern Seaboard of the USA and Canada. Water temperature data were also collected using data loggers in the Choptank River and from satellite measurements of sea surface temperature in Chesapeake Bay and the ocean. In total, 48 tags (96%) were detected at least once, 14 tagged fish (28%) were detected in the ocean migrating north to the Gulf of Maine and Bay of Fundy, and 5 tagged fish (10%) returned to the Choptank River in spring 2023. With few exceptions, tagged fish were detected at temperatures of 7–16°C across all habitats (river to ocean and back). Alewife made extensive use of tidal and non-tidal portions of the Choptank River during spring, migrated to summer habitats that are experiencing rapid warming, and passed through areas of high incidental catch on both the outgoing and return migration. This study highlights how acoustic telemetry can refine our understanding of river-specific migrations of anadromous fish and the management implications of their movements in regions with collaborative acoustic telemetry networks.

KEY WORDS: Anadromous fish · *Alosa pseudoharengus* · Acoustic telemetry · Connectivity · Phenology · Temperature

1. INTRODUCTION

Anadromous fish, which migrate between natal freshwater habitats and the ocean to complete their life cycle, are ecologically, culturally, and economically important, but are declining at a global scale (Gresh et al. 2000, Limburg & Waldman 2009, Dudgeon 2011). Their reproductive success depends on habitats and resources spread across freshwater, estuarine, and ocean ecosystems, but migration also makes them vulnerable to human activities taking place in these ecosystems, presenting unique challenges for fisheries management and conservation (Saunders et al. 2006). Traditional fisheries management approaches such as harvest restrictions and stock enhancement have had limited success at recovering anadromous fish populations, and more holistic approaches addressing threats across the watershed–ocean continuum are gaining attention (Hare et al. 2021, Ouellet et al. 2022). Understanding

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the full range of habitats and threats encountered by anadromous fishes is a critical step to developing holistic management approaches.

The alewife *Alosa pseudoharengus* exemplifies the challenges that face anadromous fish. They spawn in freshwater systems from Florida, USA, to Newfoundland, Canada, at temperatures ranging from 8–16°C, with spawning runs beginning as early as January at the southern end of the range and as late as June further north (Saila et al. 1972, Richkus 1974, Rosset et al. 2017, Lombardo et al. 2020, Legett et al. 2021). While US fisheries for alewife are mostly under moratoria, abundances are at historic lows due to past overfishing (ASMFC 2017), current incidental take in ocean fisheries (Reid et al. 2023), dams (Hall et al. 2011), and climate change (Hare et al. 2016), with many populations at <2% from their peaks (ASMFC 2017). Declines in alewife populations and the resulting losses in connectivity among freshwater, estuarine, and ocean habitats have substantially reduced the productivity of coastal ecosystems (Hall et al. 2012, Dias et al. 2019). However, a lack of detailed information on the annual migration cycle of alewife from individual rivers limits our ability to understand incidental take on river-specific stocks (Reid et al. 2023), evaluate the impacts of marine heat waves in the northwest Atlantic (Schlegel et al. 2021), or predict the outcomes of restoring connectivity, habitats, and populations.

The development of continental-scale acoustic telemetry networks makes it possible to track migrations of coastal migratory fish across large spatial and temporal scales (Bangley et al. 2020). Here, we use passive acoustic telemetry to (1) track the full annual migration cycle of alewife tagged in the Choptank River, Maryland, USA, a tributary of Chesapeake Bay, and (2) characterize the range of water temperatures potentially experienced by migrating alewife.

2. MATERIALS AND METHODS

2.1. Study site

The Choptank River is a coastal plain stream on the Eastern Shore of Chesapeake Bay in Maryland and Delaware, USA (Fig. 1). An array of 7 Innovasea (Bedford, Nova Scotia, Canada) VR2W (69 kHz) acoustic telemetry receivers was deployed in the river spanning the tidal and non-tidal portions. Water temperature was measured hourly using pendant temperature loggers (HOBO UA-003-64, Onset; accuracy: ±0.53°C) deployed in 30 cm sections of PVC pipe anchored next to the acoustic telemetry receivers. These temperature measurements were conducted following US Geological Survey standard operation procedures (Heck et al. 2018). Receivers and temperature loggers were deployed from 9 Feb 2022 to 13 June 2022 and from 13 Dec 2022 to 25 May 2023, corresponding to the timing of alewife presence in the Chesapeake Bay watershed.

2.2. Tagging

Adult alewife were captured in the mainstem Choptank River during the spring 2022 spawning run and tagged within the acoustic array at Greensboro Christian Park (between the Greensboro Christian Park and Greensboro Ramp acoustic receiver locations), near the upper end of the tidal portion of the river (Fig. 1). Innovasea V7-4L coded 69 kHz tags (7 mm diameter, 21.5 mm length, 1.8 g in air, 0.9 g in water) were used, which were set to transmit at low power with a random delay of 130–230 s (estimated tag life: 388 d). Alewife were captured using boat electrofishing, with electrofishing passes only conducted long enough to capture groups of fish to tag and not exceeding 600 s. Before tagging, captured fish were held in a live well with ambient water and aeration. Fish not used for tagging were immediately placed in a floating holding pen with a volume of approximately 1 m^3. For tagged fish, fork length and total length were measured (to the nearest 1 mm), and sex was determined by gently squeezing and noting the appearance of milt or eggs. During tagging, fish were then held ventral side up in a U-shaped tagging apparatus with ambient water flowing over the gills. A small (about 1 cm) vertical incision was made in the left ventral side of the abdomen posterior of the pectoral fin. A tag, sterilized by immersion in 95% ethanol and dried on a 12-ply 10 × 10 cm sterile gauze bandage, was inserted into the body cavity. The incision was closed with one simple interrupted suture using a 4-0 Vicryl suture incorporating a 26 mm half-circle tapered needle (J415; Ethicon). The fish was then placed into a recovery bin of ambient water with aeration. After resuming normal swimming, it was then transferred to the holding pen. When tagging was completed for a batch of fish, tagged fish were released in groups that also contained some untagged fish with the aim of enabling schooling behavior as well as reducing per capita predation risk that may increase survival (e.g. Furey et al. 2016). Alewife capture and tagging were conducted under Smithsonian Institution animal care and use proposal number SI-22005.

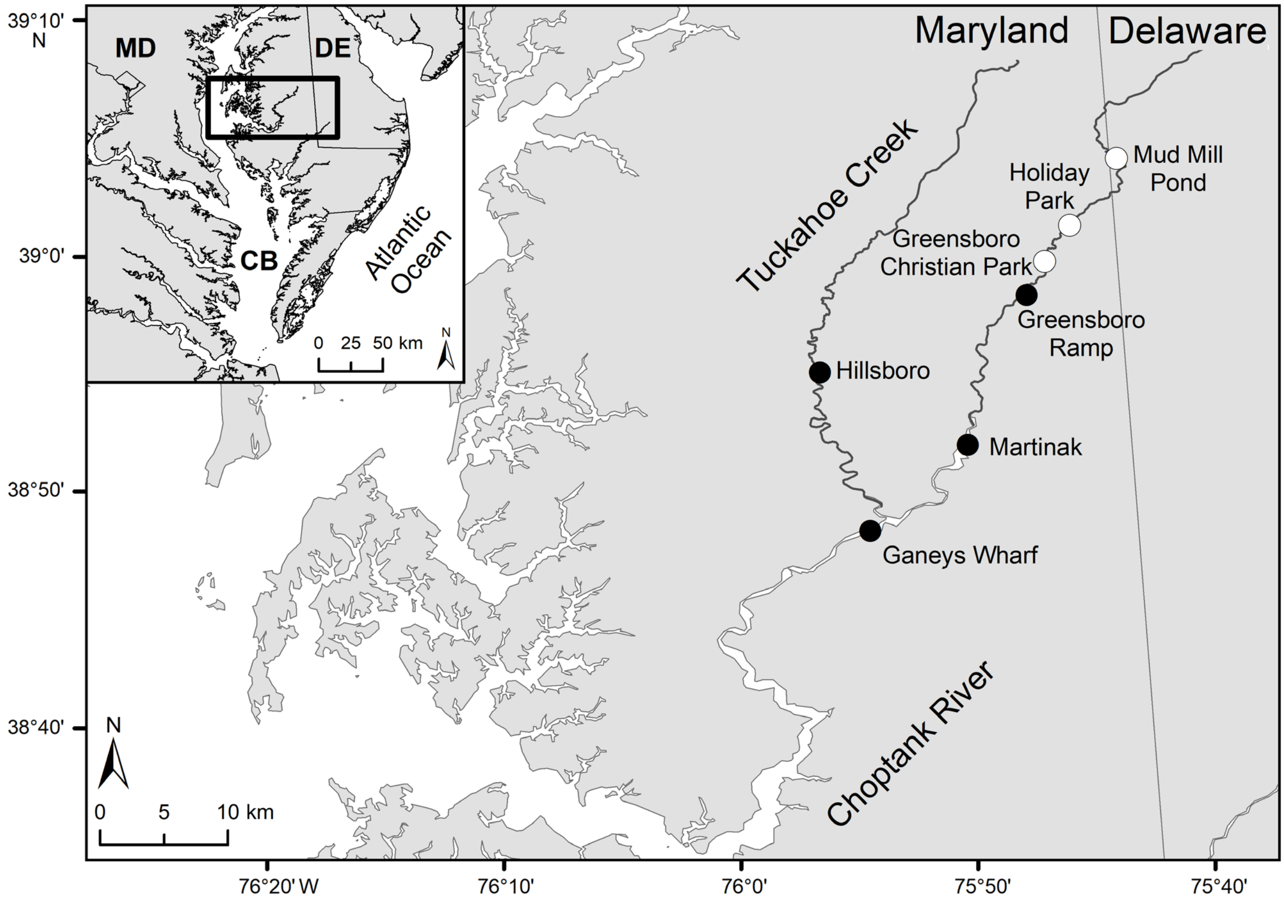

Fig. 1. Tagging location and acoustic receiver array in the Choptank River, Maryland. Inset locations are Maryland (MD), Delaware (DE), and Chesapeake Bay (CB). Acoustic receivers and temperature loggers were co-located in tidal (closed circles) and non-tidal (open circles) sites. Alewife *Alosa pseudoharengus* were captured, tagged, and released between the Greensboro Christian Park and Greensboro Ramp sites

2.3. Telemetry data

Acoustic tag detections were obtained from multiple acoustic receiver arrays. An Innovasea VR-100 unit with an omnidirectional hydrophone was used to confirm tags were operating prior to insertion. During the 2022 and 2023 spawning seasons, fish were detected on the Choptank River array deployed for the project (Fig. 1). Fish were detected exiting and then returning to the Chesapeake Bay through a collaborative Chesapeake Bay telemetry array effort on receivers attached to National Oceanic and Atmospheric Administration (NOAA) Chesapeake Bay Interpretive Buoy System buoys and the Chesapeake backbone telemetry array coordinated by NOAA Chesapeake Bay Office, Maryland Department of Natural Resources, University of Maryland Center for Environmental Science, and Virginia Marine Resources Commission. All other detections were obtained opportunistically from arrays deployed by members of the Atlantic Cooperative Telemetry (ACT) Network and the Ocean Tracking Network (see Fig. 3).

2.4. Water temperature

To characterize water temperatures potentially experienced by alewife, daily mean water temperature was calculated at the location of each acoustic tag detection. Within the Choptank River, hourly measurements of sub-surface water temperature were downloaded from the HOBO loggers. In the Chesapeake Bay and the ocean, daily sea surface temperatures were obtained from data servers in the Environmental Research Division's Data Access Program (ERDDAP), within the NOAA CoastWatch Program (https://coastwatch.noaa.gov/erddap/index.html). Sea surface temperature estimates at a 0.054° resolution were produced using multi-satellite data sets from the NOAA National Environmental Satellite, Data, and Information Service (NESDIS; https://www.nesdis.noaa.gov/), analyzed and published by the Group for High Resolution Sea Surface Temperature (GHRSST; https://www.ghrsst.org/; Fieguth et al. 1998, Fieguth 2001, Khellah et al. 2005).

2.5. Data analyses

Water temperatures measured during the alewife migration between years and among habitats were compared using independent *t*-tests. For tag detections within the Choptank River, daily mean subsurface water temperatures were compared between the 2022 and 2023 spawning seasons. For tag detections outside of the Choptank River, daily mean sea surface temperatures were compared between the northward migration from the Chesapeake Bay to ocean habitats in the Gulf of Maine (April through October 2022) and the southward migration from ocean habitats back to the Chesapeake Bay (November through February 2023). For these tests, a significance level was set at $\alpha = 0.05$. Analyses were conducted in R v.4.0.3 (R Core Team 2020).

3. RESULTS

3.1. Tag detections

A total of 50 adult alewife (247–311 mm total length; 25 each of males and females) were tagged in the Choptank River during the 2022 spawning season from 3–21 March. Following the release of fish, 48 tags (96% of total) were detected at least once by an acoustic receiver in the river, while 23 tags (46%) were detected at least once outside of the river in the Chesapeake Bay or ocean (Figs. 2 & 3), with no obvious differences among males and females. Tags were detected in the mainstem of the Choptank River, as far upstream as near the Maryland–Delaware border. After tagging, the detected fish moved further downstream before leaving the river; however, 8 tagged individuals returned further upstream again later in the 2022 spawning season. One tag was also detected in Tuckahoe Creek, the other major branch of the Choptank River, on 17 March 2022 and 6 April 2022. The last within-river detection during the 2022 spawning season occurred on 15 April.

After leaving the Choptank River, the alewife migrated south through Chesapeake Bay and then north to the Gulf of Maine. From April through early May 2022, 14 tags (28% of total) were detected at least once in the mainstem of the Chesapeake Bay, and 1 tag was detected at the mouth of the Bay on 17 April 2022 (Fig. 3). While most Chesapeake Bay detections occurred by early May 2022, 1 tag was detected on 19 May 2022 near the mouth of the Patuxent River and another was detected on 23 May in the mouth of the Potomac River. From May through October 2022, 14 tags (28%) were detected at least once along the North Atlantic coast from the mouth of Delaware Bay to the Gulf of Maine. Detections in the Gulf of Maine included 4 tags detected from 18–23 June 2022 along the southern edge of Georges Bank (2–9 detections per tag), 1 tag detected 77 times over 10 h on 2 August in the Jordan Basin, and 1 tag detected 126 times from 20–30 August 2022 across 5 receivers in the Bay of Fundy as far north as Musquash Harbor before being detected 22 times on 9–10 October 2022 in the Jordan Basin. Six tagged alewife were detected in the ocean on both the northward and southward migrations (Fig. 2).

Tagged alewife began their return migration south in late November. From 20 November 2022 to 2 February 2023, 10 tags (20%) were detected at least once from the Gulf of Maine to Delaware Bay, with detections typically occurring along the coast rather than on the continental shelf (Fig. 3). Alewife entered Chesapeake Bay in late January to early February 2023, with 1 tag detected in the mainstem of the Chesapeake Bay from 25–27 January 2023 and another tag detected at the mouth of the Chesapeake Bay on 10 February 2023. Finally, the alewife completed their migration cycle with 5 tags (10%; 2 males and 3 females) detected at least once in the Choptank River from 19 February 2023 through 14 April 2023. Tags were detected in both the tidal and non-tidal mainstem as far upstream as Greensboro Christian Park. For each of the 5 returning tagged individuals, only a single trip upstream and then back downstream was detected. One tag was detected in Tuckahoe Creek on 21 February 2023 and again on 6 April 2023. This was a different tag than the one detected in Tuckahoe Creek during the 2022 spawning season.

3.2. Comparison of tag detections and water temperature

In the Choptank River, tags were detected at water temperatures ranging from 5.9–20.8°C. The mean daily water temperature was 12.0 ± 2.5°C for detections during the 2022 spawning season, and 11.7 ± 3.7°C during the 2023 season ($t_{46} = 0.50$, p = 0.619; Fig. 4A,B). In the Chesapeake Bay and ocean, tags

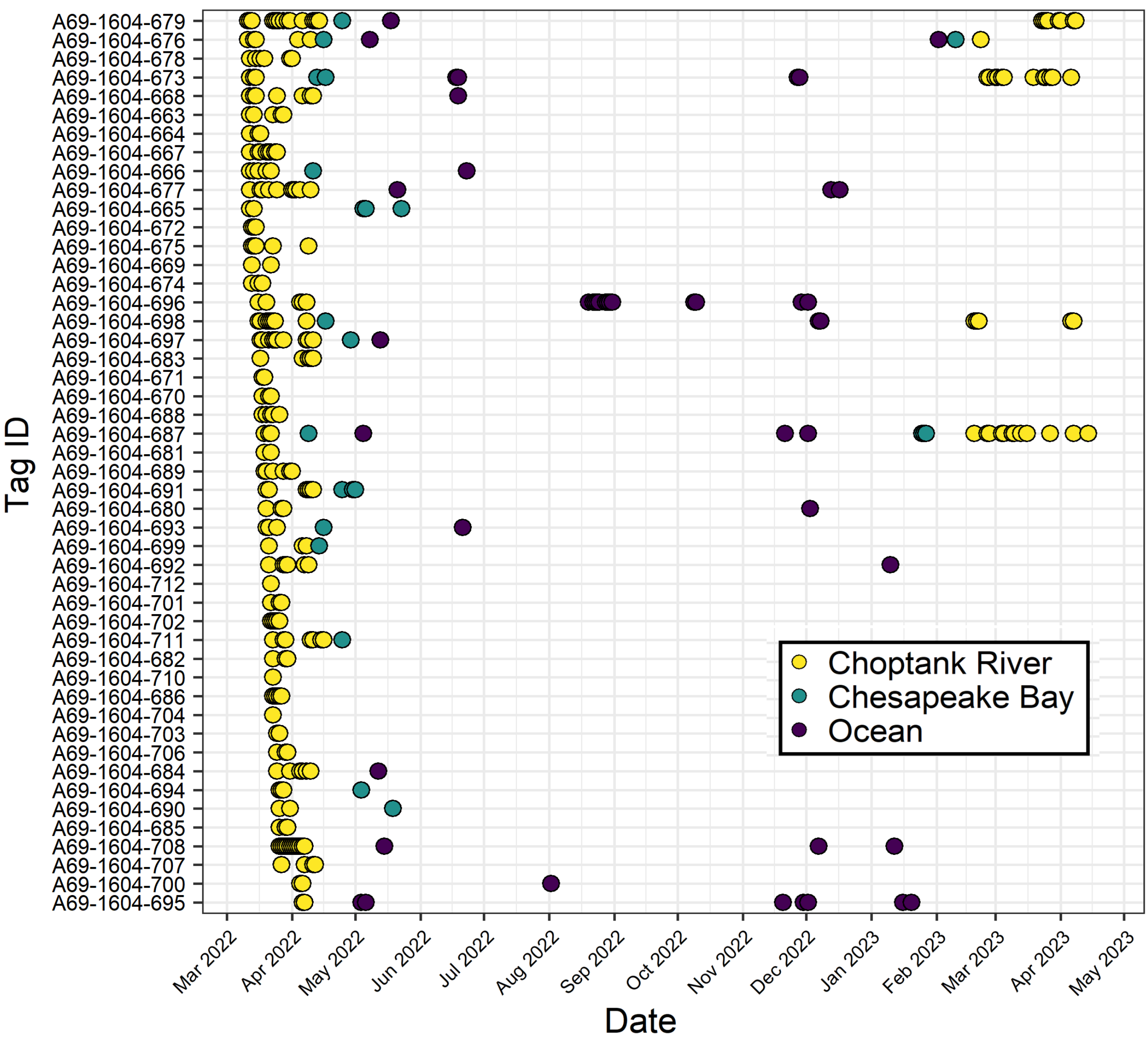

Fig. 2. Abacus plot of 48 tagged alewife *Alosa pseudoharengus* detected over the study period (each tag ID is 1 individual), with colors representing detections in the Choptank River, Chesapeake Bay mainstem, or ocean habitats (defined as any tag detection location outside of Chesapeake Bay). Detections for each individual are summarized as 1 point per day per location

were detected at sea surface temperatures ranging from 5.5–21.5°C. During the northward migration, the mean daily sea surface temperature at the location of detection was 13.5 ± 2.5°C (Fig. 4C). In comparison, during the southward migration, the mean daily sea surface temperature at the location of detection was significantly colder, at 8.6 ± 2.1°C (t_{51} = 9.50, $p < 0.001$; Fig. 4D). On 23 May 2022, 1 tag was detected for the last time at the mouth of the Potomac River at 21.5°C, and on 6 April 2023 1 tag was detected in the Tuckahoe Creek branch of the Choptank River at 20.8°C.

4. DISCUSSION

4.1. Annual migration cycle of alewife from the Chesapeake Bay

Adult alewife tagged during their spring spawning run in the Choptank River tributary of the Chesapeake Bay migrated as far north as the Bay of Fundy in the Gulf of Maine during the summer and fall and then returned to the Choptank River the following spring. The data set reported here is the first record of individual alewife tracked throughout the full annual

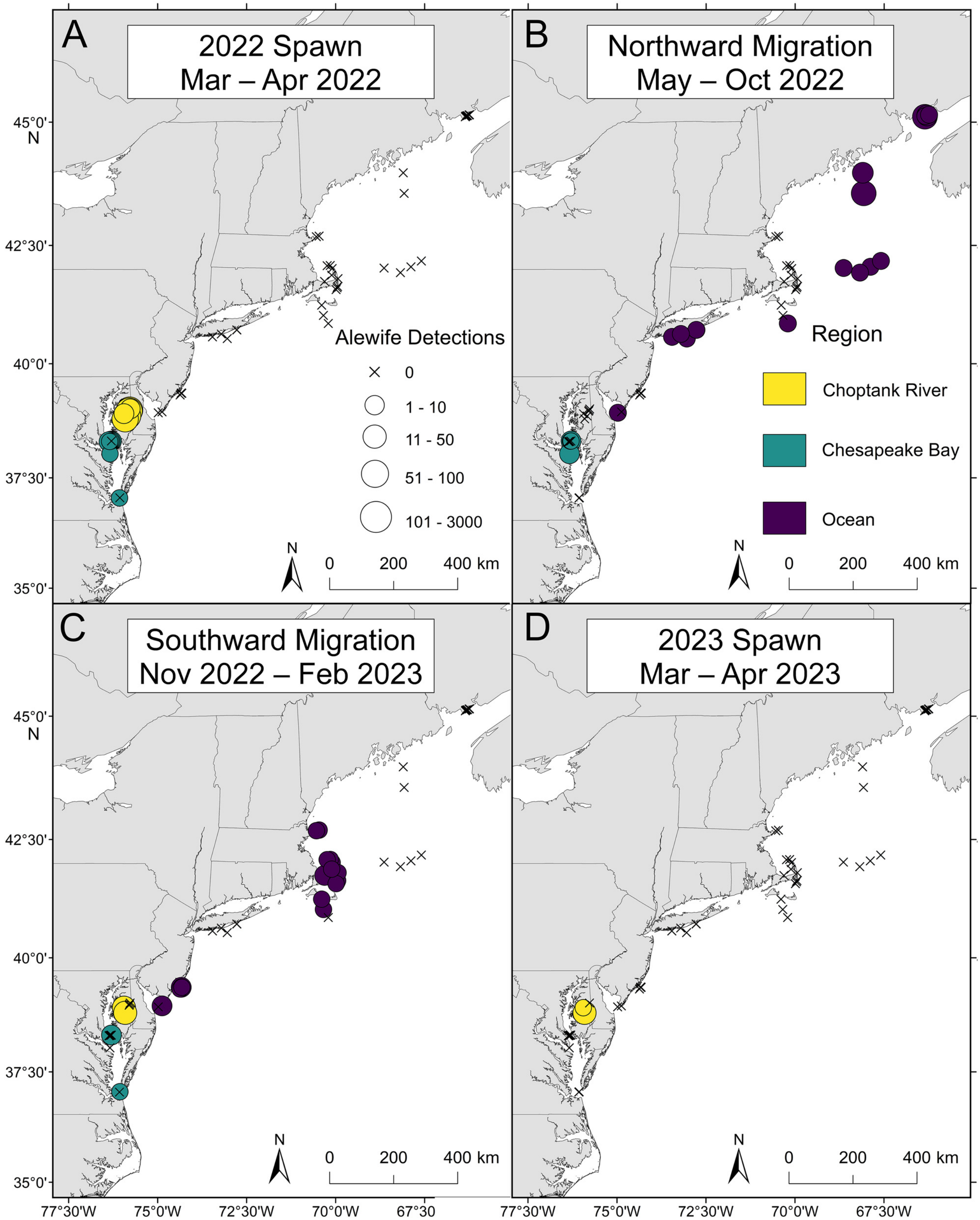

Fig. 3. Bubble plots of alewife *Alosa pseudoharengus* detections during (A) the 2022 spring spawning period in the Choptank River, (B) the northward migration from late spring to early fall, (C) the southward migration in the winter, and (D) the return to the Choptank River for the 2023 spring spawning season. Bubble size: number of detections per receiver station per time period; color: region of detection for comparison with Fig. 2; ×: acoustic receiver locations where alewife were not detected during the period depicted in the panel, but were detected in at least 1 time period

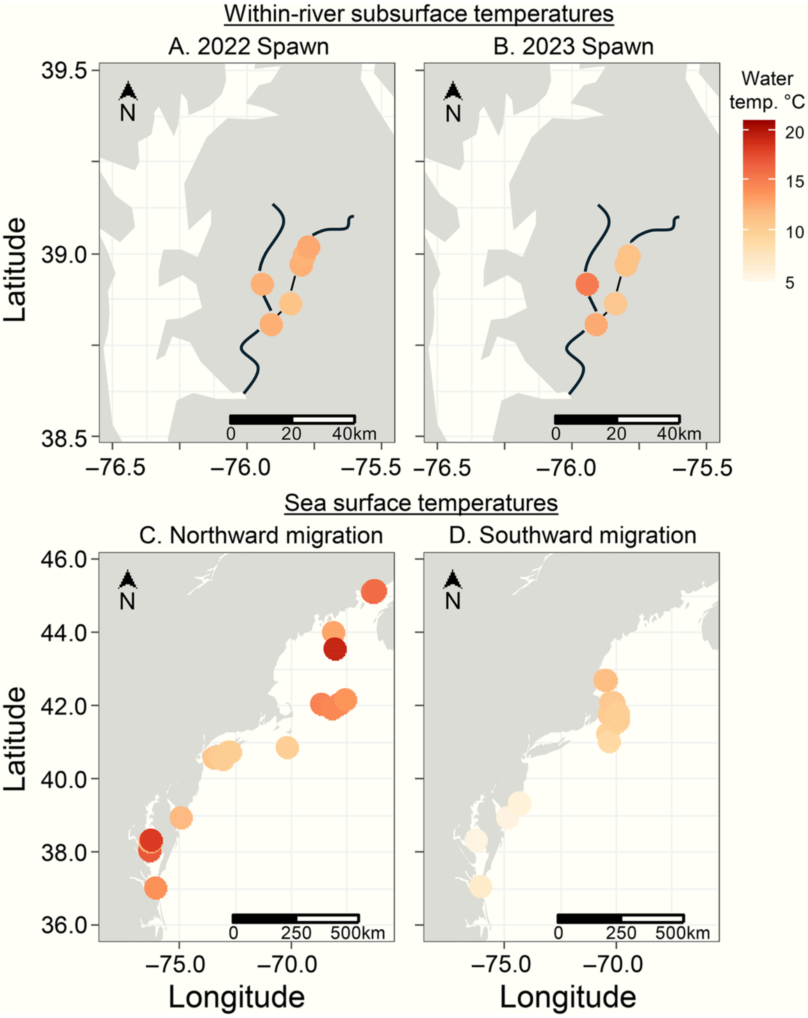

Fig. 4. Mean water temperatures of alewife *Alosa pseudoharengus* tag detections during (A) 2022 spawn (Mar–Apr 2022), (B) 2023 spawn (Mar–Apr 2023), (C) northward migration (May–Oct 2022), and (D) southward migration (Nov 2022–Feb 2023). Values at receiver locations within the Choptank River (A,B) are subsurface water temperatures. Values at receiver locations in the Chesapeake Bay and ocean habitats during the northward and southward migrations (C,D) are sea surface temperatures

Tags were detected in both main branches of the Choptank River: the mainstem and Tuckahoe Creek. The number of tagged fish detected in Tuckahoe Creek was low (only 1 tag in both years), which suggests some small amount of straying may occur within this river system. Although not a focus of this paper, we also found little evidence of alewife making multiple upstream and downstream migrations within a season, called 'oscillations', as observed in other studies using acoustic telemetry (McCartin et al. 2019). Although alewife can stray to other rivers (e.g. Spares et al. 2023), no tagged alewife were detected in other estuaries (e.g. the Delaware Bay) or rivers in the Chesapeake Bay (e.g. the Nanticoke and Patuxent rivers) with acoustic telemetry arrays deployed at the time of the study. While skipped spawning, straying, or oscillations may occur within this population, a much larger number of tagged fish would be needed to estimate rates of these behaviors.

The coastal migration of Choptank River alewife was characterized by northward movement from Chesapeake Bay in April and May, use of the Gulf of Maine and Bay of Fundy from June to October, and southward movement from November to February. Individual fish had few mainstem Chesapeake Bay or ocean detections, but tagged alewife collectively exhibited a migration consistent with the general understanding of alewife seasonal distributions. In particular, Choptank River fish were detected on George's Bank in summer and in the Jordan Basin in later summer and fall, a finding consistent with alewife habitat use patterns identified from trawl surveys (Neves 1981). Tag detections were also notable for how far north 1 individual traveled (Bay of Fundy, Canada) and the substantial spatial and temporal overlap with the incidental catch of alewife in Atlantic herring *Clupea harengus* and Atlantic mackerel *Scomber scombrus* fisheries, particularly in the nearshore regions of Southern New England and the Gulf of Maine (Bethoney et al. 2014). Incidental catch is one of several factors inhibiting recovery of river herring populations coastwide (Hare et al. 2021),

migration cycle. Tagged fish exited the Choptank River by 15 April 2022 and were detected there again from February to April 2023. Of the 50 fish tagged, 10% (5 individuals) were detected again in the Choptank River the following year. This return rate was approximately half the estimated 23% annual survival rate of Choptank River alewife based on otolith ages of fish collected in 2014 (Ogburn et al. 2017) but within the ranges estimated from otoliths and spawning marks for other US stocks (ASMFC 2017). However, given our small sample size, we use these return rates as a demonstration of the ability of acoustic telemetry to capture full annual migrations rather than as robust survival estimates.

and our results directly link fish tagged in Chesapeake Bay to the locations and times at which it occurs. This finding is consistent with genetic analyses suggesting the presence of the mid-Atlantic stock of alewife, which includes Chesapeake Bay fish, in incidental catch samples from the regional fishery statistical areas Cape Cod, Southern New England, Long Island Sound and Block Island Sound, and New Jersey–Long Island (Reid et al. 2023).

4.2. Environmental drivers of movement

Links between water temperature and alewife movement have been well established by counts of adult fish in rivers across their range (Saila et al. 1972, Richkus 1974, Rosset et al. 2017, Lombardo et al. 2020, Legett et al. 2021, Dalton et al. 2022), including in the Chesapeake Bay and Choptank River (Ogburn et al. 2017, Legett et al. 2023). Typically, alewife begin migrating into freshwater systems when spring water temperatures reach about 8–9°C and migrate out when temperatures reach ~16°C. While primarily remaining within this range, alewife left the Choptank River and migrated north in temperatures at the warmer end of the window and then left northern ocean habitats and migrated south at the colder end of the window. Although we were only able to match offshore detections with sea surface temperatures, bottom trawl surveys conducted in the northwest Atlantic also caught alewife within or below this thermal window (bottom temperatures from 3–17°C; Neves 1981). Although outside the scope of this initial study, temperature analyses could be augmented by integrating bottom temperature data from sensors (where available) or from oceanographic models.

The link between water temperature and the alewife annual migration cycle presents a conservation challenge because these fish are migrating among habitats in the Chesapeake Bay and northwest Atlantic that are rapidly warming due to climate change (Pershing et al. 2015, Hinson et al. 2022). Interannual shifts in the timing of migrations and spatial distributions have already been documented for alewife and other aquatic species in this region (Nye et al. 2009, Staudinger et al. 2019, Lombardo et al. 2020). Within rivers of the Chesapeake Bay, alewife run durations correspond with the timing of spring temperature thresholds (~8–16°C; Legett et al. 2023). Thus, warmer spring temperatures may shorten the time that within-river habitats are thermally suitable for alewife. In addition, changing seasonal temperature patterns during the summer, fall, and winter may disrupt the thermal connectivity between river and ocean habitats during the northward or southward migrations. The extent to which alewife migrations can tolerate changing temperature patterns is unknown. Future studies could examine spatial patterns in water temperatures throughout the alewife migration route to identify potential thermal bottlenecks.

4.3. Limitations and potential cases of predation

Our findings could be affected by several challenges with tracking animals using acoustic telemetry. Continental-scale collaborative acoustic receiver networks make it possible to track coastal migrants over long distances (Bangley et al. 2020), but gaps in acoustic receiver coverage resulted in large gaps between detections in both space and time. Such gaps make it difficult for us to determine the fate of tagged individuals not detected across landscapes (but see Williamson et al. 2021). Expanding the spatial coverage of acoustic receiver deployments, especially on the continental shelf, could substantially increase the level of information available on phenology and habitat use. For example, the collaborative Chesapeake backbone arrays that support this and other fisheries studies provided critical information on the timing of exit from and re-entry into Chesapeake Bay. Detections were also limited by the relatively infrequent tag transmissions (130–230 s) and low power output required to enable tracking alewife for at least a full year using the relatively small V7 tags needed for alewife (estimated tag life: 388 d). Mortality due to tagging could have reduced annual survival, and behavioral changes such as fallback (Frank et al. 2009) could have altered observed movements compared to untagged fish. For example, some detections of tagged alewife detected outside the Choptank River could be due to fallback, and the reduced percentage of tags detected (46% outside the Choptank River versus 96% in the river) could be due in part to short-term tagging mortalities. Mortality due to tagging and tag loss was not directly evaluated but was expected to be as low as 3 and 0%, respectively, as observed by Tsitrin et al. (2020), who used smaller Innovasea V5 tags with similar surgical techniques. In this study, several fish moved upstream to freshwater spawning habitats after tagging, suggesting that at least some fish continued their spawning migrations, and 46% of fish were detected after leaving the Choptank River. These results are consistent with McCartin et al. (2019), who observed multiple movements onto spawning grounds and 37% of alewife moving out of the Carman's River, New York, USA, after similar tags were implanted.

Predators such as striped bass *Morone saxatilis* and blue catfish *Ictalurus furcatus* could also consume tagged alewife, after which any detections would reflect the behavior of the predator for one to several days following consumption until the tag is evacuated from the gut (Mech 1967, Gibson et al. 2015, Schultz et al. 2015). This might have occurred for the 2 tags detected in the Choptank River and mainstem Chesapeake Bay in late May 2022 at temperatures above 20°C. Predation may also have occurred within the Choptank River and throughout the migration cycle, including by birds or mammals that could have removed tagged fish from aquatic environments, preventing further tag detections. Future studies with larger sample sizes could investigate variations in behavior characteristic of predation (Gibson et al. 2015, Klinard & Matley 2020) or could use predation tags that change their ID code upon exposure to predator stomach acids to resolve whether predation events have occurred (Halfyard et al. 2017).

5. CONCLUSIONS

This study demonstrates that Chesapeake Bay alewife that spawn in the Choptank River migrate to the Gulf of Maine in summer, moving through regions undergoing rapid warming due to climate change. During both the outgoing and return migration, tagged fish passed through multiple fisheries management jurisdictions, including regions with substantial incidental take in trawl fisheries. Within the Choptank River, alewife extensively used the tidal freshwater and oligohaline zones when they were not in non-tidal portions of the river. Similar information could be obtained in the study region for other anadromous species such as blueback herring *Alosa aestivalis*, American shad *Alosa sapidissima*, and hickory shad *Alosa mediocris* or for other anadromous species where large-scale acoustic telemetry networks are deployed. Collecting this type of detailed migration data for river-specific stocks of anadromous fish will be essential for addressing threats across the watershed—ocean continuum.

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