Wild Oceans
For the future of fishing

December 8, 2022

Dr. Chris Moore, Executive Director
Mid-Atlantic Fishery Management Council
800 North State St., Suite 201
Dover, DE 19901

RE: ***2023 Implementation Plan***

Dear Dr. Moore,

Wild Oceans commends the Mid-Atlantic Fishery Management Council for its leadership in coordinating the East Coast Climate Change Scenario Planning Initiative, and we are looking forward to the recommendations that will be presented next year. In the interim, the Council should continue to advance priorities that inform decision-making for fisheries in a changing ocean. To this end, we recommend the following actions be added to the 2023 Implementation Plan.

1. Mackerel, Squid and Butterfish (MSB)
    - During specifications, incorporate bycatch information that is currently submitted to NOAA Fisheries as part of the Environmental Assessment into the Fishery Information Documents that are viewed by the Scientific and Statistical Committee, MSB Committee, MSB Advisory Panel and full Council as input is gathered and decisions are made.

    An Environmental Assessment (EA) is compiled by Council staff and submitted to NOAA with the Council-approved specifications package. Within the EA are tables that list incidental catch and discards for each fishery. This information is valuable for tracking changes in bycatch composition over time. For example, from 2006-2010, the average annual amount of alewives taken in the longfin squid fishery was estimated at 13,600 lbs.[1] According to the 2021-2023 specifications package EA, an estimated 69,664 lbs. of alewives were caught annually from 2017-2019, nearly twice as much as was caught in the mackerel fishery for this same time period. With many fish stocks experiencing shifting distributions, it is reasonable to assume that bycatch composition is changing as well, and it is important to monitor these changes to understand the impact on non-target stocks. The EA submitted with the specifications package is often overlooked and rarely viewed by anyone other than NOAA or Council staff. This priority is not expected to add to workload. Rather it is a reorganization of tasks that are already part of the specifications process.

2. Ecosystem and Ocean Planning/Habitat
    - Develop a policy and/or process for reviewing EFP applications for new or expanding fisheries as it relates to the unmanaged forage amendment.

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[1] MAFMC. 2013. Amendment 14 to the Atlantic Mackerel, Squid, and Butterfish (MSB) Fishery Management Plan (FMP) Final Environmental Impact Statement.

Currently this 2021 recommendation from the Ecosystem and Ocean Planning Committee[2] is listed in the "Possible Additions" section of the Draft 2023 Implementation Plan. During the October meeting in Dewey Beach, the Council heard testimony from Mr. Jeff Kaelin, Director of Sustainability and Government Affairs for Lund's Fisheries, that the company has revised its Exempted Fishing Permit (EFP) application for an Atlantic thread herring fishery based on feedback from NOAA's Greater Atlantic Regional Fisheries Office (GARFO) and plans to resubmit the application for the 2023 fishing year. The Council should anticipate that EFP applications to pursue new forage fisheries may become more regular as fishermen seek opportunities to shift to available target species. Scrambling to develop a policy and process once an application has been provided to the Council for review could lead to less than desirable outcomes that are not consistent with the objective of the Unmanaged Forage Omnibus Amendment: "to prevent the development of new, and the expansion of existing, commercial fisheries on certain forage species until the Council has adequate opportunity and information to evaluate the potential impacts of forage fish harvest on existing fisheries, fishing communities, and the marine ecosystem."

3. River Herring and Shad
   - Develop 2024-2025 cap (paired with Atlantic mackerel specifications) that will implement a biologically-based bycatch cap or limit as recommended in the 2023 River Herring Benchmark Assessment.

   A biologically-based cap is needed that adequately protects the runs most vulnerable to bycatch. A newly released river herring bycatch study (appended to this letter) applied genetic stock identification analysis to river herring samples taken as bycatch by midwater and bottom trawls targeting Atlantic herring and Atlantic mackerel from 2012-2015. A majority of the alewives taken originated from Block Island and Long Island Sound, while blueback herring originated primarily from mid-Atlantic and northern New England river systems.[3] The researchers note that recent effort shift to the Hudson Canyon and the greater Mid-Atlantic Bight could impact blueback herring disproportionately. Developing the river herring and shad cap is already included in the Implementation Plan. We recommend that this priority recognize that a new river herring benchmark assessment is expected to be complete in 2023 that includes a Term of Reference (TOR) to calculate a biologically-based cap as requested by the Mid-Atlantic Council at the June meeting. The requested TOR was approved by the ASMFC's Shad and River Herring Management Board on November 8.[4]

Thank you for considering our recommendations.

Sincerely,

Pam Lyons Gromen

Pam Lyons Gromen, Executive Director

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[2] Ecosystem and Ocean Planning Committee. October 4, 2021 Webinar Meeting Summary. https://www.mafmc.org/s/Final_Oct-4_2021_EOP-Committee-Meeting-Summary.pdf.

[3] Reid, K., Hoey, J.A., Gahagan, B.I., Schondelmeier, B.P., Hasselman, D.J., Bowden, A.A., Armstrong, M.P., Garza, J.C. and Palkovacs, E.P. (2022). Spatial and temporal genetic stock composition of river herring bycatch in southern New England Atlantic herring and mackerel fisheries. *Canadian Journal of Fisheries and Aquatic Sciences.* Just-IN https://doi.org/10.1139/cjfas-2022-0144

[4] TOR #6: If possible, develop methods to calculate a biologically-based cap or limit on bycatch of river herring in ocean fisheries.
http://www.asmfc.org/files/Meetings/2022AnnualMeeting/ShadandRiverHerringBoardPresentations_Nov_2022.pdf

Spatial and temporal genetic stock composition of river herring bycatch in southern New England Atlantic herring and mackerel fisheries

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Abstract

Anadromous river herring (alewife and blueback herring) persist at historically low abundances and are caught as bycatch in commercial fisheries, potentially preventing recovery despite conservation efforts. We used newly established single-nucleotide polymorphism genetic baselines for alewife and blueback herring to define fine-scale reporting groups for each species. We then determined the occurrence of fish from these reporting groups in bycatch samples from a Northwest Atlantic fishery over four years. Within sampled bycatch events, the highest proportions of alewife were from the Block Island (34%) and Long Island Sound (22%) reporting groups, while for blueback herring the highest proportions were from the Mid-Atlantic (47%) and Northern New England (24%) reporting groups. We then quantified stock-specific mortality in a focal geographic area (~3500 km2 including Block Island Sound) of high bycatch incidence and sampling effort, where the most accurate estimates of mortality could be made. During this period, we estimate that bycatch took about 4.6 million alewife and 1.2 million blueback herring, highlighting the need to reduce bycatch mortality for the most depleted river herring stocks.

Keywords: *Alosa pseudoharengus*, *A. aestivalis*, bycatch, genetic stock identification (GSI), mixing proportion estimates, mortality estimates

1. Introduction

Anadromous fish populations represent unique sources of biological diversity (Fraser et al. 2011) but are impacted by anthropogenic activities in both their marine and freshwater environments (Limburg and Waldman 2009). In freshwater, habitat degradation and barriers to suitable spawning habitats impede successful reproduction and juvenile survival, while in marine environments, overfishing and capture in non-target fisheries (i.e., bycatch) represent additional sources of mortality (Crowder and Murawski 1998; Barbarossa et al. 2020). Catch limits on targeted and non-targeted fisheries can help to reduce overfishing and bycatch levels (Bethoney et al. 2017). However, knowing where to implement catch limits in marine systems can be challenging, as anadromous fishes tend to be highly migratory and typically aggregate into mixed stock groups. The high levels of mortality that can result from bycatch lead to increased levels of overfishing that may influence population dynamics (Crowder and Murawski 1998). To protect the most vulnerable populations, accurate identification and assessments of the stock-specific contributions to bycatch are required, but these tasks can be challenging and remain priorities in the field of fisheries management.

Genetic data are used to determine the population composition of a mixed sample, such as fisheries bycatch, with genetic stock identification (GSI) analyses. Such analyses use genotypes to assign the individuals of interest back to the potential sources, or reporting groups, with a set of reference genotypes from individuals of known population origin (Manel et al. 2005). Application of these methods are particularly useful for accurately classifying highly migratory anadromous fish back to their freshwater spawning populations, as these species generally exhibit sufficient genetic differentiation, despite geographic proximity (Shaklee et al. 1999; Seeb et al. 2000; Beacham et al. 2009, 2012; Clemento et al. 2014; Gilbey et al. 2017).

Using highly variable and/or large numbers of genetic markers with these classification methods can also help to improve accuracy (Bernatchez and Duchesne, 2000; Narum et al. 2008; Hess et al. 2011). Thus, for managed species, GSI methods are especially useful when combined with mortality estimates, as it is often the only way to assess when particular populations or stocks approach or surpass their catch allocations (Shaklee et al. 1999). Similarly, GSI methods can also be used to identify where populations of conservation concern are being captured as bycatch and which populations are most vulnerable to this additional source of mortality, allowing managers to prioritize populations more effectively for protection (Hasselman et al. 2016; Guthrie III et al. 2019; Stewart et al. 2019).

Alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*), sister species collectively called river herring, once comprised an important fishery in the Northwest Atlantic, but are now depleted to historically low levels (ASMFC [Atlantic States Marine Fisheries Commission] 2012; Bailey et al. 2017). River herring are iteroparous, anadromous species found in rivers, estuaries and Atlantic coastal habitats. Alewife are found from Newfoundland, Canada to North Carolina, USA while blueback herring range from Nova Scotia, Canada to St. Johns River, Florida, USA (Fay et al. 1983). Mature adults migrate from the ocean to freshwater in the spring to spawn. Juveniles remain in freshwater for several months before migrating to the ocean, reaching maturity at ages 2–6. River herring will return to natal freshwaters to spawn, but straying is common, and individuals will colonize new sites if there is access (Loesch 1987).

Previous research used microsatellite genetic markers and demographic characteristics to identify distinct river herring stocks (A’hara et al. 2012; McBride et al. 2014, 2015; Palkovacs et al. 2014). More recently, species-specific single-nucleotide polymorphism (SNP) markers were developed for both alewife and blueback herring across their respective species ranges and used to evaluate genetic population differentiation. These broadscale studies identified four genetic groups in alewife and five genetic groups in blueback herring (Baetscher et al. 2017; Reid et al. 2018). Both species showed significant patterns of isolation by distance, with straying among adjacent rivers, as well as additional population structure indicated by significant genetic differentiation (F_{ST} estimates ranged from 0.008 – 0.022 for alewife and 0.026 – 0.114 for blueback herring for regional groups), even among rivers within close proximity (McBride et al. 2014, 2015, Reid et al. 2018). These SNP marker datasets provide higher resolution than previously available microsatellite data (A'hara et al. 2012), expanding the set of tools available for river herring research and conservation.

Starting in the 1970s, substantial population declines have been observed in both alewife and blueback herring. River herring population declines were historically caused by a combination of dams, habitat loss, pollution of freshwaters, and overfishing (Limburg and Waldman 2009). Dam removals, habitat restoration projects, and pollution control measures have considerably improved freshwater conditions, but river herring have failed to recover in many areas, including southern New England. Due to harvest moratoria, there are no longer any major fisheries that target river herring, but bycatch of river herring in large fisheries may be limiting recovery (ASMFC 2012; Bethoney et al. 2014; Hasselman et al. 2016; Bailey et al. 2017). River herring are frequently caught as bycatch in marine fisheries targeting Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*). The estimated amount of river herring bycatch occurring in these fisheries can be as large as directed fisheries landings once were and has ranged from 34 metric tons (mt) in 2014 to 765 mt in 2007, although methodologies for estimating bycatch as well as the estimates themselves can be highly variable (Cieri et al. 2008, https://www.greateratlantic.fisheries.noaa.gov/ro/fso/reports/Mackerel_RHS/Mackerel_RHS.htm

). Voluntary bycatch avoidance programs can help mitigate incidental capture (Bethoney et al. 2017) and are encouraged to limit the bycatch of river herring, but questions remain about which stocks and rivers are most impacted.

Various approaches have been utilized to characterize the composition of river herring caught as bycatch, and to determine the rivers and/or stocks most impacted. Bethoney et al. (2014) used length-frequency distributions and life-history patterns to determine that bycatch from 2011 and 2012 was having the greatest impacts on populations from the southern New England and the New Jersey-Long Island regions. Hasselman et al. (2016) used a genetics approach, assessing the stock composition of both alewife and blueback herring bycatch in 2012 and 2013. They found that the highest proportion of bycatch originated from the most depressed genetic stocks (which included their defined southern New England reporting group for alewife and Mid-Atlantic reporting group for blueback herring). Palkovacs et al. (2014), suggested that bycatch was having the greatest negative influence on populations from the Long Island Sound region.

In this study, we used SNP genetic markers and reference datasets for alewife and blueback herring across their species' ranges to determine the composition and mortality of river herring stocks captured as bycatch in the Atlantic herring and mackerel fisheries from 2012 to 2015. We aimed to: 1) define alewife and blueback herring reporting groups at finer geographic scales than previous studies to provide additional geographic resolution on the origins of bycatch, 2) assess the frequency of these newly refined reporting groups in bycatch events sampled across a broad portion of the Atlantic herring and mackerel fishery off the Northeastern United States, and 3) assess stock-specific mortality for river herring in a 3569 km2 area off southern New England, including Rhode Island and Block Island Sounds, where bycatch monitoring was sufficient to provide reliable estimates of mortality.

2. Materials and methods

2.1 Genetic baselines for genetic stock identification in river herring

Bycatch samples were collected during opportunistic portside sampling and assigned using the reference genetic datasets for alewife (n = 5,678) and blueback herring (n = 2,247) detailed in Reid et al. (2018). Briefly, these datasets were established by extensively sampling the rangewide distribution of each species, and specimens were then genotyped with species-specific SNP panels developed by Baetscher et al. (2017). Previous results identified population structure across both species' ranges based on 93 SNPs in alewife and 95 SNPs in blueback herring, and through simulations showed that both datasets have high accuracy for resolving mixing proportions to the level of regional genetic groups (Reid et al. 2018). By taking advantage of the previously identified hierarchical genetic structure (McBride et al. 2014, 2015; Reid et al. 2018) and groupings supported by self-assignment tests (Supplementary Fig. S1), we used additional simulations to evaluate the accuracy of estimated mixing proportions to finer-scale reporting groups (RGs), defined by a smaller number of spawning rivers, than in the prior analysis by Reid et al. (2018). Finer-scale RGs were postulated based on regional proximity and biological metrics such as run timing (Table 1). To assess these newly defined RGs (indicated in Fig. 1A & 1B), simulations based on the genetic SNP datasets established in Reid et al. (2018) were conducted and consisted of 100 replicates of varying RG proportions with Dirichlet distributions. From each simulated mixture composed of the baseline RGs, 100 fish were subsampled to reflect estimates from smaller sample sizes, and mixing proportions were estimated using maximum likelihood (ML) in the *'rubias'* package (Moran and Anderson 2019) in *R* 3.4.4 (R Core Team, 2018) which implements GSI_SIM (Anderson et al. 2008). To determine the accuracy for identifying and assessing the magnitude of contribution by each RG, correlations were assessed between the simulated and estimated mixing proportions and the variance and standard deviation of each RG were estimated as measures of the accuracy of the assignments.

2.2 Sampling and genotyping of river herring bycatch samples

To characterize the stock composition, we sampled alewife and blueback herring bycatch from commercial inshore and offshore Atlantic herring and mackerel fisheries in and around southern New England from winter 2012 to 2015 (Table 2). River herring specimens were opportunistically collected from mid-water trawl and small-mesh bottom trawl vessels during portside and at-sea sampling conducted by the Massachusetts Division of Marine Fisheries (MADMF), University of Massachusetts Dartmouth School for Marine Science and Technology (SMAST), Maine Department of Marine Resources (DMR), and National Oceanic and Atmospheric Administration (NOAA) Northeast Fisheries Observer Program (NEFOP).

Samples were mainly collected in the winter (December to March) of each year (however, there is a single spring sample in May around Cape Cod), as this season has the highest incidence of bycatch encounters, and assigned to the NOAA Statistical Area where they were caught (Fig. 2A). The Statistical Areas were grouped by region and designated as follows: New Jersey-Long Island (NJLI, Statistical Area 615), Southern New England (SNE, Statistical Areas 613 & 537), Long Island Sound and Block Island Sound (LISBIS, Statistical Areas 611 & 539), and Cape Cod (CC, Statistical Area 521) (Fig. 2A).

Specimens were identified to species based on morphological features and peritoneal colour (Jordan and Evermann 1896; Scott and Crossman 1973). Collections from 2012 and 2013 were preserved in ethyl alcohol and were previously genotyped using 15 microsatellites (A'hara et al. 2012) and identified against an available microsatellite reference dataset (Palkovacs et al. 2014; Hasselman et al. 2016). Fin tissue was sampled from each specimen collected in 2014 and 2015, placed on Whatman® blotting paper, dried and stored in coin envelopes.

Genomic DNA for all the specimens from 2012 to 2015 was extracted using the DNeasy 96 Blood and Tissue Kits and a BioRobot 3000 (Qiagen, Inc.) following manufacturer's specifications. Specimens morphologically assigned to alewife and blueback herring were genotyped using SNP Type assays (Fluidigm Corporation) for their respective species-specific markers (Baetscher et al. 2017) on 96.96 Dynamic SNP Genotyping Arrays using the EP1 system (Fluidigm). These loci, which included 93 alewife-specific SNPs and 95 blueback herring-specific SNPs, were previously used to establish the rangewide reference datasets (Reid et al. 2018). Four loci were consistently genotyped in the blueback herring reference baseline but could not be amplified consistently in all the bycatch collections, and were removed from bycatch analyses in both datasets. Genotypes with more than 10% missing data were removed prior to estimating mixing proportions. In addition, for both species, alewife genotyped with the blueback herring markers and blueback herring genotyped with the alewife markers were used to genetically identify misidentified fish and hybrids. These individuals were identified through stock assignments and extremely low heterozygosity across SNP loci (Clemento et al. 2014; Reid *et al.*, 2018). After filtering, the final bycatch datasets consisted of 5,234 alewife and 1,450 blueback herring, with sample sizes for the specific region and time-period designations ranging from 42 to 1,264 for alewife and 32 to 183 for blueback herring (Table 2).

2.3 Focal region selection and strata for estimating mixing proportions

River herring are caught as bycatch in many fisheries across their entire range, but hotspots of bycatch and effort are known to occur (Cieri et al. 2008; Cournane et al. 2013; Bethoney et al. 2014, 2017). To define a region for which stock-specific mortality could be estimated, we determined the geographic area of highest sampling and capture fishing effort. First, we examined sampling and fishery effort (MADMF portside and NEFOP at-sea) from the midwater and small-mesh bottom trawls of the Atlantic herring and mackerel fisheries in the southern New England and Mid-Atlantic regions of the northwest Atlantic Ocean during the months of December to March from 2012 to 2015. Trips landing less than 2,000 pounds of Atlantic herring or mackerel were omitted. Next, we defined the focal region for assessing mortality impacts of river herring bycatch. The selected region encompassed the majority of southern New England/Mid-Atlantic trips (79.7%), sampled trips (84.8%), and genetic samples collected (76.7%). It also included Rhode Island Sound and Block Island Sound, representing a region of high fishery effort. It is hereafter referred to as the focal region (Fig. 3).

Approximately 30.1% of landings from this area were sampled during the time period analyzed in this study. The spatial extent of Atlantic herring and mackerel-target trips, sampled trips, genetic samples and fishery coverage levels was compared for individual months. It was determined that aggregating data temporally by half-winter periods (with December to January defined as HW1 and February to March as HW2) allowed for the most appropriate analysis, with detailed assignments and reasonable fishery sampling coefficients of variation (CVs) in all but one alewife stratum (2015 HW2) and three blueback herring strata (2013 HW2, 2014 HW1, 2014 HW2). These strata were characterized by low sample sizes and large CVs.

2.4 Estimating mixing proportions and mortality within the focal region

2.4.1 Mixing proportion estimates by species sample and by half winter strata

To estimate mixing proportions, the datasets were broken down by (i) species, (ii) year, region and half-winter designations, and (iii) fish that were captured in the focal region only. First, we analysed data for each species separately to assess which RGs were encountered in each dataset and to determine the frequency with which each RG occurred. Next, each species dataset was further divided into year, region and half-winter designation to evaluate the temporal and spatial occurrence of RGs in sampled bycatch events. Finally, we assessed fish only within the focal area to estimate mortality occurring in this specific area during the study period. This was the only area where we had sufficient data to confidently estimate bycatch mortality.

All mixing proportion estimates were calculated using '*rubias*' (Moran and Anderson 2018). We used the maximum likelihood (ML) and parametric bootstrap (PB) options, with sample parameters estimated from the posterior probability distribution generated with 2,000 sweeps of the MCMC algorithm, following 200 sweeps of burn-in for the ML method. We report the fraction of fish in each mixture sample assigned to each RG.

2.4.2 Estimating the number and composition of bycatch mortality within the focal area

River herring bycatch in the Atlantic herring and mackerel fisheries is highly variable in space and time (Bethoney et al. 2014). To characterize bycatch as fully and accurately as possible, we created expansions of bycatch (Cochran 1978; Bethoney et al. 2014) and combined them with stock composition estimates within the focal region. First, the total weights of alewife and blueback herring bycatch were generated for the midwater trawl and small-mesh bottom trawl

Atlantic herring and mackerel fisheries (combined) for each of the eight half-winter (HW) periods using a ratio estimator method (Cochran, 1978; Bethoney et al. 2014). Alewife and blueback herring species bycatch rates (R) were calculated for each temporal strata (R_{HW}) as

$$R_{HW} = \frac{\sum_i r_{HW,i}}{\sum_i T_{HW,i}}$$

where $r_{HW,i}$ represents the weight of observed alewife or blueback herring bycatch from trip i and half-winter HW, and $T_{HW,i}$ represents the weight of total observed catch of the target species (Atlantic herring or Atlantic mackerel) from trip i in half-winter HW. Variance was estimated as

$$var(R_{HW}) = \left(\frac{1}{n_{HW}\bar{\bar{T}}^2{}_{HW}}\right) x \left[\frac{\left(\sum_i r_{HW,i}^2\right) + R_{HW}^2\left(\sum T_{HW,i}^2\right) - 2R_{HW}\left(\sum_i r_{HW,i} T_{HW,i}\right)}{n_{HW} - 1}\right] x \left(\frac{N_{HW} - n_{HW}}{N_{HW}}\right)$$

Total river herring bycatch for each half-winter (B_{HW}) was calculated as

$$B_{HW} = R_{HW} \; x \; L_{HW}$$

where L_{HW} is the total weight of target species landings from half-winter HW based on NOAA Vessel Trip Reports. The coefficient of variation (CV) for the ratios was defined as

$$CV(R_{HW}) = \frac{\sqrt{var(R_{HW})}}{R_{HW}}$$

The variance for the bycatch in all half-winters was estimated by

$$var(B_{HW}) = L_{HW}^{2}\, x\, var(R_{HW})$$

Individual numbers of alewife and blueback herring removals were then estimated for each of the eight half-winter periods by applying a length-based expansion to estimated weights, modified from Bethoney et al. (2014). For each species, the proportion of fish in each centimetre length class *LC* from each half winter ($P_{LC,HW}$) was generated as

$$P_{LC,HW} = \frac{n_{LC,HW} x\ expW@L_{LC}}{\sum expW_{HW}}$$

where the number of fish measured as bycatch in each length class ($n_{LC,HW}$) was multiplied by the expected weight for a fish in that length class ($expW@L_{LC}$) (MADMF unpublished data) and divided by the sum of all expected weights from that half winter ($\sum expW_{HW}$). The expanded weight of bycatch for fish in each length class ($ExpaW_{LC,HW}$) was calculated as

$$ExpaW_{LC,HW} = P_{LC,HW} \times B_{HW}$$

The total number of expanded bycatch fish in each half winter ($ExpaN_{HW}$) is calculated as

$$ExpN_{HW} = \sum\nolimits_{HW} \frac{ExpW_{LC,HW}}{expW@L_{LC}}$$

A bootstrapped error estimate (1,000 iterations) around the total number of bycatch of each species in each half winter was calculated using the '*scales'* package in RStudio (3.3.0).

To calculate mortality by RG and half winter from 2012 to 2015, we multiplied the estimated proportions and CIs by the estimated number of fish caught in bycatch for each half winter.

3. Results

3.1 GSI to reporting groups

We defined 10 reporting groups (RGs) in alewife from the simulation results (Fig. 1A, Table 1 & Fig. S2). The number of rivers that comprised each RG and the geographic extent of each RG were variable (Table 1). The alewife RGs identified in Canada included the Gulf of St. Lawrence (GLS), ranging from the Garnish River to the Bras d' Or Lakes; Nova Scotia (NSC) from West River to Tusket River; and the Bay of Fundy (BOF), from the Gaspereau River to the Canadian Saint John's River. The Northern New England (NNE) RG ranged from Dennis Stream of the St. Croix River to the Merrimack River, which is the same as previously defined in Reid et al. (2018). Rivers in southern New England comprise four RGs, including Massachusetts Bay (MB) ranging from the Parker River to Stony Brook; Nantucket Sound (NUN) from the Herring River to the Monument River; Block Island Sound (BIS) from the Nemasket River to the Saugatucket River; and Long Island Sound (LIS) from the Thames River to the Carll's River. The Mid-Atlantic (MAT) RG ranged from the Hudson River to the James River while the Albemarle Sound (ALB) RG extended from the Chowan River to the Alligator River. All RGs for alewife showed highly concordant estimates among simulated and estimated mixing proportions. The RGs with the largest standard deviations (SD) among true simulated mixing proportions and estimates from our baseline RGs were NUN (SD = 0.048) and BIS (SD = 0.047). In both cases, the effect was most pronounced in larger "true" mixing proportions compared to estimated proportions.

For blueback herring, we found support for 10 RGs throughout the species range (Fig. 1B, Table 1 & Supplementary Fig. S3). Blueback herring exhibited greater genetic population structure at the southern end of their range (see Reid et al. 2018), which allowed for finer-scale partitioning, sometimes even to the level of individual rivers. The Canadian (CAN) RG ranged from the Margaree River to the Saint John's River, while the Northern New England (NNE) RG ranged from the East Machias River to the Sebasticook River. The Mid New England (MNE) RG ranged from the Oyster River to the Parker River. Rivers in southern New England comprised two RGs: the Southern New England (SNE) RG ranged from the Mystic River to Gilbert-Stuart Brook and the Long Island Sound (LIS) RG ranged from the Connecticut River to the Mianus River. Rivers in the Mid-Atlantic comprised two RGs: the Mid-Atlantic (MAT) RG ranged from the Hudson River to the James River; and the Albemarle Sound (ALB) RG extended from the Chowan River to the Neuse River. Rivers in the South Atlantic comprised three RGs: the Cape Fear (CF) River; the South Atlantic (SAT) RG that ranged from the Santee River to the Altamaha River; and the St. John's River (STR). Again, all RGs showed strong correlations between simulated "true" mixing proportions and the estimates from our baseline RGs. In blueback herring, the RGs with the highest standard deviations were CAN (SD = 0.044), NNE (SD = 0.048), and LIS (SD = 0.047).

3.2 River herring reporting group encounters in bycatch samples

The mean proportional contribution of each species-specific RG was first estimated. Overall, alewife encounters were mainly composed of fish from Block Island Sound (BIS; 0.338, 95% CIs: 0.319 – 0.356) and Long Island Sound (LIS; 0.220, 95% CIs: 0.203 – 0.237), followed by Nantucket and the Mid-Atlantic (Fig. 1C). Overall, blueback herring encounters were largely composed of fish from the Mid-Atlantic (MAT; 0.470, 95% CIs: 0.438 – 0.503) and Northern New England (NNE; 0.241, 95% CIs: 0.209 – 0.270) (Fig 1D).

These data were then further evaluated by year, half winter, and region to assess RG encounters on a spatial and temporal scale. The composition of RGs in the samples varied across regions and years for both species (Fig. 2 & Table 2), but the RGs with the highest encounters were relatively consistent. Alewife bycatch across years and regions mainly comprised NUN, BIS, LIS and MAT (Fig. 1A, 1C & 2B). Reporting groups spawning in rivers proximate to the geographical locations of bycatch encounters tended to be present at higher proportions than those spawning further away (Fig. 2A & B). For example, most of the fish encountered in the LISBIS region were from the BIS and LIS RGs. Almost no fish were encountered from the northernmost GLS RG, and fish encountered from Canadian RGs were only found in the dataset at appreciable levels in 2015 and mainly in Cape Cod (Fig. 2B). Alewife encountered in the NJLI region (Statistical Area 615) were mainly from the proximate MAT RG and not from the ALB RG (Fig. 2B). Alewife encountered in the Cape Cod region (Statistical Area 521) showed a larger proportion of bycatch from the NNE RG relative to the SNE, LISBIS, and NJLI regions, but with important differences in which RGs were detected across HWs. Within the Cape Cod region, bycatch samples were mainly represented by NNE (27%), BIS (12%), and MAT (21%) RGs in HW1, with a shift to ~65% from NNE in HW2 (Table 2).

Blueback herring bycatch encounters in the LISBIS region (Statistical Areas 611 & 539) were mainly composed of NNE and MAT RGs across years (Fig. 1B, 1D & 2C). Across all HWs, the South Atlantic RG was not frequently encountered, indicating that these fish are likely not being caught in Northeast fisheries. The MNE and SNE RGs were not frequently encountered, despite being geographically proximate to bycatch events in the LISBIS region.

3.3 Composition and mortality estimates of river herring bycatch in the focal region

Total alewife mortality from 2012 to 2015 was estimated at ~4.6 million fish (95% CIs: 2.6 – 8.0 million; Table S3). The amount of bycatch caught by year varied, with 2013 a particularly high year (~2.6 million fish) for alewife bycatch (Fig. 3B). The top contributors to alewife bycatch in the focal region were the BIS, MAT, NUN and LIS RGs, respectively. Within the focal region, the largest numbers of alewife bycatch across years came from rivers in the larger southern New England region (comprising the MB, NUN, BIS and LIS RGs), ranging from ~43% to 95% of the catch in a given year. Within the reporting groups that represent rivers in southern New England, the highest bycatch numbers came from Block Island Sound, Nantucket, and Long Island Sound (Fig. 4, Table S3). In 2013, a large proportion of alewife originating from the MAT RG were observed in both HW1 (~35% of total catch) and HW2 (~30% of total catch). The MAT RG was the second highest contributor to overall alewife bycatch mortality due to these unusually high bycatch events, which represented ~83% of total MAT alewife mortality within the focal region during the study period (Fig. 4).

Total estimated blueback herring mortality from 2012 to 2015 was ~1.2 million fish (95% CIs: ~500,000 – 2.9 million). There was no observable increase in bycatch mortality in 2013, as seen in alewife, within the focal region off of southern New England (Fig. 3B). Blueback herring bycatch mortality within the focal region was mainly composed of MAT-origin individuals (ranging from 47 – 72%) which represented ~630,000 (CIs: 306,764 – 1,196,392) fish across study years (Fig. 5, Supplementary Table S3).

4. Discussion

River herring populations have exhibited marked declines since the early 1970s (ASMFC 2012, Bailey et al. 2017). Conservation and management efforts to mitigate these declines have focused primarily on freshwater ecosystems, with much less attention paid to the marine phase of their life cycle. We applied recently developed SNP genetic markers for alewife and blueback herring to define reporting groups (RGs) at finer geographic scales than previously possible. Our reassessment allowed delineation of 10 RGs each in alewife and blueback herring, that could be accurately identified in mixed samples. We then determined the contributions of these newly refined RGs in bycatch opportunistically sampled from the Atlantic herring and mackerel fisheries from 2012 to 2015. Alewife sampled from all collected bycatch originated predominantly from Block Island Sound and Long Island Sound. In contrast, the majority of blueback herring bycatch originated from the Mid-Atlantic and Northern New England RGs and not the RGs with closer proximity to bycatch events which have shown some of the highest declines in recent years (Palkovacs et al. 2014; Bailey et al. 2017). We also observed spatial and temporal variation in bycatch composition for both species. Extensive sampling and fishery effort in a focal geographic region off of southern New England allowed us to estimate the magnitude of bycatch for that area. These results show that substantially more alewife than blueback herring were caught in the region, perhaps reflecting their current stock sizes (blueback herring have suffered more severe declines than alewife in this region; Bailey et al. 2017).

Within this focal region, rivers in southern New England (BIS, LIS, NUN RGs) and the Mid-Atlantic contributed the most to alewife mortality across the study period, with the Mid-Atlantic fish mostly coming from a single year (2013). Blueback herring mortality within this focal region mainly impacted fish originating from the Mid-Atlantic and Northern New England RGs.

4.1 Reporting groups

In this study, we utilized recently published SNP-based genetic reference datasets (Reid et al. 2018), which included more rivers throughout the alewife and blueback herring species' ranges than previous studies based on microsatellite data (Palkovacs et al. 2014; Hasselman et al. 2016). As a result of the increased number of genetic markers and more extensive geographic sampling of the entire range, we were able to define reporting groups that identify populations from smaller collections of rivers, a scale more useful for addressing conservation-focused questions in these species. Our finer-scale reporting groups allowed us to determine the origins of river herring bycatch with greater precision, especially within areas of known impact. The inclusion of the northernmost river herring populations in our reference datasets allowed us to evaluate potential impacts on Canadian populations, which was not possible in previous studies. Overall, the reliability of assignments to these reporting groups was very high (see Fig. S2 and Fig. S3) and the RGs we define are thus both suitable for assessing the occurrence of specific RGs in mixed samples, as well as providing accurate estimates of RG proportions in fishery bycatch.

4.2 The spatial and temporal occurrence of reporting groups in river herring bycatch

Our GSI results revealed that the occurrence of river herring reporting groups in bycatch events sampled from the Northeast Atlantic herring and mackerel fisheries from 2012 to 2015 was not uniform. Within these regions where bycatch encounters were occurring, finer-scale stock contributions were highly variable. We found that alewife from the BIS and LIS RGs were encountered frequently in bycatch, while the majority of blueback herring samples were from the MAT and NNE RGs. In both species, migration timing is a gradient and starts in March for each species' southernmost populations (Loesch 1987; Ellis and Vokoun 2009; ASMFC 2012), which likely influences which species and populations are encountered as bycatch during their return to spawn in natal rivers. For alewife, prior work showed that bycatch was concentrated on southern New England populations (Hasselman et al. 2016). Our results lead to a more nuanced understanding, narrowing the region of most frequent bycatch down to populations from rivers associated with Block Island and Long Island Sounds (Fig 2A, C). For blueback herring, prior work showed that bycatch was concentrated on Mid-Atlantic populations (Hasselman et al. 2016). Our results refine this area to rivers from the Hudson River to the James River (Fig. 2 B, D). Future research efforts may be able to further subdivide this large Mid-Atlantic RG into identifiable groups, but it was not possible with our SNP data, and interbasin migration may limit the ability to further discriminate fish from these river systems.

For each species, the representation of RGs in bycatch was generally consistent across years and seasons, although some variation was present. For most of the half-winter seasons, alewife from the BIS and LIS RGs occurred most frequently in bycatch, but non-trivial proportions of alewife from rivers within the NNE, NUN, and MAT RGs were also encountered.

For the LISBIS region (Statistical Areas 611 & 539), alewife from BIS and LIS were encountered particularly frequently across years in bycatch samples. As this region is immediately adjacent to the spawning rivers, it is likely that the fishery is encountering adults returning to their natal rivers to spawn and/or juveniles migrating from these rivers. Future analyses focusing on the size of fish in bycatch will provide more resolution on which life stages are being encountered in bycatch. These RGs were encountered less frequently in the other regions, suggesting that targeted management to reduce bycatch in the LISBIS region is likely to have substantial benefits for conservation of proximate alewife populations.

For the Cape Cod region (Statistical Area 521), alewife from the NNE RG made up a large portion of the sampled bycatch, particularly in February-March 2015 (Fig. 2B). The observation that alewife sampled from catch in this region are not from the adjacent rivers suggests that it is an important migration corridor, with alewife caught in this area likely migrating through, rather than returning to their immediately adjacent spawning rivers, as in the LISBIS region. Although alewife data for the Cape Cod region were only available for 2015, the onset of the spring alewife spawning migration is known to be temperature dependent and typically occurring from March through May (Loesch 1987; Ellis and Vokoun 2009; ASMFC 2012). The high occurrence of NNE fish in the bycatch sampled from the Cape Cod region may be due to shifts in diel migration patterns as daylight hours increase in the spring, which could potentially influence river herring catchability in the Atlantic herring and mackerel fisheries.

For blueback herring, bycatch from MAT and NNE were encountered most frequently across seasons and years within a region, but blueback herring from MNE, CAN, and SAT were also identified in the bycatch at appreciable rates. The frequent occurrence of MNE blueback herring in bycatch is notable, as that RG was found to be at “high risk of extinction”, but did not qualify as a Distinct Population Segment or Significant Portion of the Range in the most recent Endangered Species Act status review, so was not listed (NOAA, 2019). However, the MNE RG represents a relatively small section of coastline, with only a few rivers potentially contributing to bycatch, so the presence of MNE fish in our samples underscores the importance of potential management actions that could reduce mortality of these highly vulnerable populations.

4.3 Mortality numbers and composition in the focal area

We estimated that nearly six million individual river herring were captured as bycatch from 2012 to 2015 from trips conducted within the focal region. This estimate represents the majority of total bycatch in the Atlantic herring and mackerel fisheries south of Cape Cod, as the focal region captured 80% of trips and 70% of the total catch (i.e., total weight landed) that occurred in the NJLI, SNE, and LISBIS regions during this time. This total represents about 4.6 million alewife and 1.2 million blueback herring. Even though the species distributions of alewife and blueback herring overlap in the focal region, alewife likely suffered higher mortality than blueback herring, because alewife tend to be more common at the northern extent of the alewife-blueback herring range overlap (ASMFC 2012). New England has less blueback herring spawning habitat than the Mid-Atlantic, and while some southern New England rivers once supported very large blueback herring populations, decades of declines in southern New England have potentially resulted in fewer blueback herring from this region and hence less potential bycatch (Palkovacs et al. 2014; Bailey et al. 2017). Studies examining the spatial and intra-annual variability of river herring captured as bycatch in the Atlantic herring fishery have found that the largest bycatch incidents occurred mainly during the fall and winter months, when the Atlantic herring fishery was concentrated in waters off Cape Cod, southern New England and the northern Mid-Atlantic Bight. During spring and summer months, the fisheries operate in areas that may overlap less with river herring migration and feeding grounds. Cieri et al. (2008) found that bycatch amounts for the months of April through September accounted for less than 10% of the annual bycatch total, and Cournane et al. (2013) showed that only 17% of monitored trips that encountered river herring occurred during the period of March through October. Within the focal region from December to March, we found that alewife bycatch was consistently composed of fish from BIS, followed by NUN and then LIS. However, there was an increase in the bycatch of alewife in 2013 (Fig. 3B) that was not observed in blueback herring. This increase appeared to be driven by a prevalence of MAT-origin alewife that was not observed in other years, and which made up ~83% of estimated MAT mortality in the focal region during our study period (Fig. 4). The high bycatch in 2013 that corresponded with the prevalence of MAT-origin fish, led to the MAT RG having the second highest number of fish caught in the focal region during the study period. This result highlights the importance of tying GSI to landings by establishing and maintaining robust observing programs in high-volume fisheries.

Our findings within the focal region provide further evidence that fisheries bycatch may be disproportionately affecting populations in the southern New England region (Palkovacs et al. 2014; Hasselman et al. 2016) and could also periodically impact regions beyond southern New England. The bycatch mortality of southern New England-origin fish in southern New England waters could be contributing to the depleted nature of river herring populations in that region, despite targeted fishing moratoriums (ASMFC, 2012). Demographic and life-history shifts towards smaller and younger alewife spawners have also been observed in southern New England (Davis and Schultz 2009; Palkovacs et al. 2014), and the most recent stock assessment update indicated decreases in mean length, maximum age and repeat spawner percentage across the species range (Bailey et al. 2017). Such shifts can be indicative of overfishing and can result in reduced reproductive output (Barneche et al. 2018), which may further threaten the persistence of river herring. Explicitly linking demographic history with stock identity, as done here with our genetic analysis, will require additional investigation and a focus on developing abundance estimates for river herring across their range.

4.4 Management into the future

Anadromous river herring populations persist at historically low levels and, even though they are not targeted directly by commercial fisheries, bycatch in the Atlantic herring and mackerel fisheries may be impeding population recovery. We used high-resolution genetic reference datasets to determine the origins of river herring caught as bycatch in the southern New England Atlantic herring and mackerel fisheries and found that bycatch was an important source of mortality for alewife and blueback herring originating from rivers within the Mid-Atlantic and southern New England.

A better understanding of how stock-specific variation in life history overlaps with ecosystem drivers of river herring catchability at sea (Turner et al. 2017) and how these factors, in turn, impact demographic trends in freshwater ecosystems (Bailey et al. 2017), will be important for refining conservation measures that limit marine bycatch of the most depleted stocks (Cournane et al. 2013). In addition, the distributions of many northwestern Atlantic fisheries stocks, including alewife, Atlantic herring and Atlantic mackerel have already shifted northward and/or to deeper water (Nye et al. 2009). Further climate change-induced distributional shifts may alter the stock composition of river herring captured as incidental catch or bycatch in the future. Ongoing evaluation of spatial and temporal distributions of river herring populations and their contributions to fisheries bycatch will be important for adaptive management policies and for preserving the viability and genetic diversity of river herring populations as environmental conditions change.

Due to the collapse of the Atlantic herring fishery and subsequent regulations under Amendment 8 of the Atlantic Herring Fishery Management Plan (NOAA, 2021), major shifts in the intensity and location of fishing effort for Atlantic herring and mackerel occurred in 2019. Specifically, the effort that had historically occurred in the focal area described in this study moved south to Hudson Canyon and focused on Atlantic mackerel rather than Atlantic herring. Importantly, the effort shift to the Hudson Canyon and greater Mid-Atlantic Bight could now impact blueback herring disproportionately, as that species comprises the majority of fish sampled from those areas (MADMF, unpublished data). Abundance data for Mid-Atlantic and South Atlantic blueback herring populations are extremely limited (but see Ogburn et al. 2017a, 2017b and Plough et al. 2018), but many of the declining demographic trends seen elsewhere have also been observed in those populations (Bailey et al. 2017). The impact and conservation consequences of this new fishery effort should be examined in future work.

Amendment 8 also formerly prohibited mid-water trawls (one of the gear types in this study), from use within 12 nautical miles from shore in most of our study's focal region. However, in early 2022, this mid-water trawl exclusion zone was removed via a U.S. Federal Court ruling (https://content.govdelivery.com/accounts/USNOAAFISHERIES/bulletins/3246845), re-opening fishing in the area with the highest bycatch totals. Our results suggest that had these restrictions remained in place, they could have had significant conservation benefits for southern New England and Mid-Atlantic alewife. The re-opening of these inshore regions are now likely to have severe negative impacts for river herring in this region. Increased conservation and management strategies will be required to rebuild populations and sustain these fish into the future.

Supplementary material

Supplementary information is available with the online version of the article.

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Data Availability

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Tables

Table 1. Summary of rivers in each reporting group (RG) for alewife and blueback herring. Details of rivers in the baseline can be found in Supplementary Tables S1 and S2.

Table 2. Detailed mixing proportions with 95% CIs for alewife and blueback herring by reporting groups (RGs), region, and half winter.

Table 1. Summary of rivers in each reporting group (RG) for alewife and blueback herring. Details of rivers in the baseline can be found in Supplementary Tables S1 and S2.

Species	Country	reporting groups	code	no of rivers
Alewife	Canada	Gulf of St. Lawrence	GLS	12
	Canada	Nova Scotia coast	NSC	8
	Canada	Bay of Fundy	BOF	4
	USA	Northern New England	NNE	32
	USA	Mass Bay	MB	5
	USA	Nantucket Bay	NUN	4
	USA	Block Island Sound	BIS	4
	USA	Long Island Sound	LIS	15
	USA	Mid-Atlantic	MAT	11
	USA	Albemarle Sound	ALB	3
				98
Blueback herring	Canada	Canada	CAN	3
	USA	Northern New England	NNE	5
	USA	Mid-Northern New England	MNE	3
	USA	Southern New England	SNE	5
	USA	Long Island Sound	LIS	5
	USA	Mid-Atlantic	MAT	12
	USA	Albemarle Sound	ALB	3
	USA	Cape Fear	CF	1
	USA	South Atlantic	SAT	3
	USA	St. John's river	STR	1
				41

Table 2. Detailed mixing proportions with 95% CIs for alewife and blueback herring by reporting groups (RGs), region, and half winter.

Name	STAT regions	Code	YEAR	HW	STAT areas	Sample size	Reporting Groups									
Alewife							**GLS**	**NSC**	**BOF**	**NNE**	**MB**	**NUN**	**BIS**	**LIS**	**MAT**	**ALB**
NJLI_HW2_15	New Jersey/Long Island	NJLI	2015	2	615	92	0.008 (0.000-0.043)	0.009 (0.000-0.051)	0.000 (0.000-0.006)	0.276 (0.188-0.375)	0.062 (0.000-0.160)	0.035 (0.000-0.163)	0.073 (0.000-0.180)	0.045 (0.000-0.144)	0.464 (0.338-0.579)	0.017 (0.000-0.104)
LISBIS_HW1_15	Long Island/Block Island	SNE	2015	1	539/611	924	0.000 (0.000-0.004)	0.003 (0.000-0.009)	0.011 (0.005-0.019)	0.125 (0.102-0.150)	0.018 (0.002-0.045)	0.145 (0.106-0.184)	0.409 (0.363-0.455)	0.132 (0.102-0.167)	0.101 (0.076-0.126)	0.055 (0.036-0.076)
LISBIS_HW2_14	Long Island/Block Island	SNE	2014	2	539/611	935	0.001 (0.000-0.006)	0.000 (0.000-0.001)	0.000 (0.000-0.001)	0.001 (0.000-0.008)	0.004 (0.000-0.023)	0.170 (0.129-0.213)	0.386 (0.341-0.433)	0.390 (0.344-0.435)	0.033 (0.020-0.050)	0.013 (0.005-0.023)
LISBIS_HW1_14	Long Island/Block Island	SNE	2014	1	539/611	1264	0.001 (0.000-0.005)	0.000 (0.000-0.002)	0.000 (0.000-0.000)	0.009 (0.003-0.018)	0.001 (0.000-0.010)	0.137 (0.103-0.171)	0.371 (0.332-0.411)	0.367 (0.328-0.406)	0.095 (0.076-0.117)	0.019 (0.010-0.030)
LISBIS_HW2_13	Long Island/Block Island	SNE	2013	2	539/611	443	0.002 (0.000-0.013)	0.002 (0.000-0.010)	0.001 (0.000-0.009)	0.047 (0.025-0.072)	0.011 (0.000-0.032)	0.161 (0.110-0.217)	0.307 (0.249-0.366)	0.094 (0.050-0.149)	0.300 (0.242-0.357)	0.076 (0.040-0.118)
LISBIS_HW1_13	Long Island/Block Island	SNE	2013	1	539/611	278	0.001 (0.000-0.006)	0.001 (0.000-0.005)	0.000 (0.000-0.007)	0.101 (0.066-0.139)	0.051 (0.015-0.097)	0.142 (0.084-0.212)	0.179 (0.117-0.243)	0.044 (0.009-0.094)	0.375 (0.306-0.448)	0.105 (0.060-0.159)
LISBIS_HW2_12	Long Island/Block Island	SNE	2012	2	539/611	43	0.003 (0.000-0.030)	0.002 (0.000-0.022)	0.001 (0.000-0.013)	0.065 (0.007-0.162)	0.049 (0.000-0.189)	0.042 (0.000-0.222)	0.227 (0.057-0.439)	0.367 (0.095-0.602)	0.221 (0.088-0.388)	0.023 (0.000-0.121)
LISBIS_HW1_12	Long Island/Block Island	SNE	2012	1	539/611	342	0.001 (0.000-0.009)	0.009 (0.000-0.025)	0.000 (0.000-0.002)	0.038 (0.018-0.065)	0.007 (0.000-0.036)	0.141 (0.080-0.202)	0.623 (0.550-0.699)	0.093 (0.048-0.147)	0.084 (0.050-0.121)	0.003 (0.000-0.024)
SNE_HW2_15	Southern New England	LIBI	2015	2	537/613	288	0.001 (0.000-0.006)	0.018 (0.005-0.038)	0.015 (0.003-0.034)	0.069 (0.039-0.106)	0.084 (0.044-0.129)	0.136 (0.069-0.219)	0.398 (0.318-0.482)	0.137 (0.077-0.200)	0.113 (0.060-0.176)	0.028 (0.000-0.074)
SNE_HW2_13	Southern New England	LIBI	2013	2	537/613	62	0.009 (0.000-0.053)	0.005 (0.000-0.043)	0.001 (0.000-0.007)	0.217 (0.120-0.333)	0.037 (0.000-0.165)	0.193 (0.000-0.387)	0.067 (0.000-0.202)	0.118 (0.000-0.296)	0.321 (0.181-0.477)	0.031 (0.000-0.123)
SNE_HW1_13	Southern New England	LIBI	2013	1	537/613	52	0.003 (0.000-0.031)	0.001 (0.000-0.013)	0.001 (0.000-0.009)	0.137 (0.053-0.249)	0.008 (0.000-0.072)	0.225 (0.094-0.382)	0.253 (0.106-0.423)	0.052 (0.000-0.175)	0.256 (0.046-0.438)	0.064 (0.000-0.280)
CC_HW2_15	Cape Cod	CC	2015	2	521	42	0.004 (0.000-0.037)	0.002 (0.000-0.022)	0.130 (0.035-0.260)	0.693 (0.511-0.851)	0.029 (0.000-0.174)	0.044 (0.000-0.144)	0.008 (0.000-0.087)	0.015 (0.000-0.112)	0.074 (0.016-0.165)	0.001 (0.000-0.011)
CC_HW1_15	Cape Cod	CC	2015	1	521	426	0.002 (0.000-0.015)	0.027 (0.011-0.047)	0.068 (0.041-0.097)	0.271 (0.227-0.318)	0.016 (0.004-0.034)	0.088 (0.052-0.131)	0.120 (0.079-0.164)	0.080 (0.040-0.131)	0.209 (0.155-0.266)	0.109 (0.066-0.155)
Blueback Herring							**CAN**	**NNE**	**MNE**	**SNE**	**LIS**	**MAT**	**ALB**	**CF**	**SAT**	**STR**
NJLI_HW2_15	New Jersey/Long Island	NJLI	2015	2	615	98	0.142 (0.005-0.310)	0.355 (0.175-0.519)	0.003 (0.000-0.032)	0.025 (0.003-0.066)	0.006 (0.000-0.049)	0.453 (0.343-0.567)	0.005 (0.000-0.052)	0.000 (0.000-0.005)	0.001 (0.000-0.011)	0.000 (0.000-0.003)
LISBIS_HW1_15	Long Island/Block Island	SNE	2015	1	539/611	145	0.002 (0.000-0.018)	0.162 (0.099-0.233)	0.012 (0.000-0.045)	0.037 (0.011-0.075)	0.002 (0.000-0.017)	0.656 (0.559-0.742)	0.011 (0.000-0.072)	0.000 (0.000-0.006)	0.111 (0.065-0.169)	0.007 (0.000-0.027)
LISBIS_HW1_13	Long Island/Block Island	SNE	2013	1	539/611	183	0.074 (0.000-0.157)	0.254 (0.164-0.347)	0.053 (0.000-0.116)	0.064 (0.026-0.114)	0.078 (0.000-0.175)	0.474 (0.389-0.556)	0.001 (0.000-0.009)	0.000 (0.000-0.002)	0.000 (0.000-0.004)	0.000 (0.000-0.002)
LISBIS_HW2_12	Long Island/Block Island	SNE	2012	2	539/611	99	0.008 (0.000-0.057)	0.064 (0.009-0.133)	0.099 (0.029-0.184)	0.059 (0.019-0.120)	0.046 (0.000-0.163)	0.721 (0.602-0.827)	0.001 (0.000-0.013)	0.000 (0.000-0.002)	0.001 (0.000-0.007)	0.000 (0.000-0.002)
LISBIS_HW1_12	Long Island/Block Island	SNE	2012	1	539/611	379	0.014 (0.000-0.049)	0.120 (0.078-0.165)	0.113 (0.074-0.153)	0.106 (0.074-0.145)	0.110 (0.059-0.166)	0.516 (0.451-0.579)	0.008 (0.000-0.035)	0.000 (0.000-0.002)	0.000 (0.000-0.002)	0.011 (0.003-0.024)
SNE_HW2_15	Southern New England	LIBI	2015	2	537/613	145	0.151 (0.040-0.269)	0.550 (0.419-0.685)	0.074 (0.025-0.143)	0.028 (0.007-0.064)	0.058 (0.006-0.128)	0.137 (0.076-0.206)	0.001 (0.000-0.012)	0.000 (0.000-0.002)	0.001 (0.000-0.006)	0.000 (0.000-0.001)
SNE_HW1_12	Southern New England	LIBI	2012	1	537/613	40	0.004 (0.000-0.044)	0.093 (0.011-0.215)	0.081 (0.000-0.219)	0.003 (0.000-0.027)	0.108 (0.000-0.278)	0.695 (0.514-0.869)	0.012 (0.000-0.112)	0.001 (0.000-0.005)	0.002 (0.000-0.017)	0.000 (0.000-0.004)
CC_HW2_15	Cape Cod	CC	2015	1	521	163	0.113 (0.000-0.221)	0.458 (0.336-0.578)	0.015 (0.000-0.075)	0.001 (0.000-0.008)	0.005 (0.000-0.046)	0.379 (0.283-0.470)	0.029 (0.000-0.089)	0.000 (0.000-0.002)	0.000 (0.000-0.005)	0.000 (0.000-0.001)
CC_SP1_14*	Cape Cod	CC	2014	-	521	50	0.428 (0.196-0.657)	0.332 (0.099-0.601)	0.130 (0.001-0.260)	0.008 (0.000-0.055)	0.025 (0.000-0.121)	0.051 (0.000-0.170)	0.025 (0.000-0.112)	0.001 (0.000-0.006)	0.001 (0.000-0.014)	0.000 (0.000-0.006)
CC_HW1_13	Cape Cod	CC	2013	1	521	32	0.049 (0.000-0.236)	0.419 (0.192-0.629)	0.141 (0.032-0.288)	0.005 (0.000-0.045)	0.005 (0.000-0.049)	0.368 (0.208-0.539)	0.008 (0.000-0.079)	0.001 (0.000-0.008)	0.002 (0.000-0.025)	0.001 (0.000-0.008)
CC_HW2_12	Cape Cod	CC	2012	2	521	51	0.037 (0.000-0.145)	0.151 (0.018-0.286)	0.095 (0.000-0.221)	0.023 (0.001-0.077)	0.062 (0.000-0.237)	0.619 (0.442-0.781)	0.011 (0.000-0.106)	0.000 (0.000-0.007)	0.002 (0.000-0.016)	0.000 (0.000-0.005)

*SP1 Collected in Spring

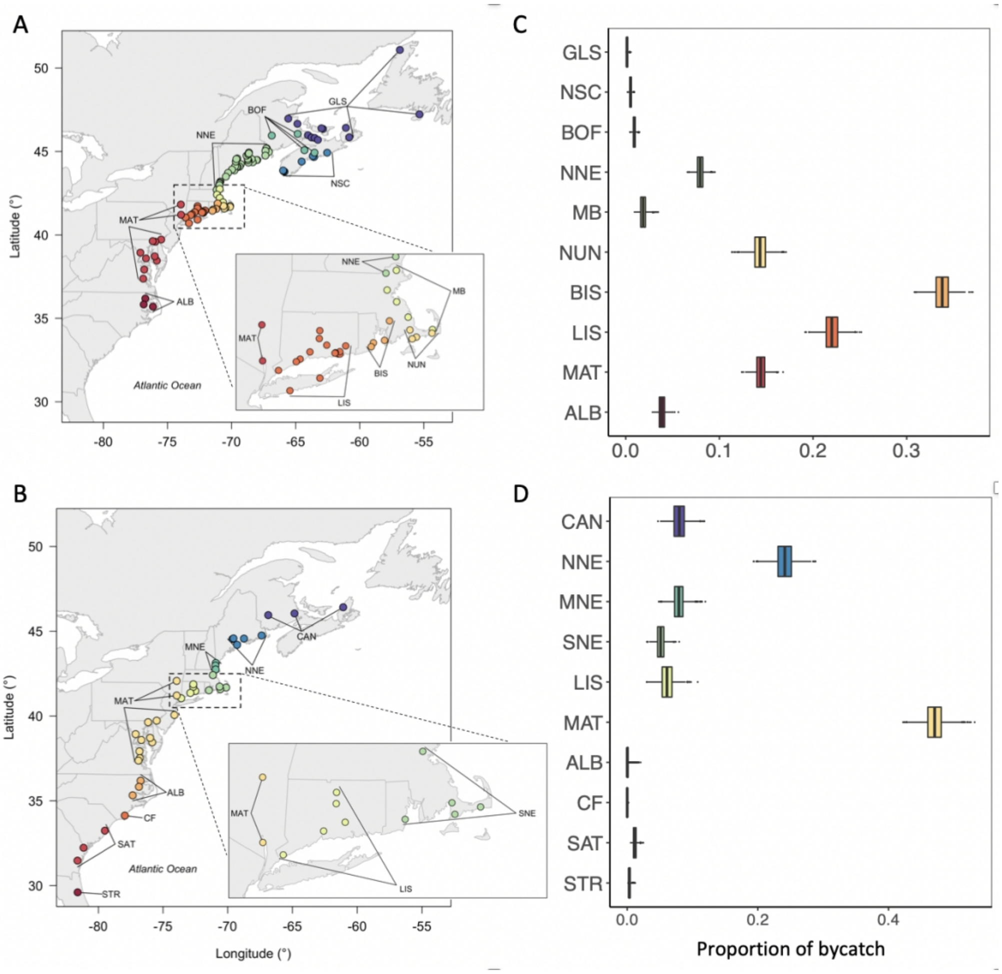
Figure 1. Sampling locations for A) alewife and B) blueback herring, with coloring of dots for each river indicating its reporting group were plotted in R. The rivers, their latitude and longitude, and reporting group information is summarized in Table 1 and detailed in Tables S1 & S2. The median mixing proportion estimates by reporting group for C) alewife and D) blueback herring. The boxplots show the lower 25% and upper 75% quantiles.

Figure 2. Posterior bootstrap mixing proportion estimates for alewife and blueback herring across space and time, where A) indicates the geographic locations of Statistical Areas with regional codes: Cape Cod (CC), Southern New England (SNE), Long Island Sound and Block Island Sound (LISBIS), and New Jersey-Long Island (NJLI) (map projection NAD83 and coordinate system UTM). Mixing proportion estimates for B) alewife and C) blueback herring by region, year, and half winter (HW). HW1 corresponds to fish caught December - January and HW2 to fish caught February - March of the corresponding winter. The missing proportions for alewife and blueback herring in 2015 are individuals that were misidentified to species in the field and were genotyped on the wrong species panel. Sample sizes are indicated in parentheses.

Figure 3. Estimated total mortality for each half-winter period within a focal region of high fisheries sampling and effort. The purple polygon A) indicates the focal region boundaries, which spans the NOAA Statistical Areas of 537, 538, 539 and 611, while B) shows the estimated mortality of alewife (orange line) and blueback herring (blue line), with the shaded area of each line indicating the 95% CI within this focal region from 2012 to 2015. The focal region included all waters bounded by the following coordinates (NAD83 UTM): 1) Coastline of mainland Massachusetts and longitude 70^{o}50’ West, due south to; 2) 41^{o}20’ North x 70^{o}50’ West (near western point of Martha’s Vineyard), southwest to; 3) 41^{o}0’N x 71^{o}30’W, due west to; 4) 41^{o}0’N x 71^{o}51.4333’W, due north to; 5) the eastern point of Montauk, New York at 41^{o}04.3333’N x 71^{o}51.4333’W, and NNW; and 6) coastline of Connecticut at longitude 71^{o}54.1’W. Data was provided by MA DMF and NEFOP.

Figure 4. Alewife mortality estimates for the focal region by reporting group (RG), year and half-winter partition.

Figure 5. Blueback herring mortality estimates for the focal region by reporting group (RG), year and halfwinter partition.



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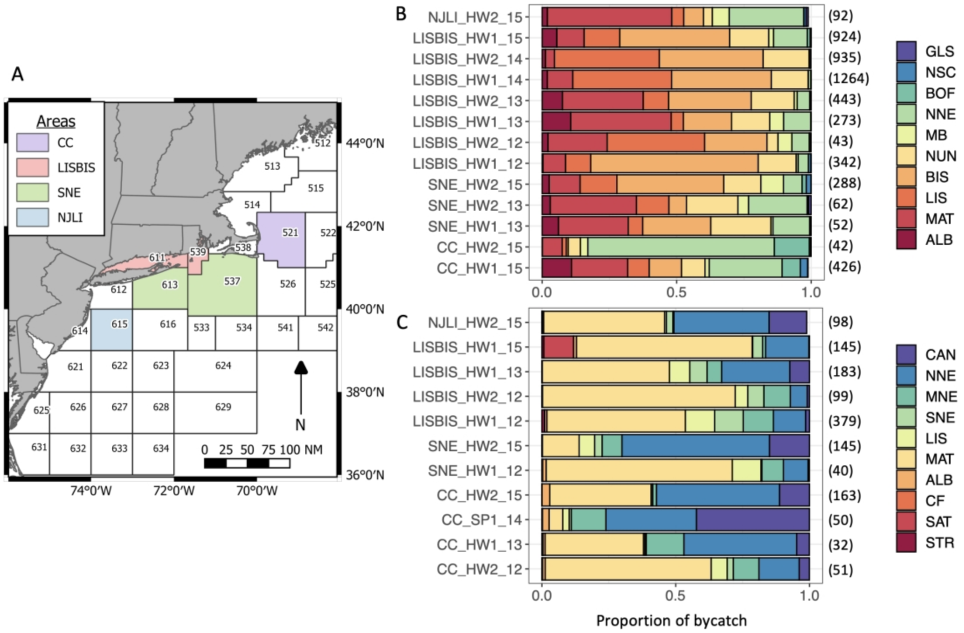

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1107x713mm (57 x 57 DPI)

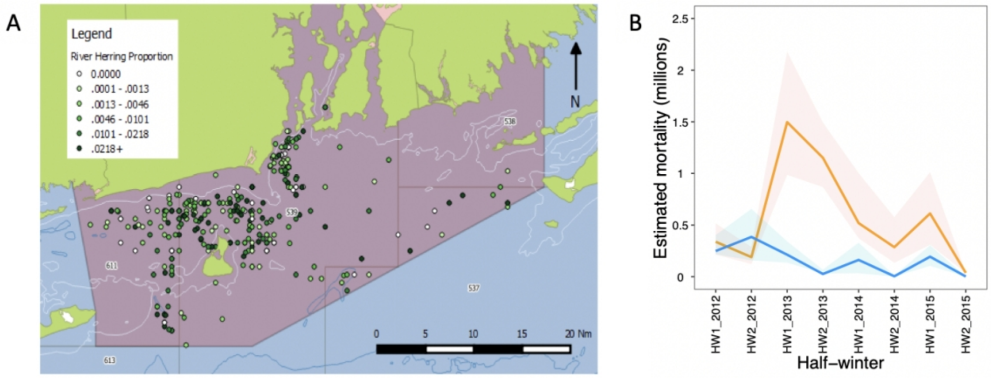

Figure 3. Estimated total mortality for each half-winter period within a focal region of high fisheries sampling and effort. The purple polygon A) indicates the focal region boundaries, which spans the NOAA Statistical Areas of 537, 538, 539 and 611, while B) shows the estimated mortality of alewife (orange line) and blueback herring (blue line), with the shaded area of each line indicating the 95% CI within this focal region from 2012 to 2015. The focal region included all waters bounded by the following coordinates (NAD83 UTM): 1) Coastline of mainland Massachusetts and longitude 70^{0}50’ West, due south to; 2) 41^{0}20’ North x 70^{0}50’ West (near western point of Martha’s Vineyard), southwest to; 3) 41^{0}0’N x 71^{0}30’W, due west to; 4) 41^{0}0’N x 71^{0}51.4333’W, due north to; 5) the eastern point of Montauk, New York at 41^{0}04.3333’N x 71^{0}51.4333’W, and NNW; and 6) coastline of Connecticut at longitude 71^{0}54.1’W. Data was provided by MA DMF and NEFOP.

626x250mm (57 x 57 DPI)

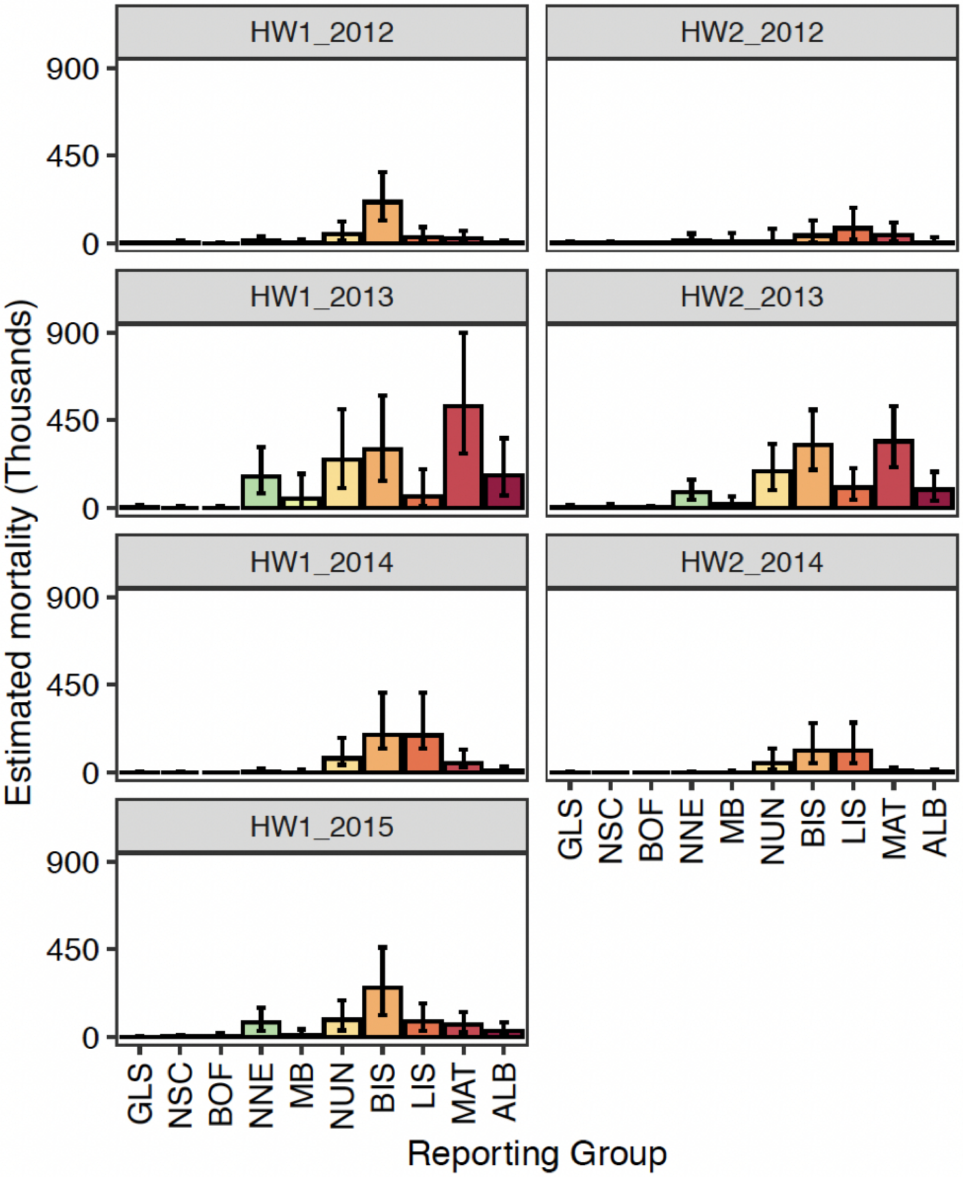

Figure 4. Alewife mortality estimates for the focal region by reporting group (RG), year and half-winter partition.

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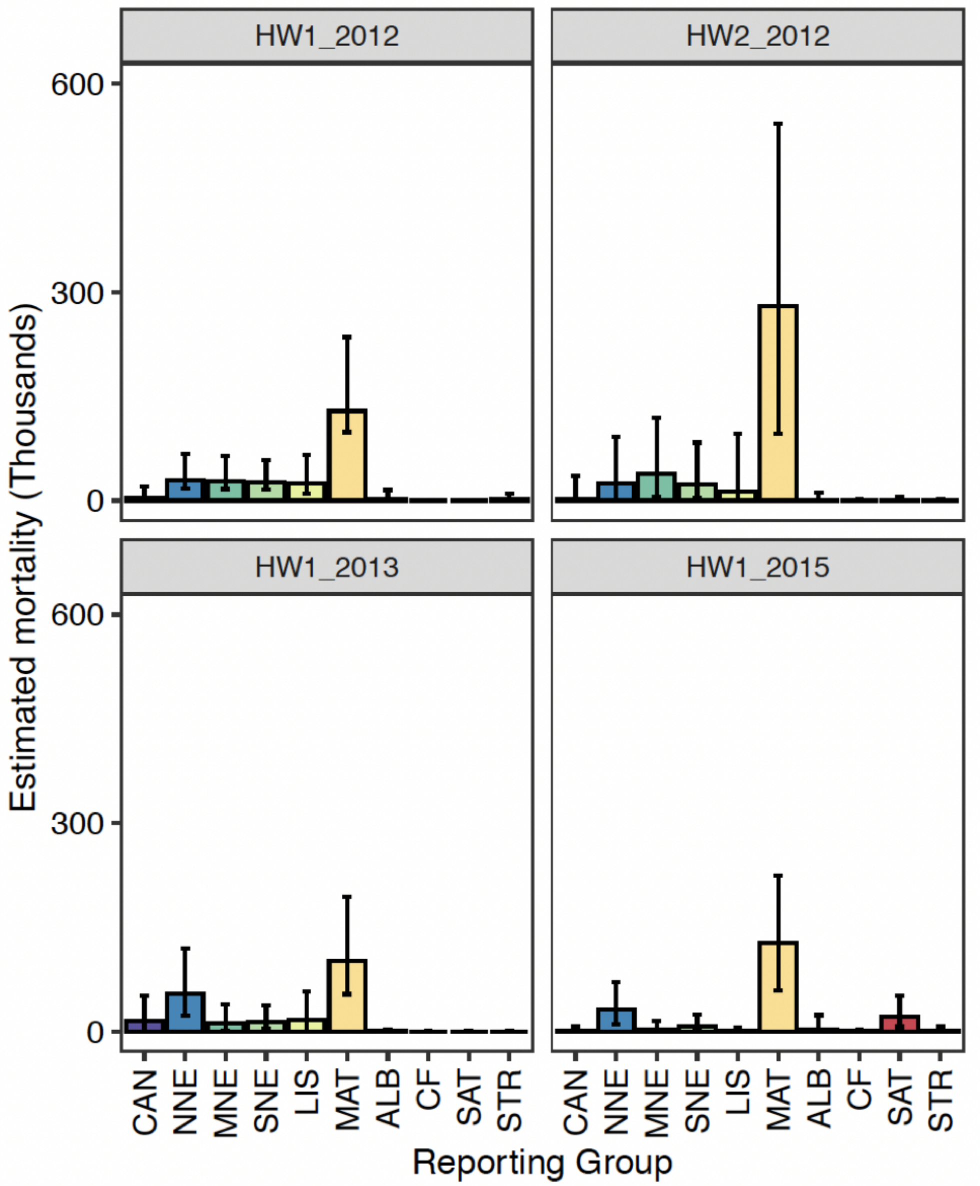

Figure 5. Blueback herring mortality estimates for the focal region by reporting group (RG), year and half-winter partition.

433x527mm (57 x 57 DPI)