EARLY RECOVERY OF RIVER HERRING SPAWNING HABITAT USE IN RESPONSE TO A LARGE-SCALE DAM REMOVAL

by

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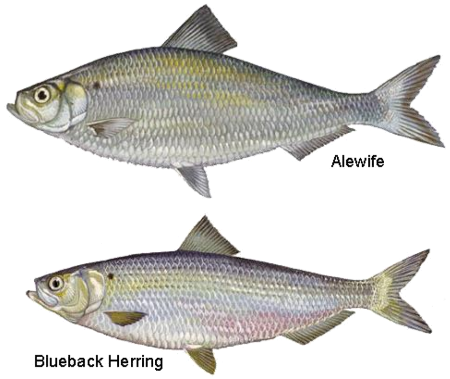
In collaboration with the Smithsonian Environmental Research Center



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EXECUTIVE SUMMARY

Historical loss of river and stream habitats due to impassable dams has contributed to the severe decline of many fish species. Anadromous fishes that migrate from the sea to freshwater streams to spawn have been especially impacted, as dams restrict these fish from accessing essential spawning habitats. This loss of habitat connectivity due to the damming of rivers has long been identified as one of the primary threats to alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), collectively known as river herring.

Dam removal is an important conservation strategy to improve migratory fish passage and habitat connectivity in rivers. In 2018, Bloede Dam was removed from the Patapsco River near Baltimore, Maryland, restoring approximately 100 km (60 mi) of potential river and tributary habitat for migratory fish. This study is the first to assess the response of river herring to Bloede Dam's removal by using a comprehensive dataset of environmental DNA (eDNA), ichthyoplankton, and passive integrated transponder (PIT) tag data collected by the Smithsonian Environmental Research Center (SERC) from 2015 to 2021, at locations upstream and downstream of the dam site during the river herring spawning migrations.

From this analysis, I documented rapid river herring habitat recolonization and expansion in the Patapsco River within three years of the dam removal, confirming that river herring are now passing the former dam location. No river herring eDNA or eggs were detected upstream of Bloede Dam prior to its removal. Post-removal, positive hits of both alewife and blueback herring eDNA were detected at restored sites upstream of the former dam site, with a higher detection likelihood for blueback herring eDNA than for alewife. Blueback herring exhibited the strongest response in recolonizing restored habitat sites, with positive eDNA detections at more sites and further upstream – including two sites upstream of Daniels Dam, a barrier still standing in the Patapsco River. Though eDNA presence in restored habitat increased post-removal, we found no evidence of increased egg abundance upstream or downstream of the former dam site, and no tagged fish were detected upstream of the dam site.

Overall, these results provide evidence of positive outcomes in support of the Bloede Dam removal's primary goals. These findings further demonstrate that: (1) eDNA served as an effective early detection tool in monitoring spatial and temporal trends of fish habitat use associated with restoration activities; (2) alewife and blueback herring respond differently to dam removal, with species-specific variability in the detection probability, abundance, and extent of upstream migration; and (3) more upstream habitat beyond the former dam site may be available to spawning river herring than originally predicted. Further monitoring is recommended to determine population-level changes associated with the removal of the Bloede Dam, and similar responses by anadromous fishes can also be expected for other barrier removal projects in the Chesapeake Bay.

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Cover image from the Maryland Department of Natural Resources.

I. INTRODUCTION

Connectivity between marine and river ecosystems is essential for the survival, growth, and productivity of anadromous fish species, which require migration access to multiple habitats to complete their lifecycles (Pess et al. 2014). However, the building of dams and other barriers has significantly fragmented habitat and migration connectivity across watersheds and coastal areas, breaking the "river continuum" (Vannote et al. 1980, Dudgeon et al. 2006). Dams inhibit the upstream movement of migratory fishes and prevent access to freshwater spawning habitat and juvenile rearing grounds, resulting in significant loss of spawning biomass (Liermann et al. 2012, Mattocks et al. 2017). In addition, historical loss of spawning habitat and productivity caused by dams further decreases fish population resilience to harvest mortalities and intensifying climate stressors (Hall et al. 2012).

Dam removal is an increasingly recognized - but challenging - strategy to restore fish habitat connectivity and conserve anadromous species (Hart et al. 2002, Kemp and O'Hanley 2010, Hare et al. 2021). Despite the construction of fish passage structures in dams, such as ladders and lifts, upstream passage efficiency remains at a low 20% for most anadromous species (Noonan et al. 2012). On the other hand, studies monitoring fish responses to dam removals have consistently observed that removing physical barriers restores longitudinal connectivity, allowing numerous migratory species to re-colonize upstream reaches (Catalano et al. 2007, Hogg et al. 2013, Watson et al. 2018, Duda et al. 2021a). A growing number of dam removal projects in North America have cited recovery of fish passage and ecological restoration as a primary goal (Doyle et al. 2003), such as Elwha Dam in Washington State, U.S. (Duda et al. 2021a) and Edwards Dam in Maine (Wippelhauser 2021).

Loss of habitat connectivity due to dams has long been identified as one of the primary threats to alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*), collectively managed as river herring (Atkins and Foster 1868, Limburg and Waldman 2009, NMFS 2019, Hare et al. 2021). These anadromous fish species are native to the North American Atlantic coast, migrating every spring from the ocean to spawn in freshwater streams and ponds (Fay et al. 1983). Although river herring were once abundant throughout their range and supported one of the most booming fisheries on the United States east coast, fishery landings have decreased by over 90% in recent decades (ASMFC 2012, 2017). The Chesapeake Bay region of the U.S. has experienced some of the most severe declines (Palkovacs et al. 2014). Landings of river herring in 2009 were less than 1% of landings from 1950-1970, dropping from approximately 3.5 million to 45,000 lbs (ASMFC 2017). While some populations in other regions, particularly New England stocks, have experienced slow increasing trends in the past decade, river herring in the Chesapeake Bay remain at historic lows (ASMFC 2017). Other factors that have contributed to this dramatic population decline include persistently elevated fishing pressure and bycatch in marine fisheries (Hasselman et al. 2016; Limburg and Walberg 2009).

Due to consistently low abundances and their ecological and economic importance, river herring are the target for species recovery on the U.S. East Coast. So far, conservation efforts have largely focused on management changes through catch regulation. In 2005, the National Marine Fisheries Service (NMFS) declared alewife and blueback herring to be “Species of Concern,” and in 2012 a moratorium was imposed on the commercial and recreational fisheries in Maryland and Virginia (ASMFC 2012). Yet conservation interventions to reduce harvest mortality may not be sufficient in recovering river herring populations if the spawning population output remains low (Mattocks et al. 2017). This is especially true for river herring as forage species since populations remain vulnerable to high natural mortality pressures via predation. Modeled changes in Alosine biomass in New England only increase to early 1900’s baselines with reduced fishing effort and substantial increases in freshwater-marine connectivity combined, whereas reducing fishing effort alone results in minimal biomass response (Dias et al. 2022).

Dam removal thus plays an important role in restoring depleted river herring populations given the species’ ecology and life history. Several studies have demonstrated improved river herring habitat connectivity and use of restored habitat after dam removals. Adult alewife and blueback herring can return to newly accessible spawning habitat within two years of restoration (Burdick and Hightower 2006; Raabe and Hightower 2014a; Raabe and Hightower 2014b; Hogg et al. 2015; Wippelhauser 2021). Successful river herring reproduction and juvenile nurseries have also been confirmed in upstream reaches of restored tributaries after dam removals (Burdick and Hightower 2006, Watson et al. 2018). In addition, some sites have documented increases in river herring abundance. In the Kennebec River in Maine, river herring counts increased 228% following the removal of Edwards Dam (1999) and over 1400% for Fort Halifax Dam (2008), when combined with additional restocking efforts (Wippelhauser 2021). Restoring aquatic connectivity for river herring spawning migrations can also help recover additional ecological functions along the land-to-sea ecosystem gradient. River herring serve as forage prey for other birds, mammals, fish like the recreationally valuable striped bass, while moving carbon and nutrients from the marine environment into freshwater ecosystems (West et al. 2010).

River herring conservation in the Chesapeake Bay is now turning to dam removal. In 2014, five mid-Atlantic state governments and federal agency partners signed the Chesapeake Bay Watershed Agreement, committing to open 132 miles of freshwater streams to fish passage every two years by 2025 (Chesapeake Bay Watershed Agreement, 2020). There are no studies, however, assessing dam removal impacts on river herring spawning migration in any Chesapeake Bay watersheds. Because dam removals face complex socio-economic, regulatory, and political hurdles, a better understanding of fish population responses using empirical data can inform environmental decision-making for restoration priorities (Doyle et al. 2003, Roy et al. 2018, Hare et al. 2021).

In this study, we assess the effectiveness of dam removal by evaluating the response of alewife and blueback herring to the removal of Bloede Dam in the Patapsco River, Maryland. Prior to its removal, annual biological surveys conducted by the Maryland Department of Natural Resources (MD DNR) detected river herring below, but not above Bloede Dam (Harbold et al. 2015). Further, Denil fish ladders installed in the dam failed to facilitate river herring passage (O'Dell et al. 1975; Harbold et al. 2013). Thus, the state of Maryland, federal agencies, and environmental nonprofits considered removing Bloede Dam as a critical step for the restoration of river herring and other anadromous fishes in the Patapsco River. We examined the spatial extent of river herring habitat use and spawning activity by applying four complimentary methods spanning four years prior to the dam removal (2015-2018) and three years post-removal (2019-2021). Monitoring efforts included the collection of ichthyoplankton (fish eggs and larvae) and environmental DNA (eDNA) to assess river herring presence and successful spawning, as well as the use of passive integrated transponder (PIT) tags to track the movements of individual adult fish within the river.

Each of the three monitoring techniques has its strengths. PIT tagging is widely used to track anadromous fish migration and assess the distribution of adult fish in relation to habitat features, including dams (e.g., Castro-Santos et al. 1996, Raabe and Hightower 2014b). Ichthyoplankton sampling of egg or larval counts can provide direct evidence of whether river herring use as habitat for active spawning (Burdick and Hightower 2006). In addition to these more traditional sampling techniques, eDNA is an emerging, non-invasive monitoring tool used to detect the presence of targeted fish species via naturally shed DNA. eDNA has previously been used in dam removal studies of salmonids (e.g., Duda et al. 2021b). eDNA concentration is also strongly correlated with relative fish abundance and biomass density, demonstrated through field and experimental studies of several anadromous species (Spear et al. 2021; Tillotson et al. 2018). For river herring in the Chesapeake Bay, Plough et al. (2018) found that relative eDNA concentrations were highly correlated with river herring adult and ichthyoplankton counts across multiple watersheds. By integrating all three methods to monitor migration and spawning activity across multiple downstream and upstream reaches of the Patapsco River, we present a robust analysis of the short-term response of river herring to dam removal.

II. METHODS

A. Study area

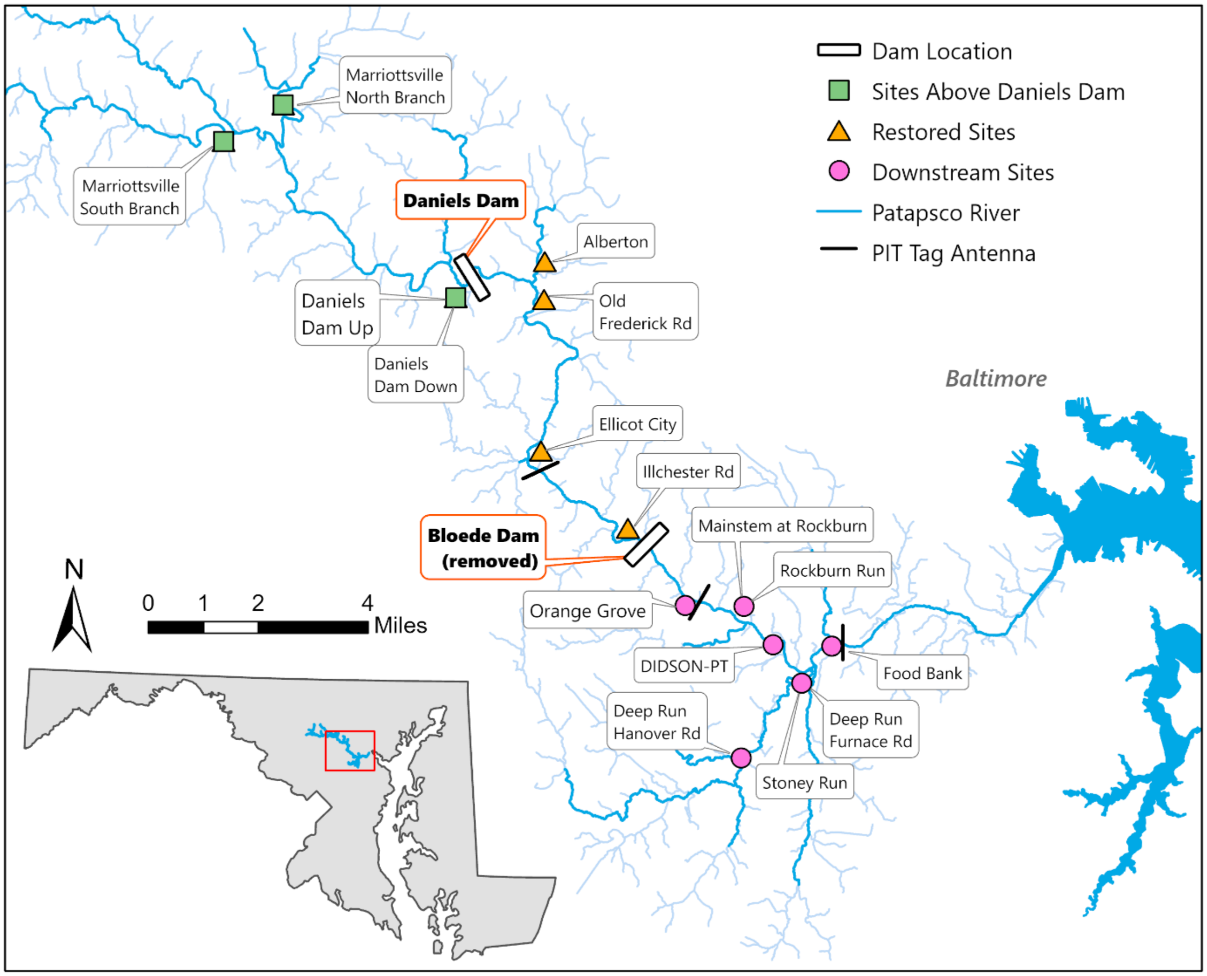

Figure 1. *Map of Patapsco River sampling sites, locations for the former Bloede Dam site and current Daniels Dam site, and the PIT tagging antenna locations in 2019.*

The Patapsco River is located in central Maryland and runs into the Baltimore Harbor of the Chesapeake Bay (Figure 1). Historically, the river valley was home to four large hydroelectric dams used to power local flour and textile mills in the early 1900s. Starting in 2010, the Maryland Department of Natural Resources (DNR), the National Oceanic and Atmospheric Administration (NOAA), American Rivers, and Friends of the Patapsco Valley State Park started a multi-year effort to restore ecological connectivity in the Patapsco River watershed. Union Dam and Simkins Dam were removed in 2010. Bloede Dam, built in 1907, was the lowermost barrier for fish passage on the Patapsco River and was located within the Patapsco Valley State Park approximately 18 km (11 mi) upstream of the Chesapeake Bay (Figure 2). The dam was designed as a flat slab buttress dam with a 10 m (34 ft) high spillway, spanning 67 m (220 ft) across the river valley (Melchior et al. 2012). In September 2018, Maryland DNR breached Bloede Dam and began full-scale restoration of the riverbanks, effectively restoring access to approximately 103 km (64 mi) of free-flowing freshwater habitat for anadromous fish species along the main stem and tributaries (Melchior et al. 2012). Currently, Daniels Dam is the only remaining structure on the Patapsco River main stem and sits 14 km (8.6 mi) upstream of Bloede Dam (Harbold et al. 2015). Daniels Dam is considered a "manmade waterfall" and is slightly smaller than Bloede Dam, at 8.2 m (26 ft) high (Harbold et al. 2015).

Figure 2. *Bloede Dam before removal in 2018 (left) and the former dam site after breaching and full bank and streambed restoration (right). Images from Maryland Department of Natural Resources.*

Samples for this study were collected from a total of 16 sites along the Patapsco River main stem and tributaries between 2015 and 2021 during the river herring migration months of March to May (Figure 1). The dataset thus represents four years of data pre-removal and three years post-dam removal (Figure 1). Habitat use samples were collected from 10 sites from 2015 to 2018, and six additional sites were added for sampling in 2019 (Figure 3). Sites were categorized into three habitat groups according to their geographic location relative to the former Bloede Dam site including sites "Downstream" of Bloede Dam (n = 8), "Restored" sites between Bloede Dam and Daniels Dam (n = 5), and "Above Daniels" sites upstream of Daniels Dam (n = 3; Figure 1, 3).

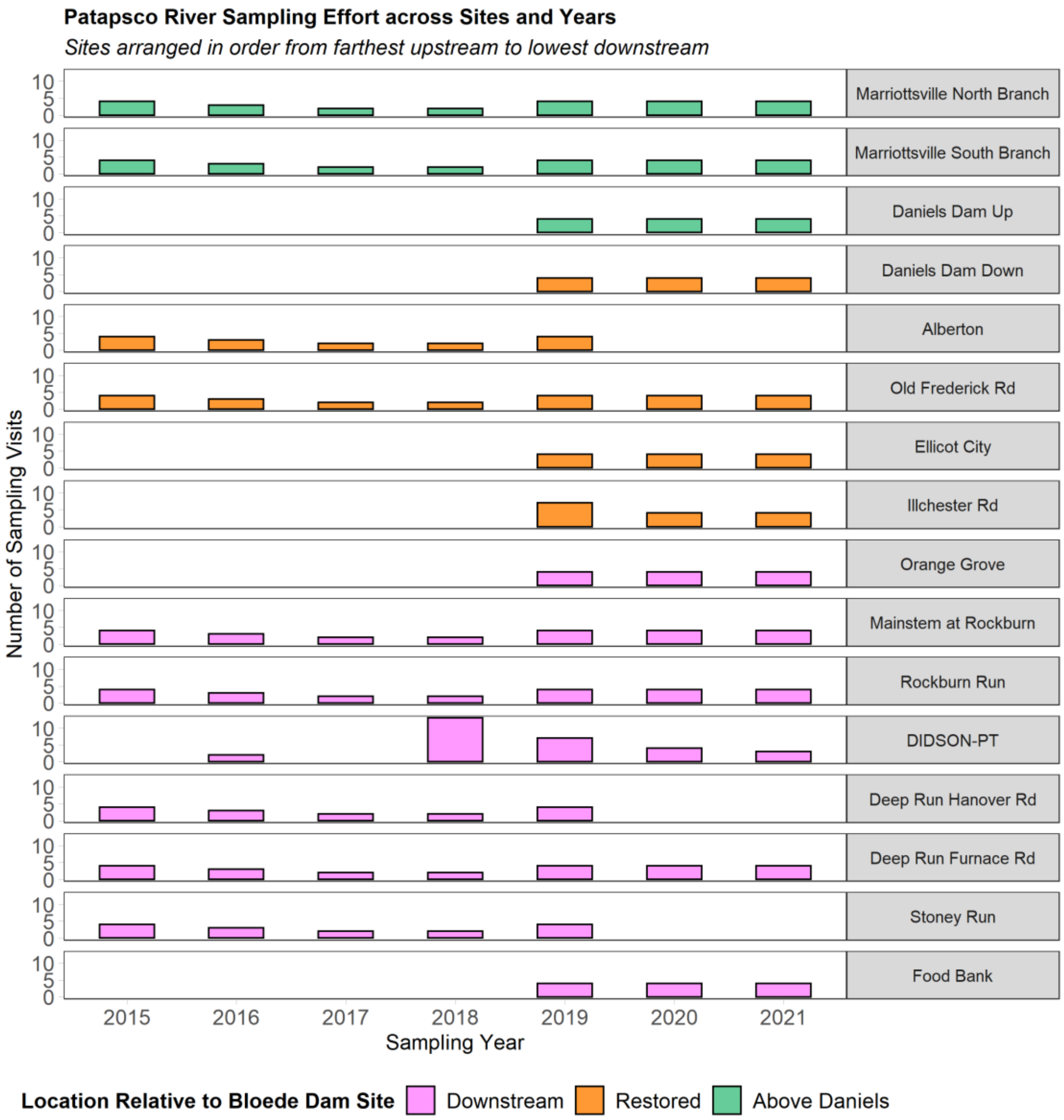

Figure 3. *Sampling effort in the Patapsco River across 16 sites and seven sampling years (2015 to 2021), arranged in order from farthest upstream to lowest downstream from top to bottom.*

B. Environmental DNA

To survey eDNA, 1-L water samples were collected from the 16 sites along the mainstem and in select tributaries of the Patapsco River from 2015 through 2021. Plough et al. (2018) developed quantitative PCR (qPCR) assay and river herring specific primers to identify river herring DNA sequences following established procedures. Following qPCR amplification, samples with at least two out of three triplicates with cycle quantification (Cq) values below 39 were considered positive eDNA detections (i.e., river herring presence) (Plough et al. 2018).

Plough et al. (2018) determined a Cq value of 39 as the conservative threshold for true eDNA detections for the river herring assay. Copy numbers from qPCR amplification were then adjusted for each sample based on the filtered water volume, calculated as the number of mtDNA copies per liter of water sampled. Duplicate samples were collected from the sites from 2019 to 2021, so copy numbers were averaged across all replicates collected at the same site and time prior to analysis. For samples with positive river herring detection, species-level identification of alewife and blueback herring was determined via Sanger sequencing. QSVAnalyser produced relative peak height ratios to estimate the relative ratio of alewife to blueback herring DNA in each sample, which was then was used to calculate the number of eDNA copies per liter for each species (Plough et al. 2018).

C. Ichthyoplankton and egg count data

Ichthyoplankton surveys of river herring eggs and larvae were conducted annually from 2015 to 2021 to investigate the spatial distribution of river herring spawning activity. Collection and processing of samples followed established protocols (Plough et al. 2018). A 46 cm x 30 cm plankton drift net with 500 μm mesh and a 200 mL cod end was deployed for 5 minutes per sample, following standard methods used by Maryland DNR (Plough et al. 2018). A total of 284 net tows were collected between 2015 and 2021. Water velocity measurements from a flowmeter (JDC Electronics Flowatch) was used to estimate sample volume at each location (Plough et al. 2018). Eggs were then retrieved, counted, and identified as “possible herring eggs.” It is not possible to visually distinguish eggs between alewife and blueback herring due to morphological similarities at the early developmental stages.

Prior to statistical analysis, a qualitative lower threshold was established for the egg count data to account for potential sampling error (methods similar to Keller et al. 1999). Observations with two or fewer eggs at any site were set as zero for “non-detection” and thus excluded from the average. The lower detection threshold would account for potential sampling cross-contamination, where residual eggs may not be thoroughly cleaned or removed from the net between new sampling events at different sites. Biological significance also informed the threshold – active river herring spawning would release thousands of eggs into the water column.

Egg abundance was converted to catch per unit effort (CPUE) across the dataset, standardized as number of eggs per 100 cubic meters. Calculating the volume of water passing through the collection net accounted for measured flow (cm/s) at each site/sample, net area (cm^2), and collection time (sec). Normalized CPUE was rounded to the nearest egg to obtain an integer count value for subsequent models. Mean egg abundance was then compared among the Patapsco River sampling sites.

D. Passive integrated transponder (PIT) tagging

Passive integrated transponder (PIT) tags are passive radio tags that allow the tracking of individual adult fish movement during their migration (e.g., Castro-Santos et al. 1996, Raabe and Hightower 2014b). Tagged fish were tracked from 2016 to 2021 using PIT antennas deployed along the bottom of the Patapsco River at three sites: “Downstream”, “Midstream”, and “Upstream.” For the first three years (2016-2018), SERC deployed all three antennas downstream of Bloede Dam. In 2019 and 2021, the antenna locations were adjusted such that the “Upstream” antenna was located upstream of Bloede Dam at Ellicott City, and the “Midstream” antenna was relocated to the Orange Grove site (Figure 1). River herring were not tagged and tracked in 2020. Each year, adult fish were captured via electrofishing, tagged, measured, and released at locations within the vicinity of the downstream antenna location. Detections for each unique tag at any given antenna were aggregated by date. The seasonal distribution of fish was assessed by estimating the percentage of tagged fish that were detected at the “Downstream” antenna also detected at either the “Midstream” or “Upstream” antennas (following Raabe and Hightower 2014a). Quantifying detections at multiple antennas in this way may account for potential tag loss during season, such as tagging stress or natural mortality.

E. **Statistical analysis**

Analysis of eDNA and egg count data in this study were conducted in R version 4.1.1 (R Core Team 2021). Spatial and temporal patterns of eDNA presence or absence and eDNA concentration were examined across the three groupings of habitat sites and compared for the time periods pre- and post-dam removal. Species-specific analyses were conducted separately for alewife and blueback herring. We fit Generalized Linear Mixed Models (GLMM) using the glmmTMB package in R, which allows for the inclusion of site locations as a spatial random factor to account for variability within habitat groupings and across habitat groupings (Brooks et al. 2017). Presence or absence was modelled with logistic regression using a logit link function to assess the main effect of dam removal on river herring eDNA detection. Separate models were run for the Downstream, Restored, and Above Daniels site groupings. Quantifying eDNA concentration allows us to further investigate river herring population dynamics in response to dam removal. Patterns of eDNA abundance were modeled using a Gaussian linear model in GLMM with log-transformed eDNA copies for Downstream sites only, because there were no positive detections for Restored and Above Daniels sites pre-removal. As in the binomial model for presence and absence, we included the main effect of dam removal as fixed factor and site as a random factor. Post-hoc pairwise comparisons were conducted between pre-removal and post-removal detection probabilities to obtain 95% confidence intervals and p-values, using the emmeans package (Searle et al. 1980, Length et al. 2019). Probabilities and standard error were back-transformed from the logistic regression to the response scale. Model assumptions and fit for all models were assessed using the *DHARMa* package (Hartig 2018).

Similar to the eDNA analysis, the ichthyoplankton data was modeled in two separate processes across the three habitat groupings independently: presence and absence and relative abundance. The probability of positive river herring egg detection was modeled using logistic regression with a log-odds link in a GLMM. The CPUE data was highly inflated with zero observations and was not normally distributed. Therefore, egg abundance from samples with positive detections was log transformed and modeled with a mixed effects ANOVA model using lmerTest package (Bates et al. 2014). For both models, we assessed removal timing as a main effect and included site as a spatial random factor. The models also included a covariate for flow in the Patapsco River. The rate of flow and precipitation-driven discharge the river affects river herring migratory behavior as well as egg retention and mobility. Daily discharge data, measured in cubic feet per second and averaged across each day, was obtained from U.S. Geological Survey (USGS) for the Patapsco River station near Elkridge, MD (01589035). We conducted post-hoc pairwise comparisons between pre-removal and post-removal detection probabilities to obtain 95% confidence intervals and p-values.

III. RESULTS

A. Distribution and abundance of alewife and blueback herring eDNA

A total of 490 eDNA samples were collected and processed across 16 sites between 2015 and 2021, including 39 control samples across the six sampling seasons. Of these samples, 189 were collected from sites downstream of Bloede Dam, 117 from sites in the restored river segment between Bloede Dam and Daniels Dam, and 97 from sites above Daniels Dam. Duplicate samples were also collected at all sites in 2019 (n = 109 out of 140 non-control samples), 2020 (n = 52 out of 105), and 2021 (n = 54 out of 102).

There were 13 samples where only alewife DNA was detected and 42 samples where only blueback herring DNA was detected. Concentration of alewife eDNA, in samples with positive detections, ranged from 20 to 103,384 copies per L, with a mean of 9,812 ± 19,469 (SD) copies per L (Figure 4). For blueback herring, concentration from positive hits ranged from 2 to 2,685,977 copies per L, with a mean of 184,846 ± 504,662 (SD) copies per L (Figure 4). After accounting for duplicates, 28% of all samples produced positive river herring eDNA detections. Duplicate samples most consistently produced positive hits in both samples at Downstream sites (68% of positive detections), whereas only 17% of positive detections for Restored sites had positive hits in both duplicate samples.

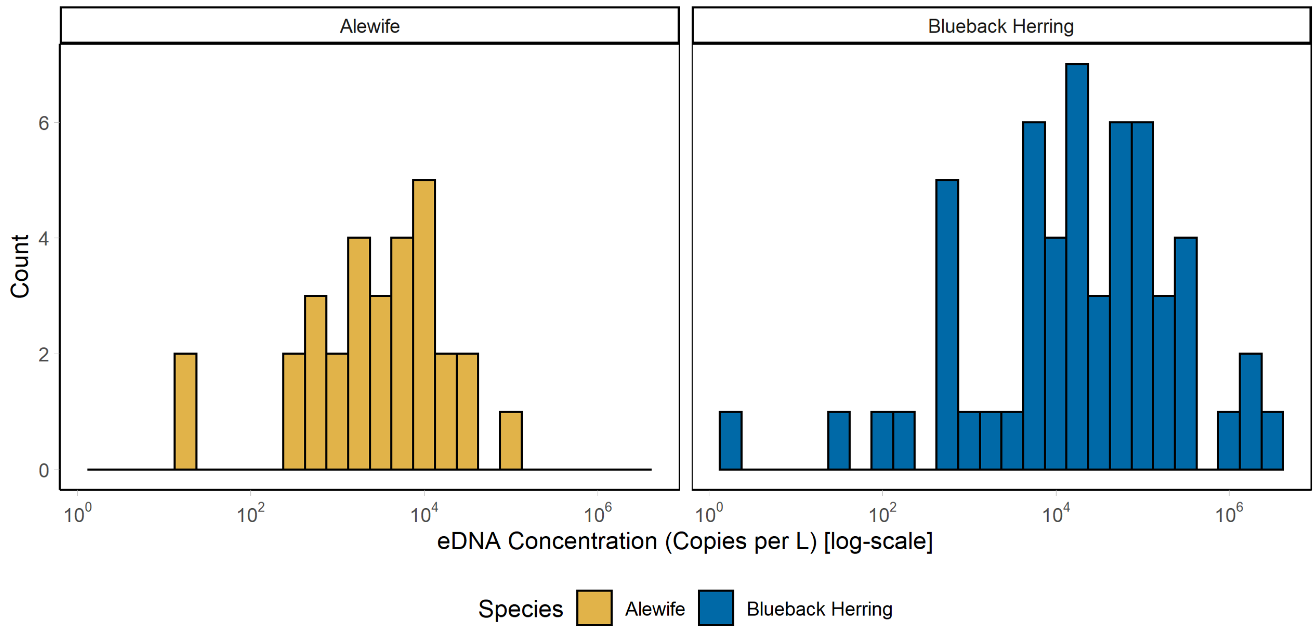

Figure 4. *Distribution of alewife and blueback herring eDNA concentration for positive detections from 2015 to 2021 sampling in the Patapsco River. eDNA abundance is normalized as number of mtDNA copies per liter.*

From 2015 to 2018, pre-dam removal, river herring eDNA was not detected at sites upstream of Bloede Dam and blueback herring and alewife DNA were both only detected at sites located on the main stem of the Patapsco River, between the Rockburn and Furnace Road sites (Figure 5).

In 2019, during the spring migration immediately after the removal of Bloede Dam, eDNA from both species were detected at the site farthest upstream in the restored segment, immediately downstream of Daniels Dam. There were also three samples with positive blueback herring DNA detections at the sites upstream of Daniels Dam (Marriottsville North and Marriottsville South Branch) in 2021 (Figure 5). However, only one out of the two duplicates resulted in a positive hit for these detections.

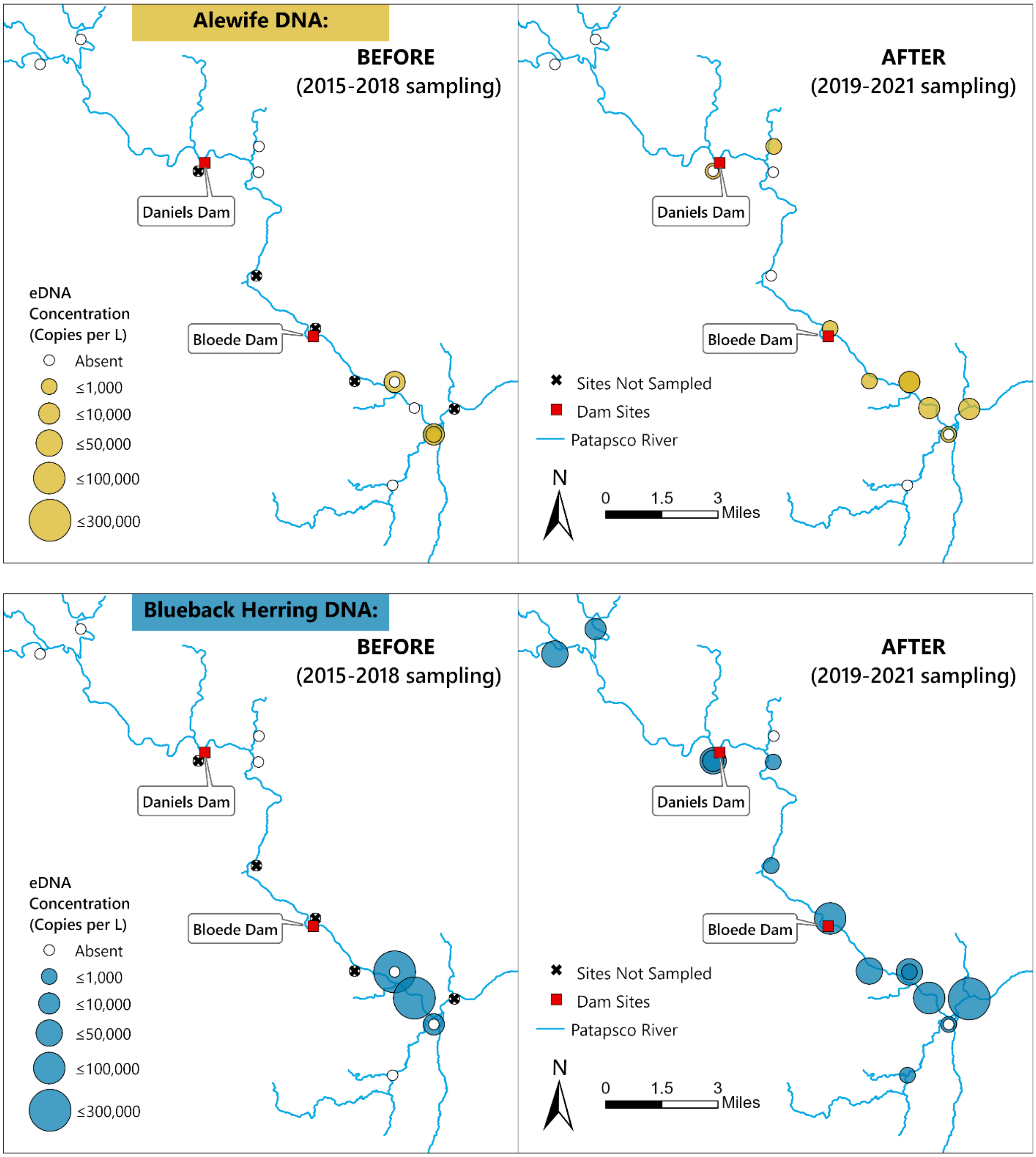

Figure 5. *Map of positive alewife (above) and blueback herring (below) eDNA detections in the Patapsco River before and after the removal of Bloede Dam. Size of the points are relative to the mean number of mtDNA copies per liter.*

Post-dam removal, the eDNA sampling revealed differences in spatial habitat use patterns between alewife and blueback herring. Overall, detection probability for blueback herring DNA was greater than that of alewife in the river after the dam was removed. At any given time during the season, there was a 12.5±4.4% (estimate ± S.E.) chance of detecting blueback herring DNA at a Restored site (95% CI 6–24.2%) and 8.3% chance of detection at sites Above Daniels Dam (95% CI 2.6–23.3%; Figure 6). On the other hand, there was only a 5.4±3.0% chance of detecting alewife DNA at a Restored site (95% CI 1.7-15.6%). The probability of detecting eDNA in the parts of the river downstream Bloede Dam was also significantly higher for both species post-removal. For blueback herring, detection probability increased from 12.0±6.0% (95% CI 4.2–29.5%) pre-removal to 34.4±10.9% (95% CI 16.9–57.6%) post-removal (p = 0.004, Z_{146} = -2.844). Detection probability for alewife DNA increased from 10.6±3.9% (95% CI 5–21.1%) pre-removal to 24±5.3% (95% CI 15.1–35.9%) post-removal (p = 0.039, Z_{146} = -3.971; Figure 6).

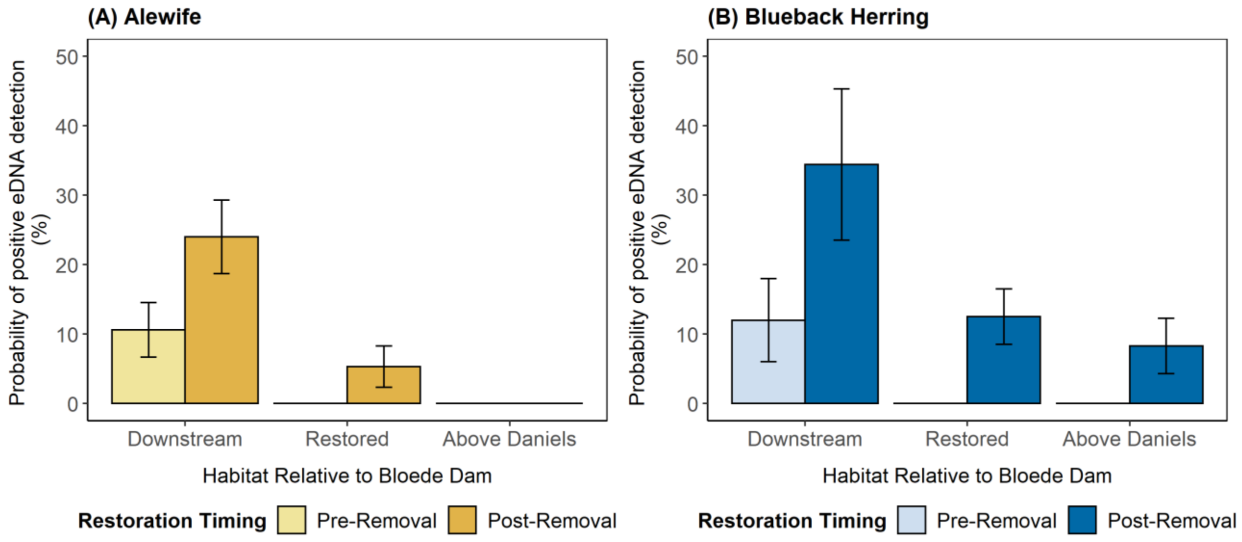

Figure 6. *Modeled detection probability of (A) alewife and (B) blueback herring DNA at sites in the Patapsco River pre- and post- removal of Bloede Dam. Probabilities and standard error are back-transformed from the logistic regression to the response scale.*

Changes in river herring eDNA abundance were only modeled at sites downstream of Bloede Dam, as there were no pre-removal detections of eDNA above the dam site in the Restored or Above Daniels sections. Overall, the change both alewife and blueback herring eDNA concentration at Downstream sites was negligible after stream restoration activity in

2018. Pre-removal, an estimated mean of 21,375 copies per L of blueback herring DNA were produced at Downstream sites (95% CI 3,229–109,097), while 8,604 copies per L were produced post-dam removal (95% CI 1,900–40,134; Figure 7). This decrease in eDNA concentration was not statistically significant ($p = 0.292$, $Z_{41} = 1.05$). For alewife, there was an average of 5,014 DNA copies per L pre-removal (95% CI 1,603–15,521) and 3,751 copies per L post-removal (95% CI 1,900–7,331). Similarly, this change was not statistically significant ($p = 0.648$, $Z_{23} = 0.456$).

In the three years following the removal of Bloede Dam, blueback herring DNA concentrations across all Patapsco River sampling sites (17,500 copies per L, 95% CI 6,311–48,533) were 180% greater than that of alewife (2835 copies per L, 95% CI 749–10,721; $p<0.001$, $Z_{62} = 3.18$). For blueback herring alone, we did not detect a significant difference in sampled eDNA concentrations between Downstream, Restored, and Above Daniels sites. However, post-removal, there was a significant difference in the concentration of alewife DNA at Downstream sites compared to Restored sites. The mean concentration of alewife DNA post-removal was 412% higher at sites downstream of the dam site than in the restored sites ($p<0.001$, $Z_{19} = -4.53$; Figure 7). On average, Downstream sites produced 3,751 (95% CI 1,881-7,480) alewife DNA copies per L and restored sites upstream of the former Bloede Dam site only produced 60 (95% CI 10–357) DNA copies per L.

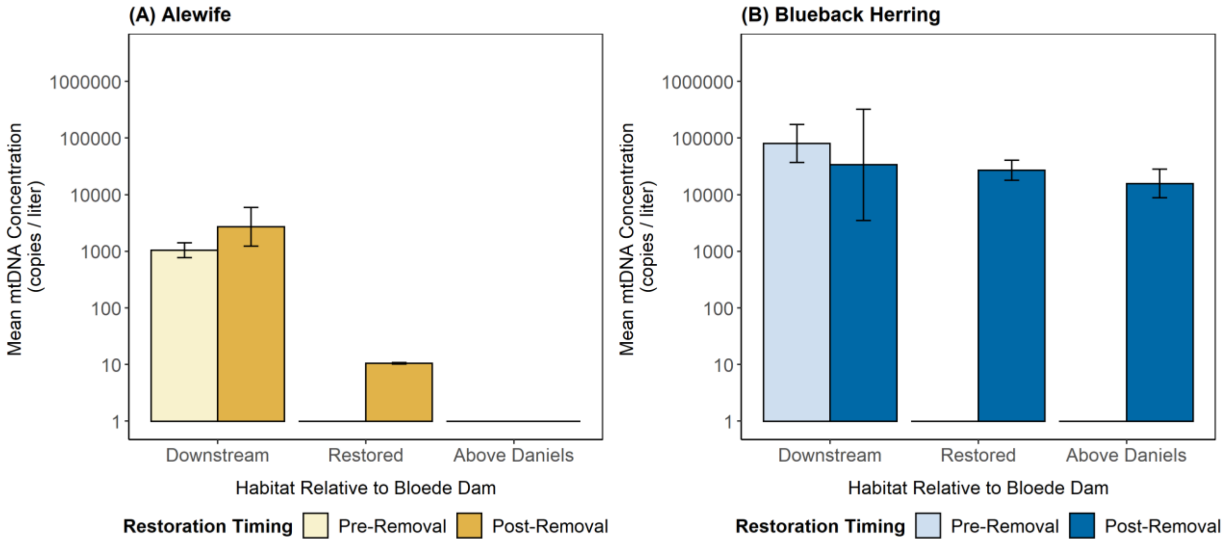

Figure 7. *Mean relative abundance of (A) alewife and (B) blueback herring eDNA at sites in the Patapsco River pre- and post-removal of Bloede Dam. Mean mtDNA copies per liter are displayed on the logarithmic scale.*

B. Distribution and relative abundance of eggs

River herring ichthyoplankton was not detected upstream of the Bloede Dam site in the three years after the dam's removal (Figure 8). There was a 14% positive detection rate for river herring eggs across all sites and sampling years. Pre-removal, river herring eggs were detected at three out of the five (60%) sampled sites in the segment of the river downstream of the dam site. Post-removal, eggs were detected at six out the seven (86%) sampled sites in the downstream segment. Notably, eggs were detected at the Orange Grove and Rockburn Run sites immediately downstream of Bloede Dam in 2019, whereas eggs had not been detected at those sites pre-removal (Figure 8).

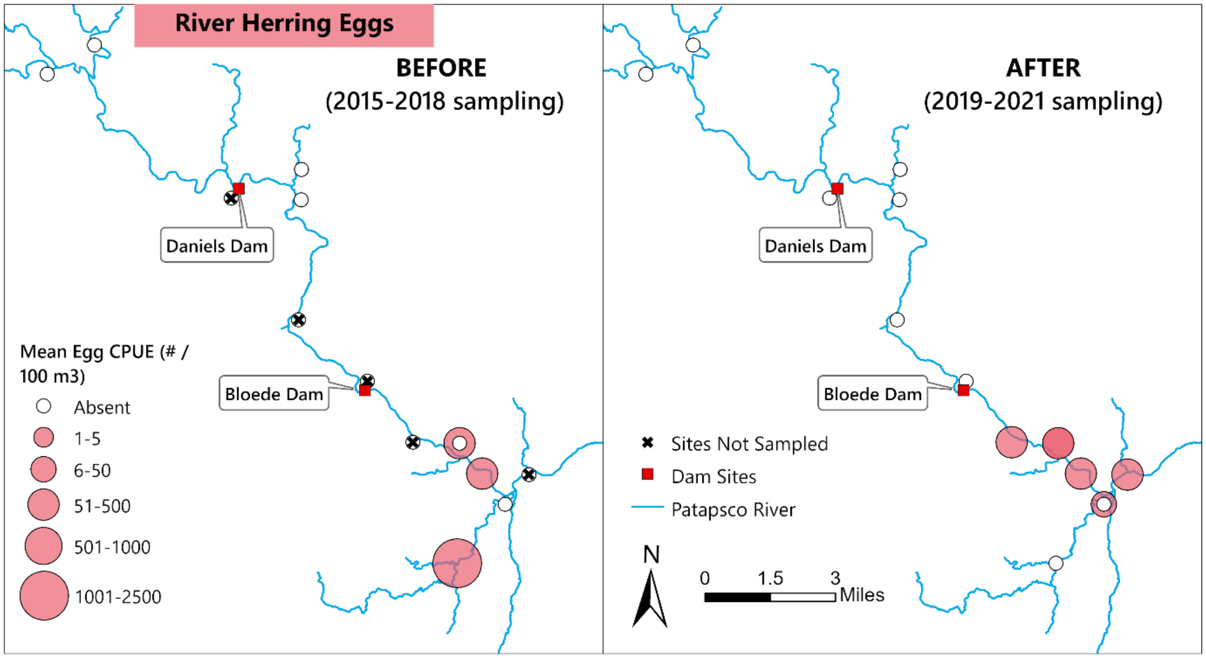

Figure 8. *Map of distribution and abundance of river herring spawning activity in the Patapsco River pre- and post-removal of Bloede Dam (9/2018). Catch per unit effort is standardized as number of eggs per 100 cubic meters.*

Comparing spatial distribution of eggs pre- and post-removal, we detected significant changes in detection probability and abundance of river herring eggs at the Downstream sites. The probability of detecting river herring eggs at any given downstream site increased from 17.2±7.2% (95% CI 7.1–36.1%) pre-removal to 25.2±8.6% (95% CI 12.0–45.4%) post-removal (p = 0.287, Z_{138} = -1.06). However, there were 69% more eggs detected at downstream sites pre-removal (837 eggs per 100 m^3, 95% CI 125–5,541) compared to post-removal (153 eggs per 100 m^3, 95% CI 25–907, p = 0.023, F = 14.81; Figure 9).

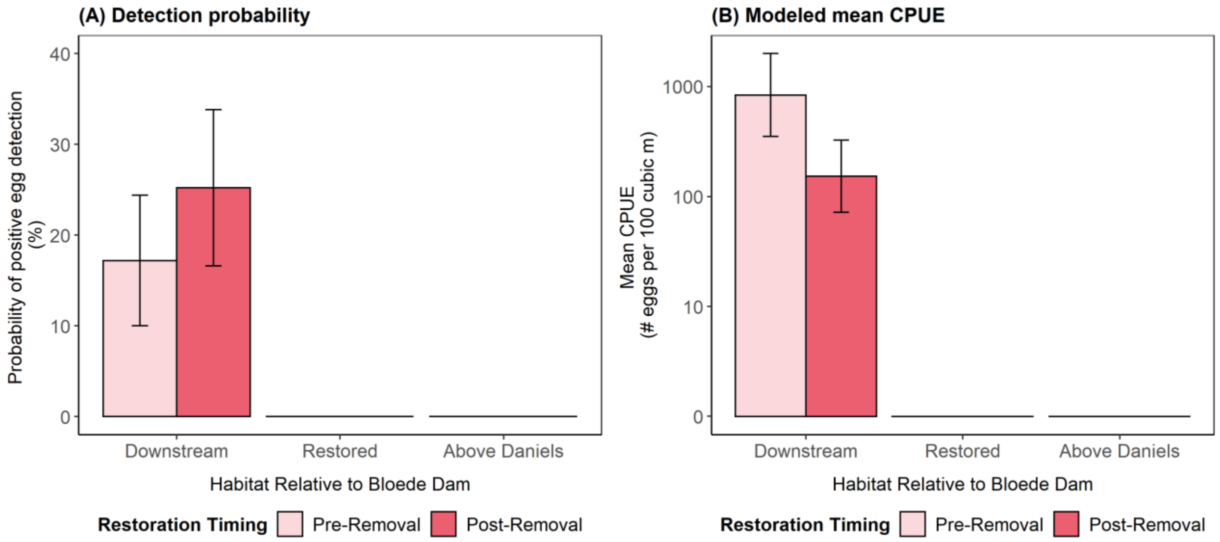

Figure 9. *Modeled (A) detection probability and (B) estimated marginal mean relative abundance of river herring eggs at sites with positive ichthyoplankton detections, pre- and post-removal of Bloede Dam. Mean catch per unit effort normalized as number of eggs per 100 cubic meters, accounting for water volume based on net size and flow and displayed on the logarithmic scale.*

The effect of flow was significant on presence and absence of eggs in the Patapsco River ($p < 0.001$). Both individual sampling years and the dam removal period was associated with significantly different flow in the river (ANOVA, $p < 0.001$). Post-hoc pairwise comparison showed that flow in the three years after Bloede Dam was removed was 157 ± 20.2 m^3 per second greater than flow during the sampling period pre-removal (2015-2018) ($p < 0.001$).

C. PIT tag migration tracking

A total of 1037 alewife (411 female and 626 male) and 1681 blueback herring (526 female, 1151 male, and 4 unspecified) were tagged over the course of this study. Prior to the removal of Bloede Dam, tagged adult river herring were consistently detected at all PIT antennas downstream of the dam site (Table 1). From 2016 to 2018, the number of tagged blueback herring individuals detected at the downstream antenna was consistently greater than that of alewife (Table 1).

Post-removal in 2019 and 2021, no tagged fish of either species were detected at the antenna located upstream of Bloede Dam site. Analysis of seasonal distribution indicates that relatively few tagged river herring migrated further upstream than the Downstream antenna. Pre-removal, less than 10% of tagged either blueback herring or alewife detected at the Downstream antenna were also detected at the Midstream antenna (Table 1). In 2019 post-removal, the greatest proportion of individual fish were detected migrating into the midstream reaches of the river, with 14% of blueback herring and 19% of alewife detected at the Downstream antenna reaching the Midstream antenna. In 2021, only between 3 to 7% of tagged individuals detected at the Downstream antenna reached Midstream antenna.

Table 1. *Number of tagged alewife (AW) and blueback herring (BB) detected at PIT receiver antenna sites along the Patapsco River from 2016 to 2021, excluding 2020. Percentage represents the proportion of fish detected at the downstream site that were also detected at the midstream or upstream site. Note that the Ellicott City antenna upstream of Bloede Dam was only installed in 2019.*

	Downstream (Food Bank)		Midstream (Orange Grove)				Upstream (Ellicott City)			
	BB Count	AW Count	BB Count	%	AW Count	%	BB Count	%	AW Count	%
2016	7	0	4	0	0	-	-	-	-	-
2017	56	29	7	10.71	1	0	-	-	-	-
2018	157	59	13	2.55	4	5.08	-	-	-	-
2019	43	43	8	13.95	15	18.6	0	0	0	0
2021	15	30	1	6.67	2	3.33	0	0	0	0

IV. DISCUSSION

A. River herring responses to dam removal

This study used multiple assessment methods from 2015 to 2021 to document the rapid recovery and expansion of river herring habitat use in the Patapsco River after the removal of Bloede Dam in 2018. Neither river herring eDNA nor eggs were present upstream of the dam when it was still in place, which is consistent with trends observed in earlier electrofishing monitoring efforts by Maryland DNR (Harbold et al. 2015). Post-removal, the eDNA data provided the strongest evidence of expanded fish presence and habitat use in the restored habitat, confirming that river herring were passing the former dam location. The probability of detecting river herring eDNA increased at sites in the restored river segment, with both alewife and blueback herring eDNA detected upstream of the former dam site by the 2019 spawning season. In every subsequent year, river herring eDNA was present at sites in the newly accessible habitat, even though tagged adult fish were not detected at the upstream antenna. This study supports trends observed in other dam removal studies in documenting recovery of habitat use. A watershed-wide assessment of river herring eDNA across the Chesapeake Bay detected river herring at nearly every sampling location where five dam removals restored aquatic connectivity (Ogburn et al., in review). Previous studies comparing responses of anadromous species to dam removal have shown that Alosine species have a relatively strong tendency to colonize new streams and expand existing habitat when dams are removed (Pess et al. 2008, Watson et al. 2018, Wippelhauser 2021). Gahagan et al. (2012) estimated a 20% straying rate for river herring across streams in Connecticut, higher than reported straying rates for West coast salmonids in the literature. This demonstrates considerable potential for river herring to colonize new habitats as long as rivers are well-connected.

The eDNA detections also displayed clear differentiation in species-specific responses to the dam removal. Recolonization of the restored habitat upstream of the former Bloede Dam site was largely driven by blueback herring. Between 2019 and 2021, blueback herring eDNA was detected at more sites across the Patapsco River tributaries, further upstream in the river, and at concentrations 180% higher than alewife. Though detection probability for alewife eDNA also increased post-removal at Downstream and Restored sites, alewife eDNA detections were restricted to fewer sites upstream of the former dam site and was not found upstream of Daniels Dam. Because eDNA concentration may be correlated with fish or egg abundance (Plough et al. 2018, Spear et al. 2021), it is possible that more blueback herring are actively using the restored habitat than alewife.

Although we hypothesized that river herring would be able access restored habitats immediately upstream of the former Bloede Dam site, it was surprising that blueback herring eDNA was present even upstream of Daniels Dam in 2021. Prior to 2018, fish passage efficiency at the Daniels Dam Denil fish ladder was impossible to measure for river herring because no Alosines were present in the river between the two dams (Harbold et al. 2015). Here, the positive detection and high concentrations of blueback herring DNA upstream of Daniels Dam in 2021 demonstrate that the fish are not only using newly open habitat immediately beyond Bloede Dam, but also potentially migrating past the Daniels Dam fish ladder. In context of conservation, this suggests that even more spawning habitat than originally estimated may now be available to spawning river herring. Each sample at these sites, however, only returned positive detections in one of the duplicates. Nevertheless, the three samples collected at the Marriottsville North and Marriottsville South sites were not trace detections due to the high concentration of DNA after amplification. It is also unlikely that sample collection on these dates coincided with a migration "surge" or spike for blueback (Greene et al. 2009), as the mean eDNA concentrations on those dates across the Downstream or Restored sites were not consistently higher than the whole river average.

Stream and watershed-level population abundances may inform these differences we observe between alewife and blueback herring. Blueback herring DNA signals may be easier to detect simply because there is a higher abundance of blueback herring in the river. Blueback herring runs tend to be stronger than alewife runs in the Patapsco River, based on long-term monitoring of run counts (Ogburn et al., unpublished data). Analysis of river herring eDNA surveys at a Chesapeake Bay-wide scale further show that watersheds on the western shore (including the Patapsco River) have greater blueback herring presence and vice versa for the eastern shore (Ogburn et al., in review). Indeed, in this sampling dataset, there was a larger proportion of positive eDNA samples with only blueback herring eDNA (n = 42 out of 79 all positive detections) compared to only alewife (n = 13 out of 79). On the Pacific coast, fish species with greater abundances pre-removal, such as Chinook salmon, also had the greatest increase in detection probability and upstream extent after a dam removal compared to rarer species, like chum salmon and pink salmon (Duda et al. 2021). It is important to note that there is also substantial interannual variability in river herring migration and spawning dynamics in the Chesapeake Bay (Ogburn et al. 2017). The relatively higher concentrations of blueback herring eDNA may correspond to sampling that coincided with years with a stronger blueback herring run.

Distinct habitat preference and migration behaviors may also contribute to the observed differences in alewife vs. blueback herring habitat use. Environmental factors such as stream water temperature (e.g., Ogburn et al. 2017, Legett et al. 2021), flow regime, and nutrient and chlorophyll concentration have been predicted to be strong drivers of variability in river herring run dynamics (Bi et al. 2021). Water velocity and substrate are also strong determinants spawning habitat suitability for each species (Green et al. 2009). Notably, alewife tend to spawn slower moving streams and gravel and pebbles for spawning, while blueback herring prefer faster flows over gravel, sand, and finer sediments (Loesch 1987, Greene et al. 2009; Supp. Table 1). Dam removal can drastically alter the hydrology and stream bed morphology within streams as bank elevation and natural flow is restored (Bednarek 2001). In the Patapsco River, the removal of Bloede Dam was predicted to shift the ecosystem from lentic to lotic flow regimes (Melchior et al. 2012), which would create restored conditions more favorable for blueback herring spawning habitat. Our analysis of USGS gauge data confirmed that average mean daily discharge in the river post-removal (406±12.6 m^3 per s) was significantly higher than pre-removal (249±15.7 m^3 per s). In 2019, the Patapsco River experienced especially high flows of water volume at 554±14 m^3 per second. Burdick and Hightower (2006) had observed spatial shifts in habitat use during a high discharge year for American shad and hickory shad post-dam removal in the Neuse River, NC. This high flow in the Patapsco River main stem during the first spawning season post-removal could have impaired habitat use and migration for alewife into upstream, restored reaches of the river.

B. Spawning and stream distribution patterns

Despite increased presence of river herring eDNA in the Patapsco River after Bloede Dam was removed, this study did not find conclusive evidence for spawning activity in the newly accessible habitat from the egg count data. After the dam was removed, river herring eggs were detected at all mainstem sites, yet there was no spawning activity detected above the former dam site. Further, the mean concentration of eggs decreased at Downstream sites post-removal. There are few prior studies that sample ichthyoplankton to monitor anadromous fish spawning after dam removals, especially for Alosines on the U.S. east coast. Studies that do document presence of eggs and/or larvae tend to be on a longer timescale. For instance, Burdick and Hightower (2006) reported upstream expansions for American shad (*A. sapidissima*) in North Carolina’s Neuse River tributaries five years after the breaching of Quaker Neck Dam.

The lack of eggs detected does not necessarily indicate a true absence of actual reproductive activity in the restored habitats. There were sampling challenges for plankton net tows due to variable flows because it was difficult to access sampling sites during high stream discharge in 2019. On the other hand, eDNA could also be derived from biological material shed during any life stage of the fish, including eggs, larvae, or other maternal tissues expelled during broadcast spawning, and there is not enough information to distinguish sequences between life stages (Thomsen and Willerslev 2015, Plough et al. 2018). The alewife or blueback herring eDNA detected in the upstream habitat post-removal could potentially encompass positive detections of eggs and/or larvae present in the water column as well. In fact, observed increases in fish eDNA in ambient water may overlap with reproduction timing and spawning events (Muha et al. 2021). Some preliminary research is assessing opportunities to distinguish broadcast spawning gamete release with eDNA primers. Spawning events of Macquarie perch, for example, produced higher relative concentrations of nuclear DNA fragments compared to mitochondrial DNA (Bylemans et al. 2016). These are potential methods to explore to complement future ichthyoplankton sampling.

The PIT tag telemetry data provides additional insight into river herring spatial migration patterns, in addition the eDNA dataset. Both tagged alewife and blueback herring were detected at the antennas installed downstream of the dam site in all years but were not pinged at the upstream antenna post-removal. On one hand, the PIT tag detections reflect a trend of decreasing abundance moving upstream across the entire monitoring period. An average of 12% of tagged river herring at the Downstream antenna were also detected at the Midstream antenna. This is consistent with the decreasing detection probability of both alewife and blueback herring eDNA moving from Downstream to Restored and Above Daniels sites. Other studies have demonstrated similar “truncated” upstream distribution patterns of anadromous species in other river systems, with significant variation between species (Catalano et al. 2007). Raabe and Hightower (2014a), for instance, observed a linear decline in PIT tagged American Shad abundance in the Little River, NC after a dam removal, with the highest proportion of detected fish remaining in downstream reaches.

The species-specific tag tracking also reveals qualitative abundance differences and changes in various reaches of the Patapsco River. From 2016 to 2018, the number of tagged blueback herring detected at the Downstream and Midstream antennas was consistently greater than that of alewife. Although we did not test correlation between eDNA and adult abundance like Plough et al. (2018), these trends generally support our hypothesis that the higher blueback herring eDNA concentrations are related to higher relative abundance of blueback herring. Interestingly, this pattern in the PIT tag data falters after Bloede Dam was removed. In 2019 and 2021, there was an equal and higher number of alewife tags detected at the Downstream and Midstream antennas, respectively. The upstream migration distribution of tagged fish in 2019 is also higher than all other years, with 14% of blueback herring and 19% of alewife from the Downstream antenna making it to the Midstream Antenna. This interannual variability may be a product of sampling challenges in the years after dam removal. High flow conditions in the Patapsco River in 2019 made it difficult to conduct electrofishing during the spring migration months, and the antennas were not able to be installed in the streambed for the entire sampling period. Consequently, detection of alewife vs. blueback herring tags may be erroneously inflated during these sampling years.

C. Advantages and limitations of eDNA

By integrating results from multiple assessment methods, we demonstrate the practical application of eDNA as an “early detection” tool to document patterns of anadromous fish habitat use in response to restoration. This is one of the first studies to combine traditional survey methods with eDNA across consistent, long-term sites to monitor fish responses to a dam removal. The eDNA assay developed by Plough et al. (2018) is highly sensitive with consistent amplification for river herring primer sequences, thus producing high confidence in this analysis that positive eDNA detections indicate true species presence. eDNA signals in freshwater systems can last typically last a few hundred meters downstream from the source and can persist from 1 to 54 days before degrading and dissipating (Barnes et al. 2016, Wilcox et al. 2016). Therefore, positive hits of river herring eDNA are likely from relatively local and recent sources of genetic material during the actual spawning season. We were also more likely to detect eDNA in the river than PIT tagged fish in the years immediately after the restoration project. These results further suggest that DNA can be detected in aquatic streams before population-level abundance changes are detectable through traditional sampling methods. In spring 2021, Maryland DNR finally caught a single alewife and blueback herring via electrofishing at a site upstream of the former dam site (MD DNR, unpublished data).

Our study adds to the growing body of literature using eDNA to assess aquatic habitat connectivity, spatial distribution, and recolonization dynamics for anadromous fish populations. Duda et al. (2021) collected eDNA at repeated sites, much like SERC's sampling design, to assess the migration of five Pacific salmon species and Pacific lamprey (*Entosphenus tridentatus*) in the Elwha River, Washington after removal of two large dams. All species were detected upstream of the removed dam sites, with species-specific trends in detection probability and spatial extent. In the Gulf of Mexico, Pfleger et al. (2016) used eDNA to test migration passage of two sturgeon species at various dams in Alabama, demonstrating only limited passage success over the barriers. Muha et al. (2021) used a similar "before-after, upstream-downstream" as this study in the river Lugg, England, finding that anadromous fish species diversity and eDNA abundance did not change after removal of a <5m tall weir.

There are potential limitations of interpreting these eDNA results. Environmental factors may affect eDNA detectability and degradation, including a combination of hydrological conditions, UV exposure, and water temperature (Tillotson et al. 2018). In addition, detectability of eDNA may also depend on species density (Muha et al. 2021). It is possible that some samples were false negatives for alewife, if the fish were indeed present at a location but in small enough numbers that the eDNA was too diffuse to detect. We also observed reduced consistency in detecting river herring eDNA across duplicate samples moving upstream the Patapsco River. 68% of samples with positive detections from duplicate samples in the Downstream sites were a "double positive," whereas only 16% positive detections the Restored sites were positive in both duplicates. Finally, eDNA data may face issues of overdispersion due to patchy spacing and density of fish in the environment (i.e., migration spikes) and movement of genetic material available to be sampled (Chambert et al. 2018). Our Gaussian GLMMs for eDNA concentration data met all model assumptions and attempted to account for spatial "clumping" of variability by including site as a random factor. Future studies using eDNA may consider exploring model fit of other distributions, such as the negative binomial model.

Finally, this long-term sampling scheme was highly robust in replicating a "before-after control-impact" (or "downstream-upstream") study design. However, it is important to note that all three survey methods – eDNA, ichthyoplankton, and PIT tagging – only capture momentary and stationary snapshots of biological events. There are ecological interactions and dynamics that were not assessed in this study but can be elucidated with further monitoring of the Patapsco River.

D. Management implications

This study contributes to the expanding evidence base for the effectiveness of dam removal in conserving anadromous fish populations, particularly Alosines. Overall, our findings here suggest that the primary objective for Bloede Dam's removal - to restore migratory fish passage in the Patapsco River – has been met for river herring (American Rivers 2018). This study could inform future efforts for river herring conservation by NOAA, Maryland DNR, and conservation groups such as American Rivers. In a 2019 Endangered Species Act listing review, National Marine Fisheries Service ranked "the present or threatened destruction, modification, or curtailment of habitat or range" due to dams as the highest threat to blueback herring and alewife (NMFS 2019). Over 400 dams remain standing in Maryland's rivers as potential barriers to anadromous fish migration (USACOE 2021; Supp. Figure 5). Notably, 31 dams were constructed pre-1950 and are now completely obsolete, serving "recreational" purposes only (USACOE 2021). Only 21 dams have been removed from rivers in Maryland since 1990, so there are additional opportunities to expand river herring spawning habitat by restoring stream connectivity (American Rivers 2021). Dam removals can fit into the broader strategy of "life cycle conservation," which considers range-wide actions for key habitats critical for anadromous lifecycles (Bowden 2015). This approach been adopted in the recovery plan for endangered Coho salmon in California, for example (NMFS 2012).

Ultimately, the conservation end-goal for habitat and fish passage restoration is to improve stock productivity and recruitment. Nine out of the fifteen of the Chesapeake Bay stocks evaluated in the previous river herring stock assessment were either "overfished or severely depleted" (ASMFC 2012). Additional assessment of river herring run counts in the Patapsco River, either through imaging sonar or biological sampling methods, should be conducted to understand changes in breeding population size in response to the restoration effort (Ogburn et al. 2017). Environmental monitoring of temperature, flow, and sediment condition in the river is also essential to characterizing habitat suitability post-restoration. Post-dam removal, elevated sediment loads and water column turbidity can extend to coastal subtidal zones and persist in the water column for years (Rubin et al. 2017). Due to the “passive sedimentation approach” adopted for Bloede Dam’s removal, the sediment deposit accumulated behind the dam released 312,000 cubic yards of sediment downstream the Patapsco River (Melchior et al. 2012, MD DNR 2021). Maryland DNR estimates that the Bloede Dam sediment load may take 6 to 10 years to fully disperse (MD DNR 2021). Sedimentation post-removal may reduce habitat quality by blanketing large gravel and pebble substrates that river herring, especially alewife, prefer. It is important to continue monitoring changes in the aquatic environment in the Patapsco to understand how potential changes to the stream may be coupled with river herring ecological needs. These are additional considerations that should be better integrated into alternatives analyses and environmental assessments for future dam removal projects (Melchior et al. 2012).

Expanded ecological and biological monitoring of anadromous fishes pre-removal at priority dam sites will also contribute valuable information to increase political, economic, and social support for this restoration strategy (Bednarek 2001, Rodeles et al. 2017). As our data show, dam removal responses can be highly species-specific and context dependent. Currently, river herring are managed under the Fishery Management Plan for American Shad and River Herring, which considers alewife and blueback herring together. Even though the Atlantic States Marine Fisheries Commission typically considers each river in the Chesapeake Bay a separate stock, the species-specific responses observed in this study suggest that conservation and management actions may also benefit from species-specific analyses at the stream level (ASMFC 2017). Long-term conservation for anadromous species should thus adopt an ecosystem-level approach, by pairing management actions such as catch regulations that reduce harvest mortality and incidental by-catch, and habitat restoration in freshwater spawning habitats (Bowden 2014, Hare et al. 2021, Dias et al. 2022).

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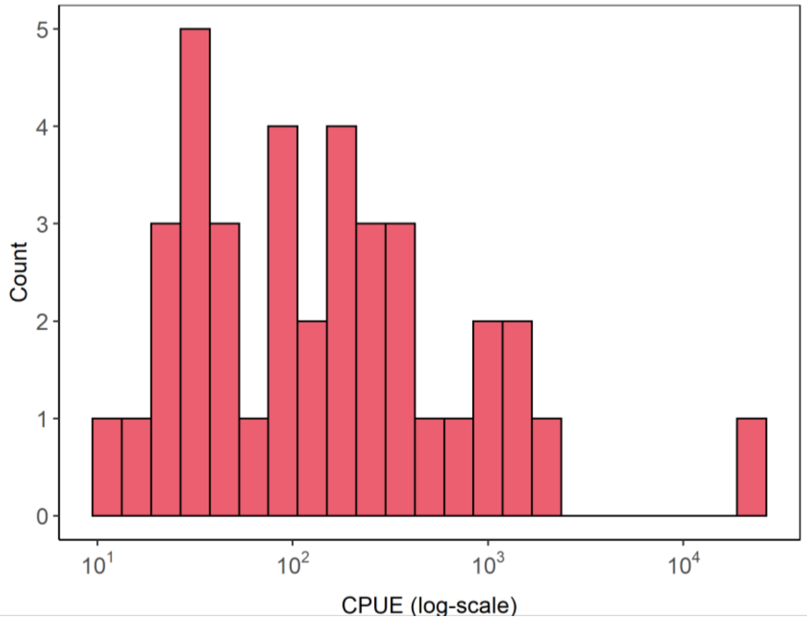
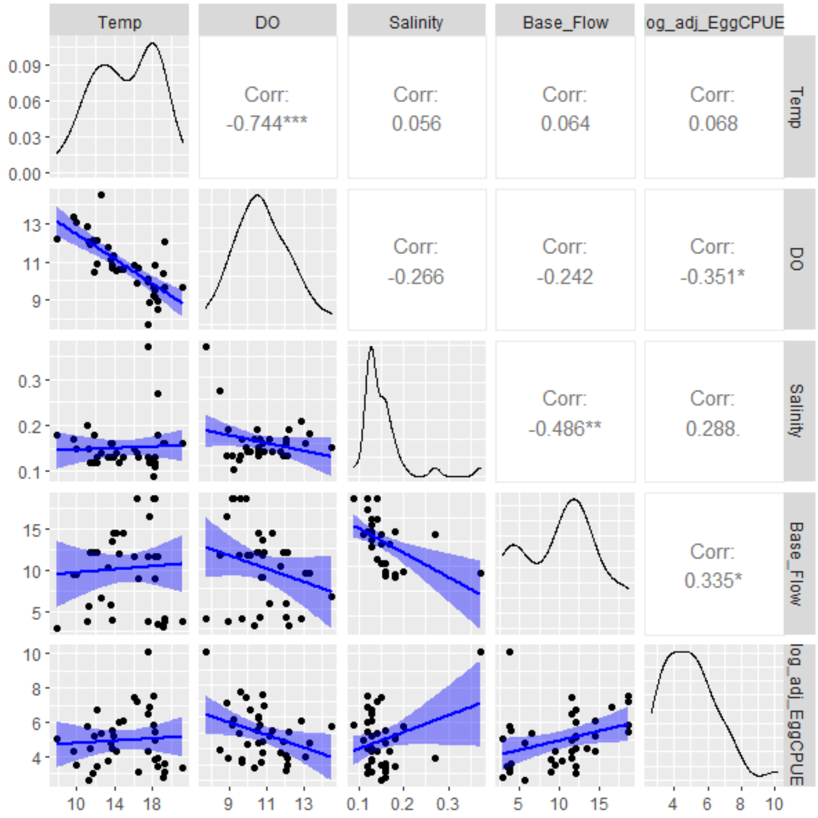
VII. APPENDIX

Supplemental Table 1. *Spawning migration and habitat requirements for alewife and blueback herring in the Chesapeake Bay region (adapted from Greene et al. 2009).*

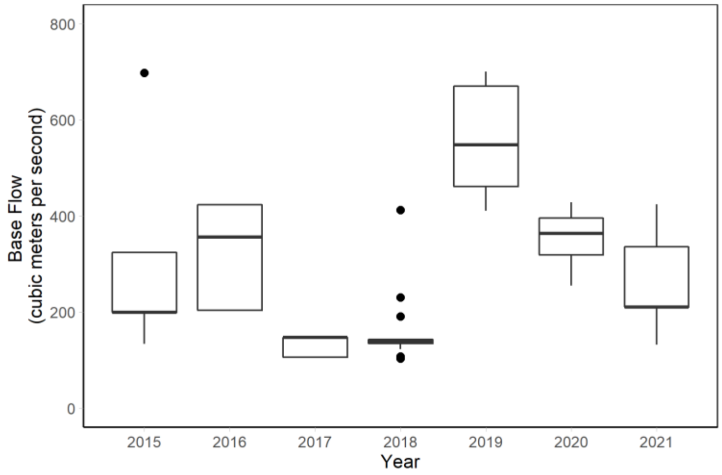
	ALEWIFE	BLUEBACK HERRING
Sexual maturity	3 years	3 years
Temperature	10-18ºC for migration 10-22ºC for spawning	13-27ºC for migration/spawning
Timing	Mid-March (2-4 weeks earlier than blueback herring). Most spawning occurs at night.	April – June Most spawning occurs in late afternoon, night.
Spawning location	Lentic environments - slow-moving, shallow streams. Ponds and lakes, shore-bank eddies or deep pools below dam/structures. Upstream movement during higher water flows.	Lotic environments - faster mainstem flow, prefer swift water flow over spawning site. Avoids slow-moving or standing water.
Substrate	Gravel, coarse stone/pebble/cobble, large pieces of organic detritus (branches, leaves, etc). Less activity in fine sediment.	Gravel, sand, other finer soft sediments and organic detritus.
Eggs	Broadcast spawn, adhesive until water-hardened, semi-demersal to pelagic.	Broadcast spawn, adhesive until water-hardened, pelagic in moving water.



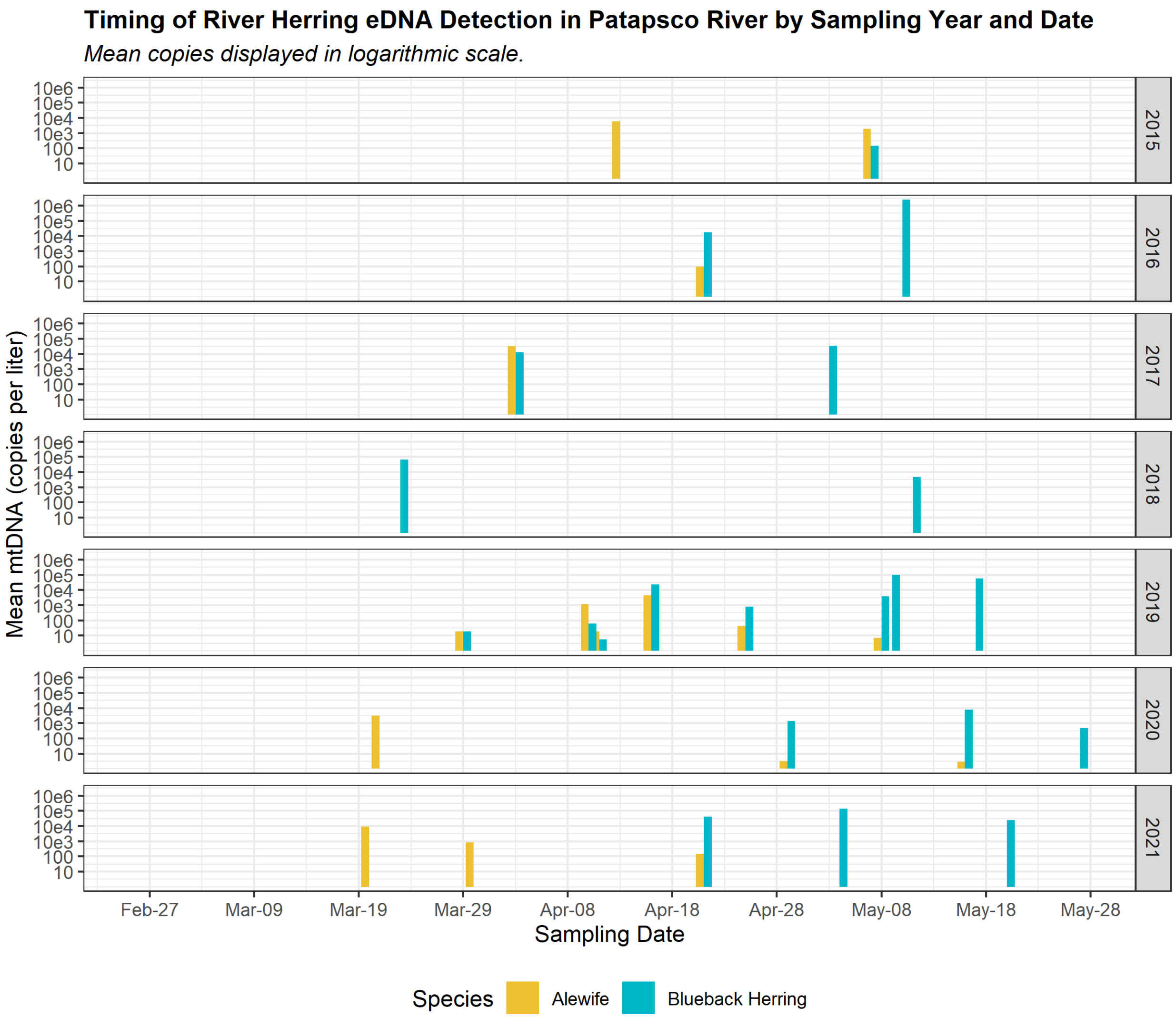
Supplemental Figure 1. *Distribution of river herring egg counts (catch per unit effort) for positive detections from 2015 to 2021 sampling in the Patapsco River. CPUE standardized as the number of eggs per 100 cubic meters of water, displayed on the logarithmic scale.*



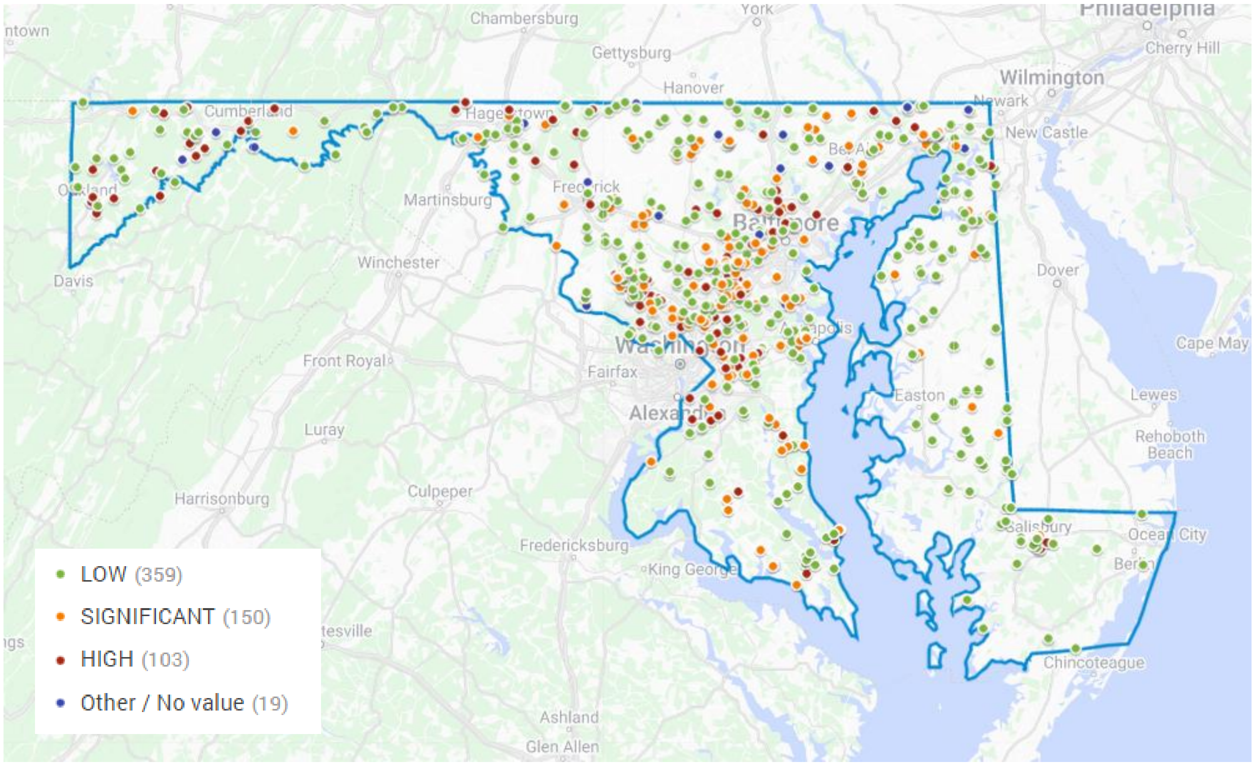
Supplemental Figure 2. *Covariate correlation plot for egg CPUE (number of eggs per 100 cubic meters) and environmental variables, including temperature, dissolved oxygen, salinity, and base flow in the Patapsco River.*



Supplemental Figure 3. *Distribution of annual mean daily discharge (cubic meters per second) measured in the Patapsco River. Data was obtained from U.S. Geological Survey (USGS) for the Patapsco River station near Elkridge, MD (01589035).*



Supplemental Figure 4. *Timing of river herring eDNA detection and relative abundance in Patapsco River by sampling year and date. Mean copies displayed in logarithmic scale.*



Supplemental Figure 5. *Inventory of dams in Maryland state, with color indicating hazard rating (red = high, orange = significant, green = low, blue = other/no value). Data derived from Maryland Department of the Environment (available here:* *https://mde.maryland.gov/programs/Water/DamSafety/Pages/maryland_dam_inventory.aspx).*