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Genetic stock composition of marine bycatch reveals disproportional impacts on depleted river herring genetic stocks

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Abstract

Bycatch of mid-trophic level anadromous fishes that connect marine and freshwater ecosystems is a growing conservation concern. Anadromous alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) are important components of coastal freshwater and marine food webs, but have experienced dramatic declines in the abundances of spawning adults. Freshwater-focused restoration efforts have yielded few consistent signs of recovery; raising concerns that bycatch in Northwest Atlantic commercial fisheries may be negating these conservation actions. Using data from 15 microsatellites genotyped for baseline populations and bycatch, we conducted genetic stock identification to understand how bycatch was partitioned among previously identified regional genetic stocks. We then combined this information with fishery observer data to estimate genetic stock-specific bycatch mortality for the southern New England Atlantic herring fishery (2012-2013). Bycatch overall, but especially in the Atlantic herring fishery, was disproportionately assigned to the most severely depleted genetic stocks (alewife Southern New England stock – 70% of assignments; blueback herring Mid-Atlantic stock – 78% of assignments). These genetic stocks overlap in the region surrounding Long Island Sound, suggesting that bycatch taken from this area in recent years may be negatively impacting recovery efforts in this region. Our study suggests that mitigating bycatch on the southern New England fishing grounds may benefit recovery efforts for alewife and blueback herring genetic stocks that have experienced the greatest declines in spawning adult abundances.

Introduction

The incidental catch of non-target species in commercial fisheries (*i.e.*, bycatch) represents a major threat to the health of marine ecosystems (Crowder and Murawski 1998; Chuenpagdee et al. 2003). Bycatch of marine megafauna has received considerable attention because of their charismatic nature and keystone role in marine food webs (Myers and Worm 2005; Lewison et al. 2014). Less focus has been directed to bycatch of mid-trophic level species, despite their importance as a key trophic link in marine ecosystems (Smith et al. 2011; Pikitch et al. 2014). Such species often make long distance migrations, transferring nutrients between ecosystems and connecting distant food webs (Bakun et al. 2010; Hall et al. 2012). Ecosystem connectivity may be particularly impacted if the flow of energy and nutrients across major ecosystem boundaries, like that between marine and freshwater environments, is disrupted. Few species traverse this boundary in large numbers, making those that do particularly important for maintaining ecosystem connectivity. Notable among these species are anadromous fishes that spawn in freshwater, but migrate to the ocean to grow and reach maturity before returning to their natal (typically) freshwater spawning grounds to reproduce. Thus, when anadromous fish populations become depleted, a key functional linkage between marine and freshwater ecosystems is lost (Schindler et al. 2005; Moore et al. 2011; Hall et al. 2012).

Along the Atlantic Coast of North America, anadromous alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) – collectively ‘river herring’ – comprise a key ecological component of coastal freshwater and marine food webs (Yako et al. 2000; MacAvoy et al. 2000; McDermott et al. 2015), and once supported an important commercial fishery. However, spawning adult abundances have declined by 93% since 1970, and many spawning populations now persist at historically low levels (Hightower et al. 1996; Limburg and Waldman 2009;

Atlantic States Marine Fisheries Commission (ASMFC) 2012). These declines have been attributed to multiple factors including overfishing, inadequate fish passage at dams, pollution, predation, water withdrawals, acidification, changing ocean conditions, and climate change (ASMFC 2012). River herring spawn in freshwater habitats from Newfoundland to Florida during the spring, and juveniles typically spend several months in freshwater before emigrating to the ocean and undertaking extensive north-south marine migrations along the Atlantic coast before returning to their natal rivers to spawn at 2-5 years of age (Messieh 1977; Neves 1981; Klauda et al. 1991). An examination of population genetic structure using microsatellites revealed that most US alewife and blueback herring spawning populations have significantly ($P<0.05$) different multi-locus allele frequency distributions, and constitute genetically distinguishable populations (hereafter ‘populations’) (see Table 2 and Table 3 in Palkovacs et al. (2014)). This interpretation is consistent with definitions of ‘population’ that place emphasis on reproductive cohesion among groups of individuals (i.e., the ‘evolutionary paradigm’; (Waples and Gaggiotti 2006)). Bayesian clustering analysis, which can provide conservative estimates of population genetic structure (Faubet et al. 2007), revealed that US alewife populations were nested within three regional genetic stocks (hereafter ‘genetic stocks’) (*i.e.*, Northern New England, Southern New England, and Mid-Atlantic), whereas US blueback herring populations were nested within four genetic stocks (*i.e.*, Northern New England, Southern New England, Mid-Atlantic, and South Atlantic) (Palkovacs et al. 2014). Palkovacs et al. (2014) also showed that recent declines in adult abundance and body size have been greatest for alewife populations from the Southern New England stock (*i.e.*, Mystic River, MA south to the Hudson River, NY) and for blueback herring populations from the Southern New England stock (*i.e.*, Mystic River, MA south to Gilbert-Stuart, RI) and Mid-Atlantic stock (*i.e.*, Connecticut River, CT south to the Neuse River, NC) (see Figure 3 in Palkovacs et al. 2014).

Restoration efforts, including habitat and water quality improvements, fish passage projects, and harvest restrictions, have focused largely on mitigating threats in freshwater habitats. However, persistent depression of population abundances, reductions in age and size of spawning adults, and few consistent signs of recovery suggest that other sources of mortality – possibly marine – may be negating these freshwater conservation actions (Nelson et al. 2011). Indeed, observed shifts in life history and demography for a southern New England alewife population (*i.e.*, decreased size, younger age structure, fewer repeat spawners in Bride Brook, CT) are consistent with the notion that marine mortality in this region has recently increased (Davis and Schultz 2009).

Bycatch in commercial fisheries of the northwest Atlantic Ocean has become a major concern for river herring conservation (ASMFC 2012; Cournane et al. 2013; Bethoney et al. 2013, 2014a). From 1989 to 2010, bycatch of alewife and blueback herring equaled or exceeded that reported for directed in-river commercial fisheries for 6 of 22 years (ASMFC 2012). Bycatch in the Atlantic herring (*Clupea harengus*) fishery off the southern New England coast is of particular concern (ASMFC 2012), because this fishery encounters river herring at relatively high rates (Cournane et al. 2013; Bethoney et al. 2014a, 2014b) and is geographically proximate to the populations and genetic stocks that have experienced the greatest declines in spawning adult abundances and body size (Palkovacs et al. 2014). Understanding the impacts of marine bycatch on populations and genetic stocks requires knowledge of how bycatch mortality is partitioned. If bycatch mortality is evenly distributed across populations, there may be minimal consequences to abundance for any particular population. However, if that same mortality is concentrated on just a few populations, major population- or genetic stock-level declines may occur.

Here, we determine how bycatch mortality for alewife and blueback herring in northwest Atlantic commercial fisheries is partitioned among genetic stocks using genetic stock identification (GSI), a commonly applied form of mixed-stock analysis (Brenden et al. 2015). Genetic stock identification involves the genotyping of individuals from a series of 'baseline' populations and from a 'mixture' sample (*e.g.*, bycatch), and the subsequent estimation of mixture proportions using a maximum likelihood or Bayesian statistical framework that relates the genotypes in the mixture sample to the expected genotype frequencies in the baseline populations (Anderson et al. 2008). This method is a standard tool in the management of mixed stock fisheries, and has been applied to a variety of species (*e.g.*, Wirgin et al. 1995; Koljonen et al. 2005; Clemento et al. 2014; Waldman et al. 2014). Using data from 15 microsatellites genotyped for populations and bycatch specimens for both species, we employed a Bayesian GSI method to assign bycatch to genetic stock of origin. We then used bycatch data collected by fishery observers to estimate the numbers of alewife and blueback herring taken as bycatch in the Atlantic herring fishery in 2012 and 2013, and applied the results from GSI to estimate genetic stock-specific mortality of alewife and blueback herring in this fishery. This combined approach allowed us to identify the regional origins of river herring bycatch, and provided valuable insight into whether bycatch may be a contributing factor in hindering recovery efforts for the most depleted genetic stocks. Our results indicate that river herring bycatch is focused primarily on those genetic stocks that have experienced the greatest declines in spawning adult abundance (*i.e.*, Southern New England stock in alewife; Mid-Atlantic stock in blueback herring).

Mitigating the impacts of river herring bycatch will be an important component of conservation efforts to rebuild these genetic stocks and restore coastal ecosystems.

Materials and Methods

Sample collections

Collections of alewife and blueback herring from populations sampled across their US ranges were obtained from 2008-2011 (see Palkovacs et al. 2014), and served as baselines in the GSI of bycatch. Before performing GSI, interspecific hybrids were removed from the baseline dataset following the procedure described in (Hasselman et al. 2014). Our resulting baselines were comprised of 1070 alewife from 21 spawning populations nested within three genetic stocks (*i.e.*, Northern New England, Southern New England, and Mid-Atlantic) and 1252 blueback herring from 21 spawning populations nested within four genetic stocks (*i.e.*, Northern New England, Southern New England, Mid-Atlantic, and South Atlantic) (Figure 1; Table S1). These genetic stocks were used for GSI because previous research demonstrated genic homogeneity and non-significant ($P>0.05$) genetic differentiation (F_{ST}) among several geographically proximate alewife and blueback herring populations within these genetic stocks, and because an analysis of molecular variance (AMOVA) revealed greater genetic variation among genetic stocks than among populations within genetic stocks for both species (Palkovacs et al. 2014).

River herring bycatch specimens (N=2928) were sampled opportunistically by fisheries observers monitoring the Atlantic herring, shrimp (*Pandalid* spp.), longfin squid (*Doryteuthis pealeii*), and Atlantic cod (*Gadus morhua*) fisheries of the northwest Atlantic Ocean (Table 1). Details about the bycatch sampling programs used to acquire specimens for this study can be found in *Supplementary Materials*. The majority of samples came from the Atlantic herring fishery, which uses single and paired midwater trawl, and bottom otter trawl fishing gear. Other sampled fisheries use only bottom otter trawls. Bycatch collections were obtained in fall (October-December) and winter (January-March) during 2011-2013 from Statistical Areas (SA) comprising five near-shore regions (*i.e.*, Gulf of Maine (GoM), SA 513/514; Cape Cod (CC), SA 521; southern New England (SNE), SA 537/539/611; New Jersey-Long Island (NJLI), SA 612/613/615; Delaware (DEL), SA 622). Although the Atlantic herring fishery also occurs on Georges Bank (SA 522, 525, 561, 562) commercial fisheries encounter almost no river herring bycatch in this off-shore region (Cieri et al. 2008; Cournane et al. 2013). Tissue (fin clip or muscle plug) was preserved in 95% ethanol until DNA extraction.

Bycatch specimens were initially identified to species based on peritoneal coloration (Scott and Crossman 1973), but were ultimately classified as alewife or blueback herring based on multilocus genotypes, using specimens of known species (n=100 per species) and the Bayesian model-based clustering method implemented in STRUCTURE v.2.3.3 (settings: K=2; correlated allele frequencies; admixture model; burn-in=50,000 steps; 250,000 steps of the Markov chain Monte Carlo (MCMC) algorithm) (Pritchard et al. 2000, Falush et al. 2003). Hybrids were identified following the same procedure applied to population baseline populations (see above; Hasselman et al. 2014). Bycatch specimens misidentified at sea were re-classified to their correct species prior to analyses. Hybrid individuals, specimens not genotyped across a minimum of six microsatellites, and instances where fewer than five specimens were sampled in a given bycatch stratum (see below) were removed from analyses. These adjustments resulted in a dataset for alewife (n=1747) and blueback herring (n=1013) bycatch that was used for GSI (Table 1).

Laboratory protocols

Bycatch specimens were genotyped across a suite of 15 polymorphic microsatellite loci developed for alewife (*Ap010*, *Ap033*, *Ap037*, *Ap038*, *Ap047*, *Ap058*, *Ap070*, *Ap071*) and blueback herring (*Aa046*, *Aa070*, *Aa074*, *Aa081*, *Aa082*, *Aa091*, *Aa093*) (A'Hara et al. 2012). These same loci were previously used to genotype anadromous populations for assessment of population genetic structure across the US ranges of these species (Palkovacs et al. 2014). Details regarding DNA isolation and genotyping protocols involving bycatch specimens were consistent with those used for baseline populations, as previously reported in (Palkovacs et al. 2014). Briefly, genomic DNA was extracted from tissue using one of two methods: Promega Wizard® SV Genomic DNA Purification System or 10% Chelex 100 (Bio-Rad, Richmond, CA). Amplification, size-fragment analysis, and scoring were conducted following (A'Hara et al. 2012). To confirm consistency in scoring and reproducibility of genotypes, positive and negative controls were used.

Genetic data analyses

Data conformance to model assumptions

Genotyping artefacts were assessed using MICROCHECKER v.2.2.3 (Van Oosterhout et al. 2004). Evidence for null alleles in baseline populations resulted in the exclusion of four loci for alewife (*Aa082*, *Ap037*, *Ap047*, *Ap070*) and two for blueback herring (*Aao81,* Ap058). Hardy-Weinberg equilibrium (HWE) among baseline populations for alewife and blueback herring, and linkage disequilibrium (LD) among loci was confirmed previously, as was selective neutrality (Palkovacs et al. 2014).

Genetic stock identification

To perform GSI, we used the mixed stock analysis program *gsi_sim* (Anderson et al. 2008) available at: https://github.com/eriqande/gsi_sim and included as an executable in the R package *gpiper* (https://github.com/eriqande/gpiper). This method provides a computationally efficient Bayesian approach and has been used for the GSI of other threatened anadromous fishes, including green sturgeon (*Acipenser medirostris*) and Chinook salmon (*Onchorhynchus tshawytscha*) (Israel et al. 2009; Satterthwaite et al. 2014; Clemento et al. 2014). This method is particularly useful for alewife and blueback herring, as several of the populations within genetic stocks for both species are not strongly differentiated (Anderson et al. 2008; Palkovacs et al. 2014).

Evaluation of baseline populations

To determine the capacity of our baseline populations for assigning bycatch and estimating mixture proportions we assessed the behavior of estimates of genetic stock and population proportions by simulation. We simulated 50 different mixing proportions for each baseline population by first simulating the genetic stock proportions from a Dirichlet distribution with all parameters equal to 1.5, and then simulating mixing proportions of each population within a genetic stock, again using a Dirichlet distribution with parameters equal to 1.5. We then took each of the 50 mixing proportions, in turn, and simulated four bycatch samples (1000 fish each) using the CV-ML method of (Anderson et al. 2008) and estimated the mixing proportions by maximum likelihood. The resulting distribution of estimates was used to assess predicted bias and precision in our estimates of the mixing proportions for assignment to genetic stock and population of origin.

Genetic stock identification of bycatch

For the GSI of bycatch, samples from the posterior probability distribution for all parameters were generated using 50,000 sweeps of an MCMC algorithm after a 20,000 sweep burn-in phase (thinning interval=10) in *gsi_sim*. To verify proper mixing of the MCMC, we conducted seven independent runs of the model for both alewife and blueback herring using different starting seeds. We estimated the mixing proportion of each genetic stock for each sample. This method provided an estimate of the fraction of fish from each genetic stock in the bycatch at the time and place where the sample was taken, and has been shown to provide a better estimate of true mixing proportions than aggregated individual assignments (Koljonen et al. 2005). Thus, we do not report individual level assignments, but rather the overall assignment of bycatch to genetic stock of origin. We then examined patterns of bycatch in two complementary ways. We first examined all bycatch collectively to understand which genetic stocks were being encountered across all fisheries. We then partitioned bycatch into 'strata' represented by unique combinations of year, season, region, target fishery, and gear type, resulting in 25 strata for alewife and 17 strata for blueback herring (Table 1). We estimated mixing proportions independently for each stratum in order to better understand the effects of these various factors on the genetic stock composition of bycatch. MCMC samples of the mixing proportions from their posterior probability distribution were used to estimate the proportion and 95% credible intervals of bycatch represented by each genetic stock for each species overall and for each bycatch stratum. Although partitioning the bycatch data resulted in relatively small sample sizes for some strata, differences in samples sizes are readily accommodated by the Bayesian method implemented in *gsi_sim*, and are reflected as wider posterior probability distributions.

The Bayesian method implemented in *gsi_sim* yields unbiased estimates of GSI accuracy only within the confines of the assumptions of the model, and particularly the assumption that all populations in the mixture sample (*i.e.*, bycatch) are accurately represented in the baseline sample (Anderson et al. 2008). We examined centered and scaled negative log-likelihood values for each fish in the bycatch (*i.e.*, Z-scores; see (Clemento et al. 2014), p. 120) from *gsi_sim* to assess the possibility that bycatch specimens may have originated from populations not included in our baselines. Empirical cumulative density functions (ECDFs) of Z-scores from all bycatch were compared with those from all baseline populations using a two-sample Komolgorov-Smirnov (K-S) test (Sokal and Rohlf 2012) implemented in the R package 'stats' (R Development Core Team 2013).

Genetic stock-specific bycatch mortality in the Atlantic herring fishery

Using data collected by fishery observers in 2012 and 2013, we estimated alewife and blueback herring bycatch mortality (*i.e.*, total number) captured with midwater single and paired trawl *vs.* bottom otter trawl gear in the Atlantic herring fishery off the coast of southern New England (SA 537/539/611). Observed weight of bycatch was converted to number of individual river herring taken in this fishery in 2012 and 2013 by each gear type using an expansion factor:

$$\mathrm{X}_{s,i} = \frac{\mathrm{W}_{s,i}}{\mathrm{w}_{s,i}},$$

that expands the number of measured individuals of species *s* to the total count of species *s* caught in trip *i*. $\mathrm{W}_{s,i}$ is the total weight of species *s* caught in trip *i* and $\mathrm{w}_{s,i}$ is the weight of species *s* in trip *i* that were measured and weighed. The total number of river herring caught for each year and gear type was estimated by:

$$\frac{\sum_{\mathrm{i}} \mathrm{X}_{s,i} * \mathrm{n}_{s,l,i}}{\left[\frac{N-n}{N}\right]}$$

where $\mathrm{n}_{s,l,i}$ is the number of measured fish of species *s* in length class *l* in trip *i*, *n* is the number of sampled trips, and *N* is the total number of Vessel Trip Reports (reports of catch required by the US federal government for every fishing trip) from mid-water trawl or small mesh bottom trawl vessels targeting Atlantic herring (Bethoney et al. 2014b). We then applied the genetic stock proportions and 95% credible intervals estimated from GSI to calculate the genetic stock-specific bycatch mortality for alewife and blueback herring taken in this fishery. A relatively large proportion of the alewife and blueback herring bycatch strata were represented by the southern New England Atlantic herring fishery (0.56 and 0.59, respectively). To examine whether the genetic stock composition of bycatch in this fishery differed between years (2012 *vs.* 2013) and gear types (midwater single and paired trawl *vs.* bottom otter trawl) we used two-sample K-S tests. This was the only fishery for which a sufficient number of samples were available to conduct such an analysis.

Results

Species identification of bycatch and incidence of hybrids

Genotyping identified 32 specimens that were misidentified to species based on peritoneal coloration by fisheries observers, representing 1.2% of the bycatch sampled. In total, 21 alewife were misidentified as blueback herring, and 11 blueback herring were misidentified as alewife. This asymmetry is not surprising given that blueback herring are generally characterized by dark peritoneal coloration, but alewife can also display some dark coloration (although typically more subtle), that can lead to misidentification (see Berlinsky et al. 2015). Given the morphological similarities between the species, our results show a high level of reliability for species identification in the field. We identified 50 specimens as hybrid individuals, representing 1.8% of the bycatch sampled; slightly lower than previously reported rangewide for anadromous adults (*i.e.*, 2.4%; Hasselman et al. 2014).

Evaluation of baseline populations

Simulations used to assess the performance of *gsi_sim* revealed concordance between the distributions of estimated and simulated mixing proportions for genetic stocks of alewife and blueback herring, indicating a high degree of reliability for genetic stock-level assignments. For alewife there was a slight upward bias for the Southern New England stock and a slight downward bias for the Mid-Atlantic stock (Figure 2a). For blueback herring, there was a slight upward bias for the Mid-Atlantic stock, and slight downward biases for the Northern New England stock and Southern New England stock (Figure 2b). These slight biases are likely due to the uneven representation of baseline populations within genetic stocks for both species (Table S1), but have a modest impact on the precision of bycatch assignment to genetic stock of origin.

Systematic bias was observed between the distribution of estimated and simulated mixing proportions at the population level for alewife (Figure S1a) and blueback herring (Figure S1b). This bias is likely due to weak differentiation among populations within genetic stocks (Palkovacs et al. 2014), and differences in samples sizes among baseline populations (Table S1) that can impact the detection of rare alleles, which contribute to assignment probabilities. Cumulatively, these self-assignment and simulation results suggested that bycatch assignment to population of origin suffers from considerable bias and may be unreliable; therefore, we focused subsequent analyses on the assignment of bycatch to genetic stock of origin.

Genetic stock identification of bycatch

Overall, the greatest proportion of alewife bycatch ($\bar{x}$=0.695) was assigned to the Southern New England stock (Figure 3a), while the greatest proportion of blueback herring bycatch ($\bar{x}$=0.782) was assigned to the Mid-Atlantic stock (Figure 3b). Other genetic stocks comprised substantially lower proportions of bycatch for both species. At a posterior probability threshold of 0.95, the Southern New England stock represented at least 67% of the total alewife bycatch, while the Mid-Atlantic stock represented at least 75% of the total blueback herring bycatch. For both species, replicate runs of the MCMC with different starting seeds generated posterior mean estimates of mixing proportions that were virtually identical to the initial run of the model (Figure S2). This result indicated that the MCMC algorithm used by *gsi_sim* to compute posterior probabilities converged well and was suitable for estimating assignment probabilities for alewife and blueback herring to genetic stock of origin.

When alewife bycatch was partitioned into strata (*i.e.*, year, season, region, target fishery, and gear type), results showed that all genetic stocks were encountered in all regions and by all fisheries. However, the greatest proportion of alewife bycatch across all fishing areas was consistently assigned to the Southern New England stock (Figure 4a), which comprised the greatest proportion of alewife bycatch for 24/25 strata (range: 0.38-0.98; $\bar{x}$=0.66), and ≥50% of bycatch for 18/25 strata (Table 1). Individual-level assignments for alewife bycatch are provided in Table S2. Although alewife bycatch was sampled from multiple fisheries, the Atlantic herring fishery was heavily represented in our bycatch dataset (20/25 strata), and largely occurred on the southern New England fishing grounds (14/20 strata). A large proportion of the alewife bycatch sampled from this fishery was assigned to the Southern New England stock (range: 0.49-0.98; $\bar{x}$=0.73). Nonetheless, a large proportion of alewife bycatch from other regions and in other fisheries were similarly assigned to the Southern New England stock (range: 0.38-0.76; $\bar{x}$=0.55). Cumulatively, these results suggest that populations from the Southern New England stock represent the largest component of alewife bycatch for several fisheries utilizing a variety of fishing gear, and occurring in several fishing areas at various times of year.

When blueback herring bycatch was partitioned into strata, results showed that all genetic stocks were encountered in all regions, but the greatest proportion of bycatch was consistently assigned to the Mid-Atlantic stock (Figure 4b). The Mid-Atlantic stock comprised the greatest proportion of bycatch for 16/17 strata (range: 0.42-0.85; $\bar{x}$=0.68), and comprised ≥50% of bycatch for 16/17 strata (Table 1). Individual-level assignments for blueback herring bycatch are provided in Table S2. Blueback herring bycatch was only encountered in the Atlantic herring fishery, and largely occurred on the southern New England fishing grounds (10/16 strata). A large proportion of the bycatch from this region was assigned to the Mid-Atlantic stock (range: 0.48-0.85; $\bar{x}$=0.70). However, bycatch from other regions also had similar proportions assigned to this genetic stock (Gulf of Maine: $\bar{x}$=0.66; Cape Cod: $\bar{x}$=0.74; New Jersey-Long Island: $\bar{x}$=0.65). Cumulatively, these results suggest that blueback herring populations from the Mid-Atlantic stock comprise a large component of bycatch in the Atlantic herring fishery utilizing midwater and bottom trawl fishing gear, and occurring in several fishing regions at various times of year.

We observed no significant difference in ECDFs (*i.e.*, Z-scores; Clemento et al. 2014) between baseline populations and bycatch for either alewife or blueback herring ($p>0.05$; K-S test); suggesting that bycatch specimens did not originate from populations that were not included in our baselines (Figure S3). This result implies that genetically differentiated populations and genetic stocks from Canada (McBride et al. 2014) were not encountered in the bycatch samples examined in this study.

Genetic stock-specific bycatch mortality in the southern New England Atlantic herring fishery

Over the two years of data examined, we estimate that more than 4.95 million river herring (95% CI: 4.11-5.79 million) were taken as bycatch in the southern New England Atlantic herring fishery (Table 2). In 2012, over 1.30 million river herring (95% CI: 1.04-1.56 million), and in 2013 over 3.65 million river herring (95% CI: 3.08-4.23), were taken as bycatch in this fishery. While more than twice as many blueback herring were taken (890 000) in 2012 compared to alewife (410 000), more than seven times as many alewife were taken (3.21 million) in 2013 relative to blueback herring (450 000). Midwater trawls and bottom trawls accounted for ~82.3% and ~17.7% of the bycatch mortality in 2012, respectively. This pattern changed in 2013, when midwater trawls accounted for ~48.5% and bottom trawls ~51.5% of the bycatch mortality.

Bycatch mortality was not evenly distributed among genetic stocks for either species (Table 2). For alewife, 72.5% of the bycatch across both years examined was assigned to the Southern New England stock, while 20% and 7.5% was assigned to the Mid-Atlantic stock and Northern New England stock, respectively. The proportional genetic stock composition of alewife bycatch was not significantly different between gear types (KS test: D=0.019, $p > 0.1$) or between years (KS test: D=0.19, $p > 0.1$). For blueback herring, 80% of the bycatch across both years was assigned to the Mid-Atlantic stock, while 9%, 10%, and 1% was assigned to the

Northern New England stock, Southern New England stock and South Atlantic stock, respectively. The genetic stock composition of blueback herring bycatch did not differ significantly between gear types (KS test: D=0.042, p > 0.1) or between years (KS test: D=0.06, p > 0.1).

Despite consistency in the proportional representation of genetic stocks *within species* across years, different species dominated bycatch mortality in 2012 *vs.* 2013, leading to major differences in genetic stock-specific mortality. In 2012, when blueback herring dominated bycatch, the Mid-Atlantic stock of blueback herring (711 800 fish taken) represented 54.7% of the total river herring mortality. In 2013, when alewife dominated bycatch, the Southern New England stock of alewife (2.32 million fish taken) represented 64% of the total river herring mortality.

Discussion

Our study reveals that bycatch mortality in commercial fisheries, particularly the Atlantic herring fishery, is not evenly distributed among genetic stocks, but is disproportionately assigned to the most depleted genetic stocks (*i.e.*, alewife: Southern New England stock; blueback herring: Mid-Atlantic stock) and could be hindering recovery efforts. Mitigating the impacts of commercial bycatch is an important component of alewife and blueback herring recovery efforts, and will aid in restoring connectivity between marine and freshwater environments and restoring the health of coastal ecosystems.

Genetic stock identification of bycatch

The genetic composition of alewife and blueback herring bycatch overall and by strata revealed that all genetic stocks from both species were taken in commercial fisheries. This finding supports prior research that populations mix extensively at sea (Neves 1981; Rulifson 1984; Stone and Jessop 1992) and suggests that alewife and blueback herring from across their ranges are susceptible to bycatch across a broad geographic area. However, the alewife Southern New England stock and blueback herring Mid-Atlantic stock comprised the largest proportions of genetic assignments overall (Figure 3) and dominated bycatch across years, seasons, regions, target fisheries, and gear types (Figure 4). Although our mixture simulations revealed slight upward biases for the alewife Southern New England stock (Figure 2a) and the blueback herring Mid-Atlantic stock (Figure 2b), these biases are not substantial enough to account for the differences in the proportion of overall bycatch assignment to these genetic stocks for either species, and do not dramatically impact our key results. Further, replicate runs of the MCMC underlying *gsi_sim* generated nearly identical posterior mean estimates of mixing proportions (Figure S2), confirming model convergence and supporting the reliability of our assignments to genetic stock of origin.

The geographic boundaries for the alewife Southern New England stock and blueback herring Mid-Atlantic stock overlap in the region of Long Island Sound due to species specific differences in population genetic structure (Figure 1; Palkovacs et al. 2014). Thus, alewife populations from rivers that drain into Long Island Sound would be assigned to the Southern New England stock, while blueback herring populations from these same rivers would be assigned to the Mid-Atlantic stock. A relatively large proportion of the alewife and blueback herring bycatch strata examined (0.56 and 0.59, respectively) came from the southern New England Atlantic herring fishery that occurs in areas adjacent to Long Island Sound (*i.e.*, SA

537/539/611; Figure 4). Thus, it seems reasonable to postulate that bycatch in the southern New England Atlantic herring fishery may be disproportionately impacting the alewife and blueback herring populations in and around Long Island Sound that have experienced some of the greatest declines in spawning adult abundances (Palkovacs et al. 2014). Relative to other marine fisheries, the Atlantic herring fishery encounters the highest level of river herring bycatch (Cieri et al. 2008; Cournane et al. 2013), and our results are consistent with previous studies that demonstrated that river herring bycatch is greatest just offshore of the region where populations have declined the most (Bethoney et al. 2013, 2014a). However, this should be interpreted cautiously, as the boundaries for the alewife Southern New England stock and blueback herring Mid-Atlantic stock extend beyond the Long Island Sound region (Figure 1).

Massachusetts, Rhode Island, and Connecticut are all adjacent to the Long Island Sound region, and were among the first states to detect population-level declines and to implement a series of conservation actions that placed moratoria on directed in-river fisheries and increased access to historical spawning habitat (ASMFC 2012). Unfortunately, these conservation actions have provided few consistent signs of recovery (Nelson et al. 2011). While there are numerous threats that may limit the recovery of river herring in this region (Hartman 2003; Atlantic States Marine Fisheries Commission 2012; Davis et al. 2012; Lynch et al. 2014; Tommasi et al. 2015), our study suggests bycatch mortality may be an important contributing factor. However, bycatch should be evaluated in conjunction with other sources of mortality to fully assess its direct impact on river herring populations.

Genetic stock-specific bycatch mortality in the southern New England Atlantic herring fishery

We estimate that approximately 3.6 million alewife and 1.3 million blueback herring were taken as bycatch in the southern New England Atlantic herring fishery in 2012 and 2013 (Table 2). The greatest alewife bycatch came from the Southern New England stock (2.62 million fish), while the greatest blueback herring bycatch came from the Mid-Atlantic stock (1.07 million fish). The amount of river herring caught in the southern New England Atlantic herring fishery is typically < 0.5% of the catch of the target species (Bethoney et al. 2014a), but the magnitude of bycatch mortality estimated for these genetic stocks may be substantial. Recent research suggests that bycatch mortality in the Atlantic herring fishery may be similar to that previously generated by directed fisheries (Cieri et al. 2008). However, linking the magnitude of bycatch mortality to declines in spawning adult abundances at the genetic stock (or population) level, and evaluating the impacts of bycatch on recovery efforts, is complicated by the absence of reliable spawning run count data for many populations. What spawning run count data are available have been enumerated using different methods (*i.e.*, electronic fish counters, visual counts, video counts) with variable accuracy. Nonetheless, bycatch mortality is considerable when compared to the size of individual spawning runs (ASMFC 2012).

We observed extreme inter-annual variability in the magnitude and species composition of bycatch in the southern New England Atlantic herring fishery. While the genetic stock composition of bycatch was stable across years, we observed a notable increase in bycatch in 2013, but a reduced contribution from blueback herring. Such variability is evident across a longer time series of coastwide bycatch dating back to 2005 (Mid-Atlantic Fisheries Management Council (MAMFC) 2013). Thus, our results present a snapshot of a highly variable fisheries management problem.

Future directions

Our results show that bycatch may be disproportionately impacting the most severely depleted river herring genetic stocks; however, we cannot presently assign bycatch to population of origin with high confidence. Our simulations revealed some bias for population-level assignment for both alewife and blueback herring (Figure S2). This result may stem from moderate levels of gene flow among populations within genetic stocks and the resolution of the microsatellite markers employed (Manel et al. 2005). Using the same suite of microsatellites, Palkovacs et al. (2014) found relatively weak (but significant; $P<0.05$) levels of genetic differentiation among populations of alewife (global $F_{ST}=0.049$) and blueback herring (global $F_{ST}=0.030$) from across the US, and non-significant differentiation among some geographically proximate populations within genetic stocks. Similar patterns were observed for Canadian populations (McBride et al. 2014). This result is consistent with other studies of anadromous fishes that detected genetic structure on broad spatial scales, but insufficient differences among populations within genetic stocks to confidently allocate mixture samples back to population of origin (Gharret et al. 1987; Templin et al. 2011). For alewife and blueback herring, this finding may be due to a combination of gene flow via natural straying and, in some areas, human-mediated gene flow via inter-basin stock transfers (McBride et al. 2015).

Increased accuracy of genetic assignments for alewife and blueback herring bycatch on finer spatial scales will benefit from the inclusion of additional baseline populations from across the species' entire geographic ranges. Assignment accuracy may also be improved through the application of Single Nucleotide Polymorphisms (SNPs), particularly if some of those SNPs show signatures of selection that help differentiate populations (Ackerman et al. 2011, Nielsen et al. 2012). SNPs are currently being developed for alewife and blueback herring (Baetscher, D., Hasselman, D.J., Palkovacs, E.P., and Garza, J.C. *in prep*), and their application shows promise for improving the spatial resolution of GSI (e.g., (Larson et al. 2014). Combining SNPs with microsatellites (Hess et al. 2011, Beacham et al. 2012), morphometrics (Cronin-Fine et al. 2013) or otolith microchemistry (Barnett-Johnson et al. 2010; Brennan et al. 2015; Martin et al. 2015; Turner et al. 2015) could provide particularly powerful approaches for improving the spatial resolution of assignments.

Collection of bycatch samples for this study was largely opportunistic, leading to large variation in sample sizes across bycatch strata. Although our overall results were consistent across strata, we were limited to small sample sizes in some areas. Thus, future efforts should attempt to implement a standardized sampling regime for bycatch.

Conservation and management implications

Our study suggests that bycatch in marine fisheries, particularly the southern New England Atlantic herring fishery, may be a contributing factor in the persistent depression of population abundances observed for the most depleted river herring genetic stocks. Our results may help partially explain why freshwater restoration efforts in Massachusetts, Rhode Island, and Connecticut have not yielded consistent regional signs of recovery. The geographically concentrated nature of river herring bycatch reported herein places severely depleted genetic stocks and populations at risk, but also suggests that reducing bycatch on the southern New England fishing grounds (SA 537/539/611) may serve to increase spawning population abundances, particularly for populations in the Long Island Sound region.

These genetic stocks and populations are important to the overall alewife and blueback herring metapopulation genetic structure (Palkovacs et al. 2014; McBride et al. 2014), and the extirpation of these populations would create a geographic discontinuity in the ranges of both species that could increase the risk of further extirpations, as connectivity and the potential for stabilizing portfolio effects is lost (Schindler et al. 2010). The threat posed by climate change makes it especially important to reduce bycatch mortality in order to increase the resiliency of populations in the face of an unpredictable future (Lynch et al. 2014; Tommasi et al. 2015). Therefore, reducing bycatch mortality for these genetic stocks should be a priority for river herring conservation.

River herring catch limits based on past bycatch levels in the Atlantic herring fishery were established in late 2014 with the goal of preventing high levels of bycatch, such as those observed in 2007 and 2013, from occurring in the future (NEFMC 2013). However, more refined bycatch mitigation techniques may be achieved through a combination of ‘real-time’ genetic monitoring of bycatch (Schwartz et al. 2007), coupled with the implementation of genetic stock-based catch caps, and the continuation of flexible and dynamic voluntary time and area closures (Bethoney et al. 2013). Some of these measures along with bycatch reduction devices have successfully reduced bycatch of Chinook salmon and rockfish (*Sebastes* spp.) in Pacific coast commercial fisheries (Lomeli and Wakefield 2012; Ianelli and Stram 2015; Stram and Ianelli 2015). The recovery of river herring may be assisted by the successful implementation of similar bycatch mitigation measures.

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Literature Cited

A'Hara, S.W., Amouroux, P., Argo, E.E., Avand-Faghih, A., Barat, A., Barbieri, L., Bert, T.M., Blatrix, R., Blin, A., Bouktila, D., Broome, A., Burban, C., Capdevielle-Dulac, C., Casse, N., Chandra, S., Cho, K.J., Cottrell, J.E., Crawford, C.R., Davis, M.C., Delatte, H., Desneux, N., Djieto-Lordon, C., Dubois, M.P., El-Mergawy, R.A.A.M., Gallardo-Escárate, C., Garcia, M., Gardiner, M.M., Guillemaud, T., Haye, P.A., Hellemans, B., Hinrichsen, P., Jeon, J.H., Kerdelhué, C., Kharrat, I., Kim, K.H., Kim, Y.Y., Kwan, Y.-S., Labbe, E.M., LaHood, E., Lee, K.M., Lee, W.-O., Lee, Y.-H., Legoff, I., Li, H., Lin, C.-P., Liu, S.S., Liu, Y.G., Long, D., Maes, G.E., Magnoux, E., Mahanta, P.C., Makni, H., Makni, M., Malausa, T., Matura, R., McKey, D., McMillen-Jackson, A.L., Méndez, M. A., Mezghani-Khemakhem, M., Michel, A.P., Paul, M., Muriel-Cunha, J., Nibouche, S., Normand, F., Palkovacs, E.P., Pande, V., Parmentier, K., Peccoud, J., Piatscheck, F., Puchulutegui, C., Ramos, R., Ravest, G., Richner, H., Robbens, J., Rochat, D., Rousselet, J., Saladin, V., Sauve, M., Schlei, O., Schultz, T.F., Scobie, A.R., Segovia, N.I., Seyoum, S., Silvain, J.-F., Tabone, E., Van Houdt, J.K.J., Vandamme, S.G., Volckaert, F.A.M., Wenburg, J., Willis, T.V., Won, Y.-J., Ye, N.H., Zhang, W., and Zhang, Y.X. 2012. Permanent genetic resources added to Molecular Ecology Resources Database 1 August 2011-30 September 2011. Mol. Ecol. Resour. **12**(1): 185–9. doi: 10.1111/j.1755-0998.2011.03088.x.

Ackerman, M.W., Habicht, C., and Seeb, L.W. 2011. Single Nucleotide Polymorphisms (SNPs) under diversifying selection provide increased accuracy and precision in mixed-stock analyses of sockeye salmon from the Copper River, Alaska. Trans. Am. Fish. Soc. **140**(3): 865–881. doi: 10.1080/00028487.2011.588137.

Anderson, E.C., Waples, R.S., and Kalinowski, S.T. 2008. An improved method for predicting the accuracy of genetic stock identification. Can. J. Fish. Aquat. Sci. **65**(7): 1475–1486. doi: 10.1139/F08-049.

Atlantic States Marine Fisheries Commission (ASMFC). 2012. River Herring Benchmark Stock Assessment Volume I. Stock Assessment Report 12-02. 392 pp. ASMFC, Washington, DC.

Bakun, A., Babcock, E.A., Lluch-Cota, S.E., Santora, C., and Salvadeo, C.J. 2010. Issues of ecosystem-based management of forage fisheries in "open" non-stationary ecosystems: The example of the sardine fishery in the Gulf of California. Rev. Fish Biol. Fish. **20**(1): 9–29. doi: 10.1007/s11160-009-9118-1.

Barnett-Johnson, R., Teel, D.J., and Casillas, E. 2010. Genetic and otolith isotopic markers identify salmon populations in the Columbia River at broad and fine geographic scales. Environ. Biol. Fishes **89**(3): 533–546. doi: 10.1007/s10641-010-9662-5.

Beacham, T.D., Jonsen, K., and Wallace, C. 2012. A comparison of stock and individual identification for Chinook salmon in British Columbia provided by microsatellites and single nucleotide polymorphisms. Mar. Coast. Fish. **4**(1): 1–22. doi: 10.1080/19425120.2011.649391.

Berlinsky, D.L., DiMaggio, M.A., Breton, T.S., Walsh, J., and Kovach, A.I. 2015. Peritoneal Pigmentation in Purebred and Hybrid River Herring. Trans. Am. Fish. Soc. **144**(4): 717–723. doi: 10.1080/00028487.2015.1037017.

Bethoney, N.D., Schondelmeier, B.P., Stokesbury, K.D.E., and Hoffman, W.S. 2013. Developing a fine scale system to address river herring (Alosa pseudoharengus, A. aestivalis) and American shad (A. sapidissima) bycatch in the U.S. Northwest Atlantic mid-water trawl fishery. Fish. Res. **141**: 79–87. Elsevier B.V. doi: 10.1016/j.fishres.2012.09.003.

Bethoney, N.D., Stokesbury, K.D.E., and Cadrin, S.X. 2014a. Environmental links to alosine at - sea distribution and bycatch in the Northwest Atlantic midwater trawl fishery. Ices J. Mar. Sci. **71**: 1246–1255.

Bethoney, N.D., Stokesbury, K.D.E., Schondelmeier, B.P., Hoffman, W.S., and Armstrong, M.P. 2014b. Characterization of River Herring Bycatch in the Northwest Atlantic Midwater Trawl Fisheries. North Am. J. Fish. Manag. **34**(4): 828–838. doi: 10.1080/02755947.2014.920736.

Brenden, T.O., Bence, J.R., Liu, W., Tsehaye, I., and Scribner, K.T. 2015. Comparison of the accuracy and consistency of likelihood-based estimation routines for genetic stock identification. Methods Ecol. Evol. **6**: 817–827. doi: 10.1111/2041-210X.12377.

Brennan, S.R., Zimmerman, C.E., Fernandez, D.P., Cerling, T.E., McPhee, M. V., and Wooller, M.J. 2015. Strontium isotopes delineate fine-scale natal origins and migration histories of Pacific salmon. Sci. Adv. **1**(4): e1400124. doi: 10.1126/sciadv.1400124.

Chuenpagdee, R., Morgan, L.E., Maxwell, S.M., Norse, E.A., and Pauly, D. 2003. Shifting gears: assessing collateral impacts of fishing methods in US waters. Front. Ecol. Environ. **1**(10): 517–524. doi: 10.1890/1540-9295(2003)001[0517:SGACIO]2.0.CO;2.

Cieri, M., Nelson, G., and Armstrong, M. 2008. Estimates of river herring bycatch in the directed Atlantic herring fishery. *In* Atlantic States Marine Fisheries Commission. Available from http://www.alewifeharvesters.org/wp-content/uploads/2010/03/River-Herring-Bycatch-Estimates-10-29-081.pdf.

Clemento, A.J., Crandall, E.D., Garza, J.C., and Anderson, E.C. 2014. Evaluation of a single nucleotide polymorphism baseline for genetic stock identification of Chinook Salmon (Oncorhynchus tshawytscha) in the California Current large marine ecosystem. Fish. Bull. **112**(2-3): 112–130. doi: 10.7755/FB.112.2-3.2.

Cournane, J.M., Kritzer, J.P., and Correia, S.J. 2013. Spatial and temporal patterns of anadromous alosine bycatch in the US Atlantic herring fishery. Fish. Res. **141**: 88–94. Elsevier B.V. doi: 10.1016/j.fishres.2012.08.001.

Cronin-Fine, L., Stockwell, J.D., Whitener, Z.T., Labbe, E.M., Willis, T.V., and Wilson, K.A. 2013. Application of morphometric analysis to identify alewife stock structure in the Gulf of Maine. Mar. Coast. Fish. **5**: 11–20. doi: 10.1080/19425120.2012.741558.

Crowder, L.B., and Murawski, S.A. 1998. Fisheries Bycatch: Implications for Management. Fisheries **23**(6): 8–17. doi: 10.1577/1548-8446(1998)023<0008:FBIFM>2.0.CO;2.

Davis, J.P., and Schultz, E.T. 2009. Temporal shifts in demography and life history of an anadromous alewife population in Connecticut. Mar. Coast. Fish. **1**(1): 90–106. doi: 10.1577/C08-003.1.

Davis, J.P., Schultz, E.T., and Vokoun, J.C. 2012. Striped bass consumption of blueback herring during vernal riverine migrations: does relaxing harvest restrictions on a predator help conserve a prey species of concern? Mar. Coast. Fish. **4**(1): 239–251. doi: 10.1080/19425120.2012.675972.

Falush, D., Stephens, M., and Pritchard, J.K. 2003. Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. Genetics **164**(4): 1567–1587. Available from ISI:000185248000029.

Faubet, P., Waples, R.S., Gaggiotti, O.E., and Science, N.F. 2007. Evaluating the performance of a multilocus Bayesian method for the estimation of migration rates. Mol. Ecol. **16**(6): 1149–1166. doi: 10.1111/j.1365-294X.2006.03218.x.

Gharret, A.J., Shirley, S.M., and Tromble, G.R. 1987. Genetic relationships among populations of Alaskan Chinook salmon (Oncorhynchus tshawytscha). Can. J. Fish. Aquat. Sci. **44**: 765–774.

Hall, C.J., Jordaan, A., and Frisk, M.G. 2012. Centuries of anadromous forage fish loss: consequences for ecosystem connectivity and productivity. Bioscience **62**(8): 723–731. doi: 10.1525/bio.2012.62.8.5.

Hartman, K.J. 2003. Population-level consumption by Atlantic coastal striped bass and the influence of population recovery upon prey communities. Fish. Manag. Ecol. **10**(5): 281–288. doi: 10.1046/j.1365-2400.2003.00365.x.

Hasselman, D.J., Argo, E.E., McBride, M.C., Bentzen, P., Schultz, T.F., Perez-Umphrey, A.A., and Palkovacs, E.P. 2014. Human disturbance causes the formation of a hybrid swarm between two naturally sympatric fish species. Mol. Ecol. **23**(5): 1137–1152. doi: 10.1111/mec.12674.

Hess, J.E., Matala, A.P., and Narum, S.R. 2011. Comparison of SNPs and microsatellites for fine-scale application of genetic stock identification of Chinook salmon in the Columbia River Basin. Mol. Ecol. Resour. **11**(Suppl/. 1): 1–13. doi: 10.5061/dryad.7986.

Hightower, J.E., Wicker, A.M., Endres, K.M. 1996. Historical Trends in Abundance of American Shad and and river herring in Albemarle Sound, North Carolina. North Am. J. Fish. Manag. **16**: 257–271.

Ianelli, J.N., and Stram, D.L. 2015. Estimating impacts of the pollock fishery bycatch on western Alaska Chinook salmon. Ices J. Mar. Sci. **72**(4): 1159–1172.

Israel, J.A., Bando, K.J., Anderson, E.C., and May, B. 2009. Polyploid microsatellite data reveal stock complexity among estuarine North American green sturgeon (Acipenser medirostris). Can. J. Fish. Aquat. Sci. **66**(9): 1491–1504. doi: 10.1139/F09-091.

Klauda, R.J., Fischer, S.A., L. W. Hall, J., and Sullivan, J.A. 1991. Alewife and blueback herring; Alosa pseudoharengus and Alosa aestivalis. *In* Habitat requirements for Chesapeake Bay living resources, 2nd edition. *Edited by* S.L. Funderburk, M. J.A., S.J. Jordan, and D. Riley. Chesapeake Bay Program Living Resources Subcommittee, Annapolis, MD. pp. 10.1–10.29. Available from http://www.dnr.state.md.us/irc/docs/00000260_10.pdf.

Koljonen, M.L., Pella, J.J., and Masuda, M. 2005. Classical individual assignments versus mixture modeling to estimate stock proportions in Atlantic salmon (Salmo salar) catches from DNA microsatellite data. Can. J. Fish. Aquat. Sci. **62**(9): 2143–2158. doi: 10.1139/f05-128.

Larson, W.A., Seeb, J.E., Pascal, C.E., Templin, W.D., and Seeb, L.W. 2014. Single-nucleotide polymorphisms (SNPs) identified through genotyping-by-sequencing improve genetic stock identification of Chinook salmon (Oncorhynchus tshawytscha) from western Alaska. Can. J. Fish. Aquat. Sci. **71**: 1–11.

Lewison, R.L., Crowder, L.B., Wallace, B.P., Moore, J.E., Cox, T., Zydelis, R., McDonald, S., DiMatteo, A., Dunn, D.C., Kot, C.Y., Bjorkland, R., Kelez, S., Soykan, C., Stewart, K.R., Sims, M., Boustany, A., Read, A.J., Halpin, P., Nichols, W.J., and Safina, C. 2014. Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. Proc. Natl. Acad. Sci. U. S. A. **111**(14): 5271–6. doi: 10.1073/pnas.1318960111.

Limburg, K.E., and Waldman, J.R. 2009. Dramatic declines in North Atlantic diadromous fishes. Bioscience **59**(11): 955–965. doi: 10.1525/bio.2009.59.11.7.

Lomeli, M.J.M., and Wakefield, W.W. 2012. Efforts to reduce Chinook salmon (Oncorhynchus tshawytscha) and rockfish (Sebastes spp.) bycatch in the U.S. west coast Pacific hake (Merluccius productus) fishery. Fish. Res. **119-120**: 128–132. Elsevier B.V. doi: 10.1016/j.fishres.2011.11.003.

Lynch, P.D., Nye, J.A., Hare, J.A., Stock, C.A., Alexander, M.A., Scott, J.D., Curti, K.L., and Drew, K. 2014. Projected ocean warming creates a conservation challenge for river herring populations. Ices J. Mar. Sci. doi: 10.1093/icesjms/fsu134.

MacAvoy, S.E., Macko, S.A., McIninch, S.P., and Garman, G.C. 2000. Marine nutrient contributions to freshwater apex predators. Oecologia **122**(4): 568–573. Available from ISI:000086455000016.

Manel, S., Gaggiotti, O.E., and Waples, R.S. 2005. Assignment methods: matching biological questions techniques with appropriate. Trends Ecol. Evol. **20**(3): 136–142. Available from ISI:000227661200008.

Martin, J., Rougemont, Q., Drouineau, H., Launey, S., Jatteau, P., Bareille, G., Berail, S., Pécheyran, C., Feunteun, E., Roques, S., Clavé, D., Nachón, D.J., Antunes, C., Mota, M., Réveillac, E., and Daverat, F. 2015. Dispersal capacities of anadromous Allis shad population inferred from a coupled genetic and otolith approach. Can. J. Fish. Aquat. Sci. **72**: 991–1003.

McBride, M.C., Hasselman, D.J., Willis, T.V., Palkovacs, E.P., and Bentzen, P. 2015. Influence of stocking history on the population genetic structure of anadromous alewife (Alosa pseudoharengus) in Maine rivers. Conserv. Genet. **16**(5): 1209-1223. doi: 10.1007/s10592-015-0733-1.

McBride, M.C., Willis, T.V., Bradford, R.G., and Bentzen, P. 2014. Genetic diversity and structure of two hybridizing anadromous fishes (Alosa pseudoharengus, Alosa aestivalis) across the northern portion of their ranges. Conserv. Genet. **15**(6): 1281-1298. doi: 10.1007/s10592-014-0617-9.

McDermott, S.P., Bransome, N.C., Sutton, S.E., Smith, B.E., Link, J.S., and Miller, T.J. 2015. Quantifying alosine prey in the diets of marine piscivores in the Gulf of Maine. J. Fish Biol.: n/a–n/a. doi: 10.1111/jfb.12692.

Messieh, S.N. 1977. Population structure a biology of alewives (Alosa pseudoharengus) and blueback herring (A. aestivalis) in the Saint John River, New Brunswick. Environ. Biol. Fishes **2**(3): 195–210.

Mid-Atlantic Fisheries Management Council (MAFMC). 2013. Amendment 14 to the Atlantic Mackerel, Squid, and Butterfish (MSB) fishery management plan (FMP) environmental impact statement and public hearing document. Dover, DE.

Moore, J.W., Hayes, S.A., Duffy, W., Gallagher, S., Michel, C.J., and Wright, D. 2011. Nutrient fluxes and the recent collapse of coastal California salmon populations. Can. J. Fish. Aquat. Sci. **68**: 1161–1170. doi: 10.1139/F2011-054.

Myers, R.A., and Worm, B. 2005. Extinction, survival or recovery of large predatory fishes. Philos. Trans. R. Soc. Lond. B. Biol. Sci. **360**(1453): 13–20. doi: 10.1098/rstb.2004.1573.

Nelson, G.A., Brady, P.D., Sheppard, J.J., and Armstrong, M.P. 2011. An Assessment of River Herring Stocks in Massachusetts. Massachusetts Division of Marine Fisheries. Report No. TR-46.

Neves, R.J. 1981. Offshore distribution of alewife, Alosa pseudoharengus, and blueback herring, Alosa aestivalis, along the Atlantic coast. Fish. Bull. **79**(3): 473–485.

New England Fisheries Management Council (NEFMC). 2013. Amendment 5 to the Fishery Management Plan for Atlantic Herring Volume I. 696 pp.

Nielsen, E.E., Cariani, A., Aoidh, E. Mac, Maes, G.E., Milano, I., Ogden, R., Taylor, M., Hemmer-Hansen, J., Babbucci, M., Bargelloni, L., Bekkevold, D., Diopere, E., Grenfell, L., Helyar, S., Limborg, M.T., Martinsohn, J.T., McEwing, R., Panitz, F., Patarnello, T., Tinti, F., Van Houdt, J.K.J., Volckaert, F.A.M., Waples, R.S., Albin, J.E.J., Vieites Baptista, J.M., Barmintsev, V., Bautista, J.M., Bendixen, C., Bergé, J.-P., Blohm, D., Cardazzo, B., Diez, A., Espiñeira, M., Geffen, A.J., Gonzalez, E., González-Lavín, N., Guarniero, I., Jeráme, M., Kochzius, M., Krey, G., Mouchel, O., Negrisolo, E., Piccinetti, C., Puyet, A., Rastorguev, S., Smith, J.P., Trentini, M., Verrez-Bagnis, V., Volkov, A., Zanzi, A., and Carvalho, G.R. 2012. Gene-associated markers provide tools for tackling illegal fishing and false eco-certification. Nat. Commun. **3**(851). doi: 10.1038/ncomms1845.

Van Oosterhout, C., Hutchinson, W.F., Wills, D.P.M., and Shipley, P. 2004. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol. Ecol. Notes **4**(3): 535–538. doi: 10.1111/j.1471-8286.2004.00684.x.

Palkovacs, E.P., Hasselman, D.J., Argo, E.E., Gephard, S.R., Limburg, K.E., Post, D.M., Schultz, T.F., and Willis, T.V. 2014. Combining genetic and demographic information to prioritize conservation efforts for anadromous alewife and blueback herring. Evol. Appl. **7**(2): 212-226. doi: 10.1111/eva.12111.

Pikitch, E.K., Rountos, K.J., Essington, T.E., Santora, C., Pauly, D., Watson, R., Sumaila, U.R., Boersma, P.D., Boyd, I.L., Conover, D.O., Cury, P., Heppell, S.S., Houde, E.D., Mangel, M., Plagányi, É., Sainsbury, K., Steneck, R.S., Geers, T.M., Gownaris, N., and Munch, S.B. 2014. The global contribution of forage fish to marine fisheries and ecosystems. Fish Fish. **15**(1): 43–64. doi: 10.1111/faf.12004.

Pritchard, J.K., Stephens, M., and Donnelly, P. 2000. Inference of population structure using multilocus genotype data. Genetics **155**(2): 945–959. Available from ISI:000087475100039.

R Development Core Team. 2013. R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rulifson, R.A. 1984. Tagging studies of river herring (Alosa aestivalis and A. pseudoharengus) in Bay of Fundy, Nova Scotia. North Carolina Division of Marine Fisheries, Completion Report No. AFC-22, East Carolina University, Greenville, NC, USA. 26 pp.

Satterthwaite, W.H., Mohr, M.S., O'Farrell, M.R., Anderson, E.C., Banks, M.A., Bates, S.J., Bellinger, M.R., Borgerson, L.A., Crandall, E.D., Garza, J.C., Kormos, Brett, J., Lawson, P.W., and Palmer-Zwahlen, Melodie, L. 2014. Use of genetic stock identification data for comparison of the ocean spatial distribution , size at age , and fishery exposure of an untagged stock and its indicator: California coastal versus Klamath River Chinook Salmon. Trans. Am. Fish. Soc. **143**: 117–133.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. Nature **465**(7298): 609–12. doi: 10.1038/nature09060.

Schindler, D.E., Leavitt, P.R., Brock, C.S., Johnson, S.P., and Quay, P.D. 2005. Marine-derived nutrients, commerical fisheries, and production of salmon and lake algae in Alaska. Ecology **86**(12): 3225–3231. Available from http://www.esajournals.org/doi/pdf/10.1890/04-1730.

Schwartz, M.K., Luikart, G., and Waples, R.S. 2007. Genetic monitoring as a promising tool for conservation and management. Trends Ecol. Evol. **22**(1): 25–33. doi: 10.1016/j.tree.2006.08.009.

Scott, W.B., and Crossman, E.D. 1973. Freshwater fishes of Canada. J. Fish. Reseach Board Canada **184**: 1–966.

Smith, A.D.M., Brown, C.J., Bulman, C.M., Mackinson, S., Marzloff, M., and Shannon, L.J. 2011. Impacts of fishing low-trophic level species on marine ecosystems. Science **333**: 1147–1150. doi: 10.1126/science.1209395.

Sokal, R.R., and Rohlf, F.J. 2012. Analysis of Frequencies. *In* Biometry. W.H. Freeman and Co., New York, New York. pp. 703–816.

Stone, H.H., and Jessop, B.M. 1992. Seasonal distribution of river herring Alosa pseudoharengus and A. aestivalis off the Atlantic coast of Nova Scotia. Fish. Bull. **90**(2): 376–389. Available from ISI:A1992JF22700011.

Stram, D.L., and Ianelli, J.N. 2015. Evaluating the efficacy of salmon bycatch measures using fishery-dependent data. Ices J. Mar. Sci. **72**(4): 1173–1180. doi: 10.1093/icesjms/fst048.

Templin, W.D., Seeb, J.E., Jasper, J.R., Barclay, A.W., and Seeb, L.W. 2011. Genetic differentiation of Alaska chinook salmon: the missing link for migratory studies. Mol. Ecol. Resour. **11**: 226–246. doi: 10.1111/j.1755-0998.2010.02968.x.

Tommasi, D., Nye, J., Stock, C., Hare, J.A., Alexander, M., and Drew, K. 2015. Effect of environmental conditions on juvenile recruitment of alewife (Alosa pseudoharengus) and blueback herring (Alosa aestivalis) in fresh water: a coastwide perspective. Can. J. Fish. Aquat. Sci. **72**: 1037–1047.

Turner, S.M., Limburg, K.E., Palkovacs. 2015. Can different combinations of natural tags identify river herring natal origin at different levels of stock structure ? Can. J. Fish. Aquat. Sci. **72**(6): 845–854.

Waldman, J., Hasselman, D., Bentzen, P., Dadswell, M., Maceda, L., and Wirgin, I. 2014. Genetic mixed-stock analysis of American shad in two Atlantic coast fisheries: Delaware Bay, USA, and inner Bay of Fundy, Canada. North Am. J. Fish. Manag. **34**(6): 1190–1198. doi: 10.1080/02755947.2014.954067.

Waples, R.S., and Gaggiotti, O. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity 1. Mol. Ecol. **15**(6): 1419–1439. Available from ISI:000236798200001.

Wirgin, I., Jessop, B., Courtenay, S., Pedersen, M., Maceda, S., and Waldman, J.R. 1995. Mixed stock analysis of striped bass in rivers of the Bay of Fundy as revealed by mitochondrial DNA. Can. J. Fish. Aquat. Sci. **52**(5): 961–970. Available from ISI:A1995RX74900008.

Yako, L.A., Mather, M.E., and Juanes, F. 2000. Assessing the contribution of anadromous herring to largemouth bass growth. Trans. Am. Fish. Soc. **129**(1): 77–88. Available from ISI:000089076300006.

Data Accessibility

Microsatellite data used in this manuscript and all scripts needed to reproduce the analyses using *gsi_sim* as well as Table S2 are deposited in DRYAD Digital Repository: XXX

Table 1: Bycatch strata for alewife (n=25) and blueback herring (n=17) with genetic stock-level posterior mean estimated mixing proportions (95% CI) calculated using *gsi_sim* (Anderson et al. 2008).

								Posterior Mean of Mixture Proportion[6] (95% CI)			
Strata[1]	**Year**	**Season**	**Region[2]**	**SA[3]**	**Fishery[4]**	**Gear[5]**	**N**	**NNE**	**SNE**	**MAT**	**SAT**
Alewife											
1	2011	Fall	GoM	513	AH	PMOT	28	0.1653 (0.0017-0.3808)	0.6687 (0.4079-0.8986)	0.1660 (0.0319-0.3514)	-
2	2012	Fall	GoM	514	AC	BOT	16	0.3246 (0.0721-0.6150)	0.3863 (0.0782-0.7320)	0.2892 (0.0636-0.5817)	-
3	2012	Fall	GoM	513	AH	SMOT	16	0.4641 (0.1648-0.7603)	0.4994 (0.1857-0.8154)	0.0392 (0.0000-0.2162)	-
4	2012	Fall	GoM	514	Unk	BOT	7	0.3691 (0.0573-0.7628)	0.4205 (0.0190-0.8408)	0.2103 (0.0018-0.6118)	-
5	2012	Winter	CC	521	AH	PMOT	38	0.2620 (0.1044-0.4504)	0.5649 (0.2898-0.8103)	0.1773 (0.0006-0.4206)	-
6	2012	Winter	GoM	514	PS	BOT	26	0.3652 (0.1236-0.6395)	0.5143 (0.2203-0.7936)	0.1206 (0.0107-0.3072)	-
7	2012	Winter	SNE	539	AH	Unk	20	0.0161 (0.0000-0.1302)	0.9607 (0.8047-1.000)	0.0232 (0.0000-0.1437)	-
8	2012	Winter	SNE	539	AH	BOT	149	0.1130 (0.0491-0.1909)	0.8831 (0.8035-0.9487)	0.0039 (0.0000-0.0255)	-
9	2012	Winter	SNE	539	AH	PMOT	120	0.0056 (0.0000-0.0354)	0.9355 (0.8678-0.9902)	0.0589 (0.0068-0.1343)	-
10	2012	Winter	SNE	539/611	AH	BOT	37	0.2113 (0.0657-0.3992)	0.6411 (0.4410-0.8242)	0.1476 (0.0290-0.3122)	-
11	2012	Winter	SNE	539/611	AH	PMOT	21	0.0273 (0.0000-0.1862)	0.8479 (0.5789-0.9991)	0.1249 (0.0000-0.3663)	-
12	2012	Winter	SNE	611	AH	BOT	40	0.0716 (0.0014-0.1977)	0.8764 (0.6928-0.9895)	0.0520 (0.0000-0.2065)	-
13	2013	Winter	DEL	622	LS	BOT	40	0.3427 (0.1916-0.5068)	0.6091 (0.4318-0.7725)	0.0481 (0.0001-0.1562)	-
14	2013	Winter	CC	521	AH	PMOT	20	0.4108 (0.1768-0.6661)	0.4326 (0.1528-0.7219)	0.1566 (0.0093-0.3960)	-

15	2013	Winter	GoM	514	PS	Unk	65	0.5571 (0.3959-0.7172)	0.4095 (0.2411-0.5781)	0.0334 (0.0005-0.1091)	-
16	2013	Winter	NJLI	613	AH	PMOT	20	0.0217 (0.0000-0.1599)	0.7399 (0.3877-0.9917)	0.2384 (0.0026-0.5816)	-
17	2013	Winter	SNE	537	AH	PMOT	75	0.1281 (0.0252-0.2577)	0.6780 (0.5184-0.8257)	0.1938 (0.0867-0.3243)	-
18	2013	Winter	SNE	539	AH	BOT	350	0.0282 (0.0065-0.0571)	0.6685 (0.5914-0.7385)	0.3033 (0.2373-0.3770)	-
19	2013	Winter	SNE	539	AH	SMOT	125	0.1109 (0.0436-0.1925)	0.6372 (0.5182-0.7631)	0.2519 (0.1440-0.3573)	-
20	2013	Winter	SNE	539	AH	PMOT	55	0.2525 (0.1137-0.4141)	0.4827 (0.2902-0.6758)	0.2648 (0.1339-0.4125)	-
21	2013	Winter	SNE	539/611	AH	BOT	228	0.0985 (0.0465-0.1555)	0.6703 (0.5777-0.7610)	0.2311 (0.1583-0.3112)	-
22	2013	Winter	SNE	611	AH	Unk	20	0.0089 (0.0000-0.0754)	0.5546 (0.3015-0.7972)	0.4365 (0.1968-0.6900)	-
23	2013	Winter	SNE	611	AH	BOT	109	0.0382 (0.0000-0.1015)	0.8566 (0.7542-0.9367)	0.1052 (0.0404-0.1924)	-
24	2013	Winter	SNE	611	AH	PMOT	95	0.0317 (0.0000-0.0937)	0.6241 (0.4981-0.7469)	0.3442 (0.2326-0.4610)	-
25	2013	Winter	Unk	Unk	AH	PMOT	27	0.0160 (0.0000-0.1226)	0.7072 (0.4664-0.9046)	0.2767 (0.0876-0.5095)	-
Blueback herring											
1	2011	Fall	GoM	513	AH	PMOT	73	0.0323 (0.0000-0.1190)	0.0324 (0.0000-0.0937)	0.6794 (0.5230-0.8184)	0.2579 (0.1348-0.3992)
2	2012	Fall	GoM	513	AH	PMOT	19	0.2875 (0.0145-0.6088)	0.0144 (0.0000-0.1221)	0.6769 (0.3600-0.9594)	0.0203 (0.0000-0.1412)
3	2012	Winter	CC	521	AH	PMOT	51	0.1052 (0.0038-0.2396)	0.0298 (0.0000-0.1308)	0.8334 (0.6614-0.9611)	0.0316 (0.0000-0.1297)
4	2012	Winter	NJLI	613	AH	PMOT	46	0.0525 (0.0000-0.1761)	0.0144 (0.0000-0.1065)	0.8993 (0.7424-0.9966)	0.0338 (0.0000-0.1221)
5	2012	Winter	SNE	539	AH	BOT	88	0.0084 (0.0000-0.0611)	0.2917 (0.1629-0.4229)	0.6594 (0.5196-0.7953)	0.0406 (0.0053-0.1116)
6	2012	Winter	SNE	539	AH	PMOT	282	0.1318 (0.0807-0.1907)	0.0537 (0.0155-0.1067)	0.8115 (0.7371-0.8671)	0.0030 (0.0000-0.0203)

7	2012	Winter	SNE	539/611	AH	BOT	16	0.0267 (0.0000-0.2142)	0.1619 (0.0000-0.4896)	0.7782 (0.4120-0.9939)	0.0332 (0.0000-0.2133)
8	2012	Winter	SNE	539/611	AH	PMOT	62	0.1588 (0.0499-0.2931)	0.0069 (0.0000-0.0543)	0.8021 (0.6443-0.9263)	0.0322 (0.0000-0.1327)
9	2012	Winter	SNE	611	AH	Unk	99	0.0525 (0.0000-0.1241)	0.1351 (0.0519-0.2376)	0.8089 (0.6912-0.9161)	0.0035 (0.0000-0.0243)
10	2012	Winter	SNE	611	AH	PMOT	35	0.0295 (0.0000-0.1735)	0.0227 (0.0000-0.1515)	0.9372 (0.7535-0.9999)	0.0107 (0.0000-0.0755)
11	2013	Winter	CC	521	AH	PMOT	17	0.2816 (0.0017-0.5977)	0.0184 (0.0000-0.1561)	0.6643 (0.3345-0.9576)	0.0357 (0.0000-0.2074)
12	2013	Winter	NJLI	612	AH	PMOT	28	0.4507 (0.2231-0.6915)	0.0795 (0.0000-0.2527)	0.4408 (0.1659-0.7017)	0.0290 (0.0000-0.1721)
13	2013	Winter	SNE	539	AH	BOT	111	0.0470 (0.0000-0.1629)	0.0391 (0.0000-0.1079)	0.9107 (0.7837-0.9908)	0.0029 (0.0000-0.0199)
14	2013	Winter	SNE	539	AH	SMOT	7	0.2953 (0.0023-0.7051)	0.0211 (0.0000-0.1788)	0.5065 (0.0452-0.9100)	0.1771 (0.0000-0.6956)
15	2013	Winter	SNE	539	AH	PMOT	5	0.2003 (0.0000-0.6368)	0.0793 (0.0000-0.4814)	0.6025 (0.1064-0.9792)	0.1179 (0.0000-0.5517)
16	2013	Winter	SNE	539/611	AH	BOT	65	0.1637 (0.0545-0.3106)	0.1190 (0.0320-0.2339)	0.7127 (0.5414-0.8566)	0.0046 (0.0000-0.0321)
17	2013	Winter	Unk	Unk	AH	SMOT	9	0.0246 (0.0000-0.2065)	0.2111 (0.0000-0.5789)	0.5121 (0.0232-0.9771)	0.2522 (0.0000-0.7177)

[1] Strata numbers correspond to those in pie charts provided in Figure 4a,b.

[2] Region: GoM (Gulf of Maine), CC (Cape Cod), SNE (southern New England), DEL (Delaware), NJLI (New Jersey-Long Island), Unk (unknown). See Figure 4ab for map depicting fishing regions.

[3] SA: Statistical Area: See Figure 4ab for map depicting statistical sampling areas.

[4] Fishery: AH (Atlantic herring), AC (Atlantic cod), PS (Pandalid shrimp), Longfin squid (LS), Unk (unknown).

[5] Gear: PMOT (Paired Midwater Otter Trawl), SMOT (Single Midwater Otter Trawl), BOT (Bottom Otter Trawl), Unk (unkown).

[6] Stock abbreviations: Northern New England (NNE), Southern New England (SNE), Mid-Atlantic (MAT), South Atlantic (SAT)

Table 2: Number of alewife and blueback herring estimated to be removed from various genetic stocks by the Atlantic herring fishery off the coast of Southern New England (SA 537/539/611) in 2012 and 2013 by midwater trawl and bottom trawl fishing gear. The range represents 95% credible intervals of estimated mixing proportions.

	2012		**2013**		**Total**
	Midwater Trawl	**Bottom Trawl**	**Midwater Trawl**	**Bottom Trawl**	
Alewife					
Northern New England	20 400	9 800	127 300	108 300	265 800
	(9 000 – 31 300	(4 300 – 15 000)	(56 600 – 195 500)	(48 200 – 166 400)	(118 100 – 408 200)
Southern New England	201 300	96 000	1 255 900	1 068 200	2 621 400
	(181 500 – 222 700)	(86 500 – 106 200)	(1 132 200 – 1 388 900)	(963 000 – 1 181 400	(2 363 200 – 2 899 200)
Mid-Atlantic	55 900	26 600	348 500	296 400	727 400
	(45 900 – 64 700)	(21 900 – 30 900)	(286 100 – 403 900)	(243 400 – 343 600)	(597 300 – 843 100)
Sub-total	277 600	132 400	1 731 700	1 472 900	3 614 600
	(236 400 – 318 700)	(112 700 –152 100)	(1 474 900 – 1 988 300)	(1 254 600 – 1 691 400)	(3 078 600 – 4 150 500)
Blueback herring					
Northern New England	75 400	9 300	3 900	38 600	127 200
	(40 500 – 113 200)	(5 000 – 14 000)	(2 100 – 5 700)	(20 800 – 58 000)	(68 400 – 190 900)
Southern New England	72 700	9 100	3 700	37 200	122 700
	(35 800 – 107 500)	(4 500 – 13 200)	(1 800 – 5 400)	(18 400 – 55 100)	(60 500 – 181 200)
Mid-Atlantic	633 600	78 200	32 400	324 800	1 069 000
	(537 100 – 715 000)	(66 400 – 88 300)	(27 400 – 36 500)	(275 300 – 366 500)	(906 200 – 1 206 300)
South Atlantic	10 400	1 400	500	5 300	17 600
	(700 – 34 400)	(100 – 4 200)	(0 – 1 800)	(300 – 17 600)	(1 100 – 58 000)
Sub-total	792 100	98 000	40 500	405 900	1 336 500
	(614 100 – 970 100)	(76 000 – 119 700)	(31 300 – 49 400)	(314 800 – 497 200)	(1 036 200 – 1 636 400)
Grand total	1 069 700	230 400	1 722 200	1 878 000	4 951 100
	(850 500 – 1 288 800)	(188 700 – 271 800)	(1 506 200 – 2 037 700)	(1 569 400 – 2 188 600)	(4 114 800 – 5 786 900)

Figure Legends

Figure 1: Map showing the baseline populations and genetic stocks for (a) alewife and (b) blueback herring used in genetic stock identification. Populations are color-coded to coincide with their genetic stock designations provided in legend (inset). Population abbreviations for both species are provided in Table S1.

Figure 2: Simulated and estimated mixing proportions by genetic stock for (a) alewife and (b) blueback herring. Upward bias is indicated where data points fall above the 1:1 (dashed) line, whereas downward bias is indicated where data point fall below the 1:1 (dashed) line.

Figure 3: Boxplots showing the proportion (posterior median, with 10th, 25th, 75th, and 95th percentiles of the posterior distribution) of overall bycatch assignment for (a) alewife and (b) blueback herring to genetic stock. Genetic stock designations: Northern New England (NNE), Southern New England (SNE), Mid-Atlantic (MAT), and South Atlantic (SAT).

Figure 4: Relative proportion of assignments to genetic stocks for each bycatch stratum for (a) alewife and (b) blueback herring. The map shows the baseline populations color-coded to coincide with their genetic stock designations (as per Figure 1; see legend), and the NOAA Statistical Areas where bycatch was sampled (grouped by region using various degrees of shading). Pie charts illustrate the relative proportion of bycatch for each stratum, grouped by region, that was assigned to each genetic stock. The number in the center of each pie chart refers to a specific bycatch stratum (see Table 1). Descriptions of bycatch strata (*i.e.*, year, season, region, statistical area, target fishery, gear type, and sample size) are provided in Table 1.

Alewife stratum #25 and blueback herring stratum # 17 were excluded from consideration because the region where the bycatch sample was collected was unknown.

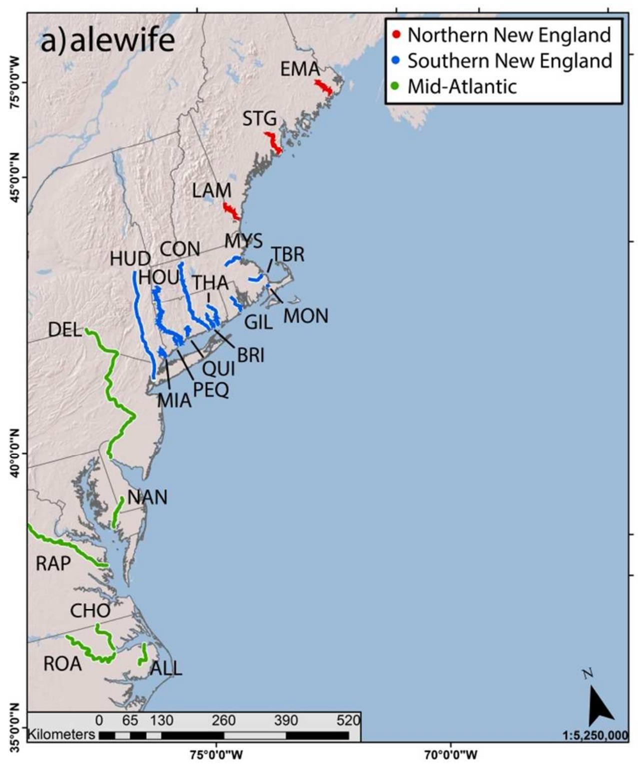

Figure 1a

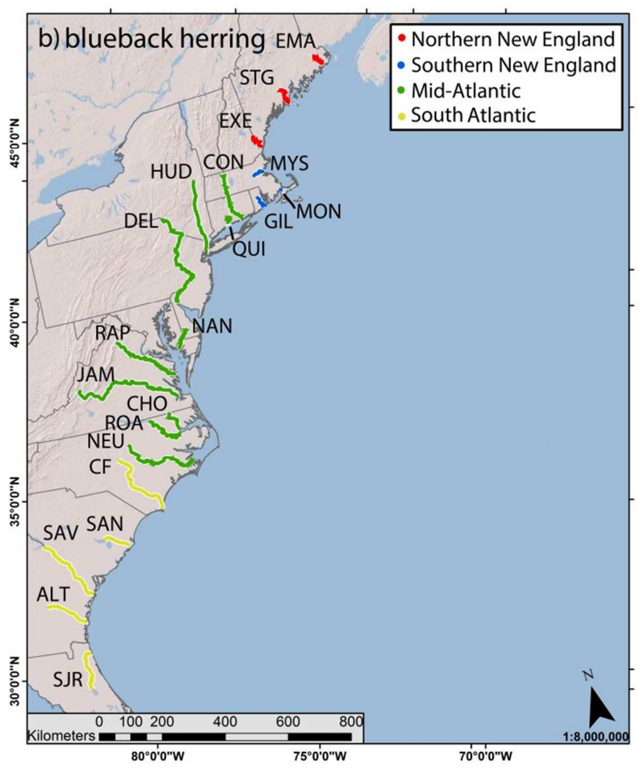

Figure 1b

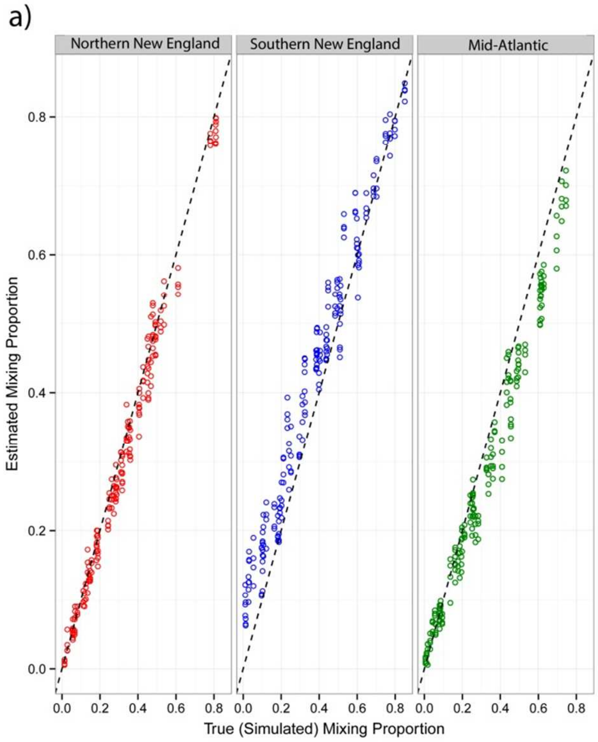

Figure 2a

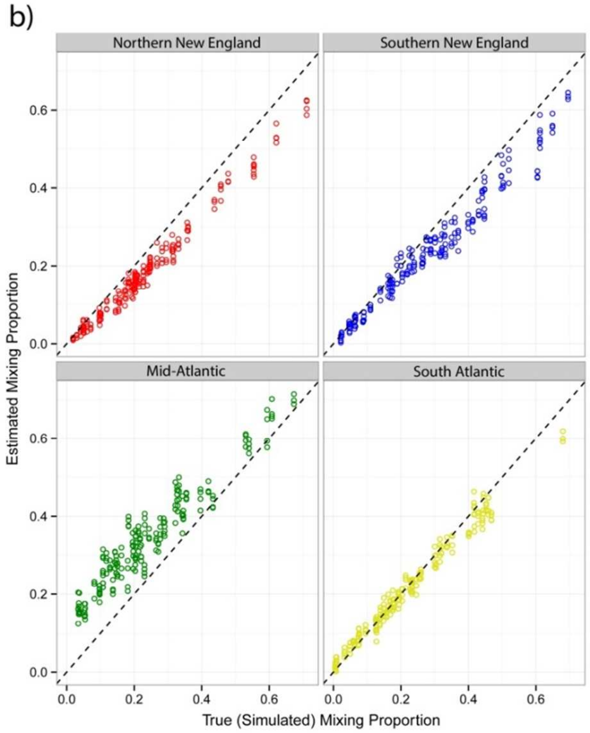

Figure 2b

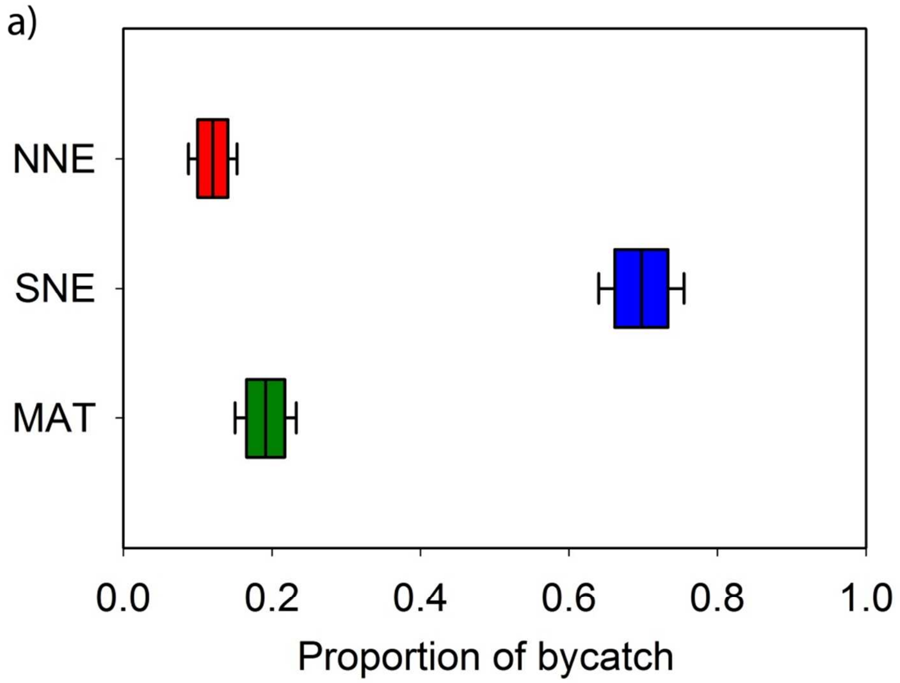

Figure 3a

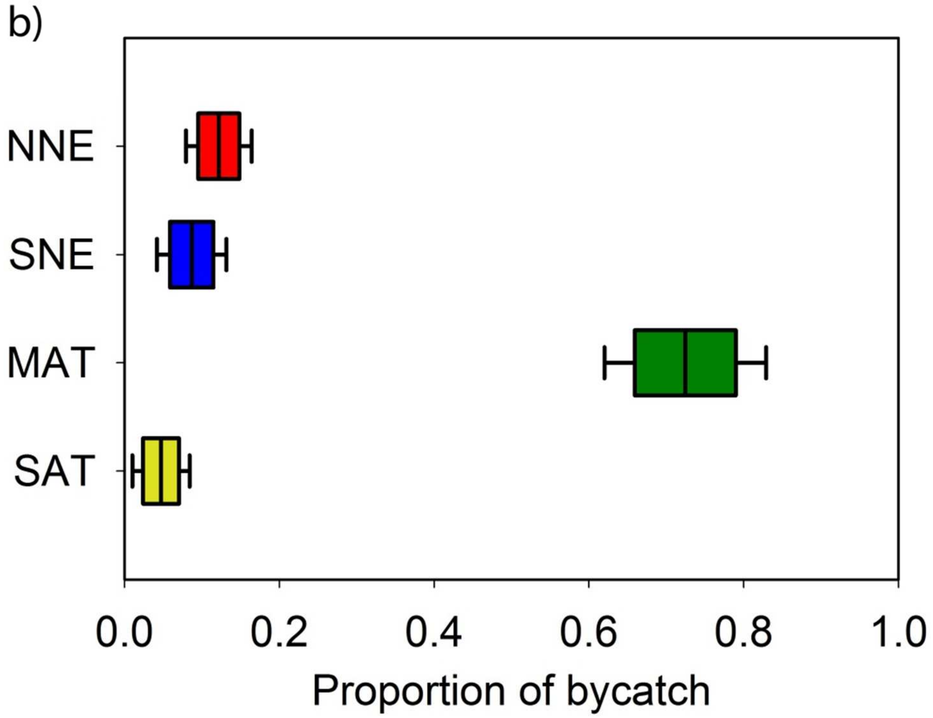

Figure 3b

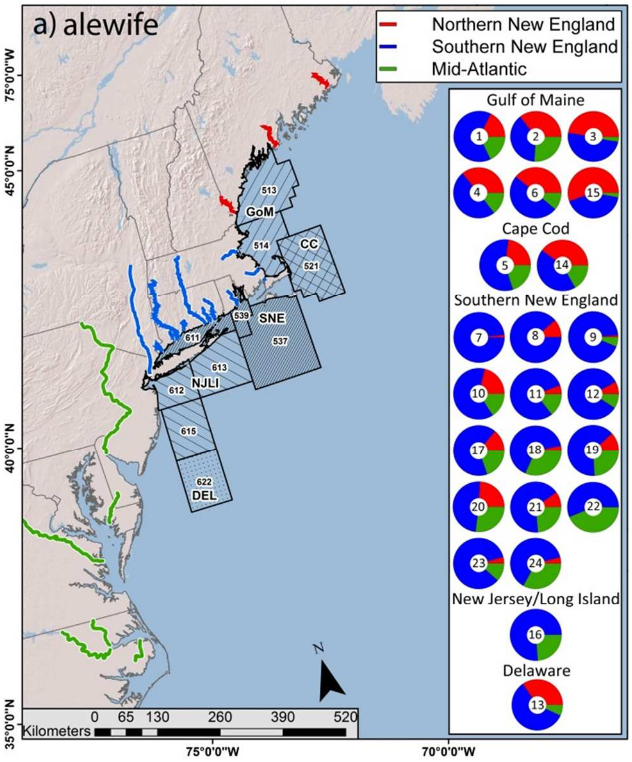

Figure 4a

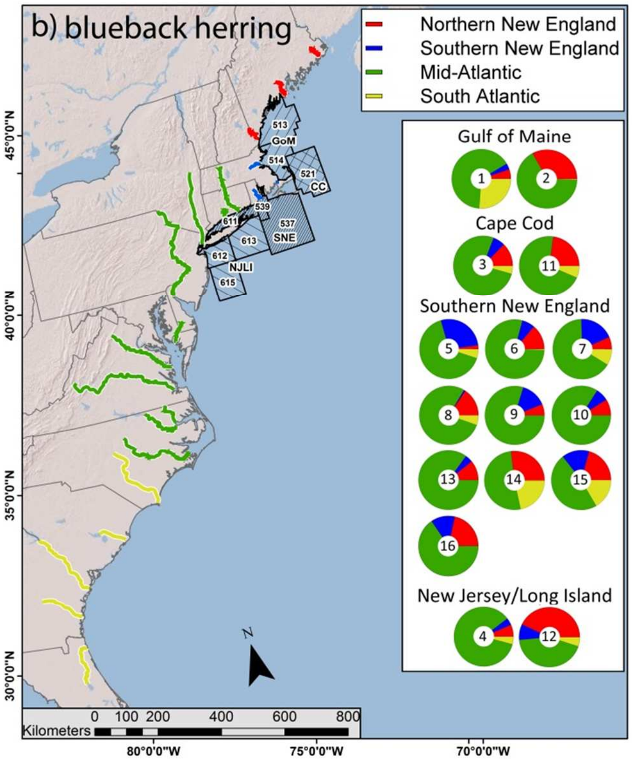

Figure 4b