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Larger body size and earlier run timing increase alewife reproductive success in a whole lake experiment

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Title: Larger body size and earlier run timing increase alewife reproductive success in a whole lake experiment

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Abstract

Environmental conditions can influence biological characteristics like phenology and body size with important consequences for organismal fitness. Examining these fitness consequences under natural conditions through genetic pedigree reconstruction offers a lens into potential population responses to changing environments. Over three years (2013-2015), we introduced adult alewife (*Alosa pseudoharengus*), anadromous, iteroparous clupeids, into one Massachusetts (USA) lake to complete the first detailed examination of this species' mating system and assess relationships between body size, reproductive timing, and seasonal reproductive success. We reconstructed pedigrees using 15 microsatellites and genotypes from all possible parents and samples of naturally produced offspring within four months of hatching. Within each of the three study years, spawning adults had multiple mates and spawned multiple times. Larger females that arrived and were translocated earlier had higher reproductive success. Declining body size and altered migration timing over time, through an influence on reproductive success, can influence population vital rates and productivity.

16 Introduction

17 Individual reproductive success provides an important link between phenotypic variation
18 and population dynamics (Kinnison and Hairston 2007; Pelletier et al. 2007; Wright and Trippel
19 2009; Schoener et al. 2011). Parental characteristics and reproductive phenology (timing)
20 strongly influence individual reproductive success in many taxa (Schultz 1993; Dawson and
21 Clark 2000; Cargnelli and Neff 2006). In fishes, hypotheses involving a relationship between
22 timing of hatch and survival have been central to fisheries ecology since the seminal publication
23 of Hjort (1914) that identified critical periods in early life where exceedingly high mortality
24 shaped future recruitment success. The match-mismatch hypothesis expanded upon Hjort (1914)
25 and proposed that synchrony between hatching and prey abundance is critical to driving the
26 survival of offspring for many marine fishes (Cushing 1969, 1975). Additional research has
27 employed indirect measures of relative fitness to explore the relationship between parental
28 characteristics, reproductive timing, and reproductive success. For example, indirect associations
29 between age-specific egg contribution and temporal patterns of juvenile abundance in haddock
30 (*Melanogrammus aeglefinus*, Linnaeus 1758) suggest that older and earlier spawning individuals
31 had higher relative fitness (Wright and Gibb 2005). Advances in methods, such as pedigree
32 construction in natural populations, can help elucidate the relationship between reproductive
33 success and parental traits like body size and reproductive timing.

34 Pedigrees are a useful tool for understanding reproductive and mating patterns in wild
35 (Pemberton 2008) and laboratory (Malvezzi et al. 2015) populations. For example, long term
36 pedigrees for Soay sheep (*Ovis aries*, Linnaeus 1758) have been used to extensively explore life
37 history traits, including how reproductive success relates to body size (Milner et al. 1999; Milner
38 et al. 2000; Wilson et al. 2006) and habitat use (Regan et al. 2016). In the past, pedigree related

studies were biased towards taxa like ungulates and birds, whose life history traits were more conducive to individual observation (Kruuk and Hill 2008). However, availability of molecular markers and advances in analytical approaches have increased the taxa for which pedigrees can be constructed towards estimating lifetime or annual reproductive success (Pemberton 2008; Jones and Wang 2010). For example, the use of pedigrees has expanded to evaluate reproductive patterns in wild anadromous fish species, including sockeye (*Oncorhynchus nerka*, Walbaum 1792) (Peterson et al. 2014; Lin et al. 2016) and Atlantic salmon (*Salmo salar*, Linnaeus 1758) (Perrier et al. 2014). Pedigree construction for additional species will provide a better understanding of reproductive patterns and the influence of environmental change.

Alewife (*Alosa pseudoharengus*, Wilson 1811) are clupeids that are native to the Atlantic coast of North America. They are iteroparous, maturing after 2-5 years, with asynchronous oocyte development and indeterminate fecundity (Ganias et al. 2015). Adults make migrations from the ocean into freshwater lakes between March and June, depending on latitude (Neves 1981; Loesch 1987; Turner et al. 2015) and return to the ocean after spawning. Adult outmigration can be following a substantial amount of time in fresh water (3-82 days (Kissil 1974); 2-5 weeks (Gahagan et al. 2010); (43-76 days) Rosset et al. 2017). During this time, adult alewife are likely to feed on invertebrates and fish eggs in fresh water, as do the closely related blueback herring (*Alosa aestivalis*), although there are no studies to confirm this in alewife (Creed 1985; Simonin et al. 2007). Juveniles feed on freshwater plankton and tend to emigrate to the ocean from early summer to late fall (Kosa and Mather 2001; Iafrate and Oliveira 2008; Gahagan et al. 2010). For multiple-batch spawners, including alewife, larger and older females tend to have higher fecundity and spawn for a longer duration (DeMartini and Fountain 1981; Parrish et al. 1986; Kjesbu et al. 1996, Trippel et al. 1997; Secor 2000; Wright and Gibb 2005;

Claramunt et al. 2007; Ganas et al. 2015). Batch spawning in alewife has been demonstrated through asynchronous development of oocytes (Ganas et al. 2015), but no studies provide direct observations of multiple batches from a single adult. In general, little information is available regarding alewife mating systems, family size, and factors related to reproductive success.

Alewife have experienced centuries-long population declines (Hall et al. 2012) related, in part, to anthropogenic stressors that likely negatively affect individual reproductive success (Loesch 1987; ASMFC 2012). Early declines in alewife populations resulted from industrialization of landscapes, resulting loss of habitat available for spawning alewife (ASMFC 2012; Hall et al. 2012; Mattocks et al. 2017). Bycatch mortality has also been associated with population declines in alewife (Palkovacs et al. 2014; Hasselman et al. 2016). Meanwhile, recent abundance and demographic trends indicate shifts in phenology (Ellis and Vokoun 2009) and geographic range (Nye et al. 2012), as well as decreased age and size at maturity (Davis and Schultz 2009; ASMFC 2012). Specifically, mean adult body size from one alewife population declined by 10% between 1966 and 2006 (Davis and Schultz 2009) and river herring are projected to have earlier migrations across their range due to increased ocean and stream temperatures (Nye et al. 2012; Lynch et al. 2015). It is not clear to what extent climate and body size influence reproductive patterns, recruitment potential, and ultimately population dynamics for alewife. Disentangling these different components requires a better understanding of mating systems and the fitness consequences of current reproductive strategies.

The goals of this study were to provide novel information on reproductive biology of anadromous alewife and to provide the first test of whether reproductive success is related to parental sex, body size, and migration timing for this species. We conducted experimental translocations of adult alewife on multiple discrete dates in each of three successive years to a

historical, but extirpated, alewife spawning pond that is currently inaccessible to upstream migrants due to dams. We used genotypic (microsatellite) information from adult and juvenile alewife to reconstruct pedigrees and assign individual reproductive success to each stocked adult. Our study design and constructed pedigrees allowed us to test the hypothesis that alewife are batch spawners by examining the pattern of reproduction within and across translocation dates. Additionally, we predicted that adults would exhibit an early arrival advantage due to an increased number of reproductive opportunities and an increased chance that batches of offspring would encounter conditions favorable to survival. We also predicted that larger fish would have more offspring because larger females have higher fecundity. Our results provide novel information on the reproductive biology of alewife and fitness consequences of spawn timing and body size that will aid in understanding possible population-level consequences of anthropogenic environmental change and will help inform management for this species.

Materials and Methods

Study Site

This project was conducted in Pentucket Pond, located in Georgetown, Massachusetts. Pentucket Pond is 0.35 km² (86 acres) in area, has a maximum depth of 7.9 m and an average depth of 4.6 m, and is moderately developed. The Parker River flows from this pond 13.4 km to the Atlantic Ocean. Anthropogenic and natural barriers currently prevent adult alewife in the Parker River from entering the pond; however, adults and their offspring are capable of outward migration to the ocean.

106 *Adult Fish Translocation and Sampling*

107 In collaboration with the Massachusetts Division of Marine Fisheries (MDMF), we
108 translocated adult alewife from the lower Parker River to Pentucket Pond between April and
109 May in 2013, 2014, and 2015. Stocking dates varied among years roughly reflecting the natural
110 run timing. In 2013, 423 adult fish were transported on five different stocking dates (4/19: $N =$
111 100, 4/29: $N = 100$, 5/3: $N = 16$, 5/8: $N = 134$, 5/10: $N = 73$; Table S1). In 2014, 266 adult fish
112 were transported in four events (4/24: $N = 78$, 5/5: $N = 100$, 5/12: $N = 76$, 5/19: $N = 12$; Table
113 S1). In 2015, 409 adult fish were transported in three events (4/29: $N = 144$, 4/30: $N = 57$, 5/6: N
114 $= 208$; Table S1). We attempted to only stock alewife, but they are morphologically similar to
115 blueback herring and are difficult to distinguish without lethally sampling to observe peritoneal
116 coloration (Berlinsky et al. 2015). Blueback herring spawn later in the season than alewife
117 (Collette and Klein-MacPhee 2002), thus translocations occurred early in the spring to minimize
118 the presence blueback herring. We used genetic methods to test for presence of blueback herring
119 and hybrids between the two species in the stocked population. For all transplanted fish, sex and
120 length were recorded and fin clips were collected for genetic analyses. Fin clips were preserved
121 in Whatman paper and dried overnight in a drying oven.

122 *Juvenile Fish Sampling*

123 Young-of-year (YOY) produced by translocated adults were sampled using multiple
124 methods and over multiple sampling rounds between May and August in 2013 ($n = 117$), 2014 (n
125 $= 242$), and 2015 ($n = 843$). (Table S2). In 2013, YOY were sampled by boat electrofishing. In
126 2014 and 2015, a pelagic purse seine (30.5 m x 4.3 m, 2.22-mm mesh) was deployed from a boat
127 powered by an electric motor in 3 to 5 random locations per sampling night (Table S2). Random
128 locations were selected by dividing the lake into a numbered 50-m grid and using a random

number generator to select three primary and three alternate grid number locations. Alternate locations were used when a primary location was unsuitable for safe deployment due to shallowness or other obstacles (e.g., excess vegetation). In 2014, YOY were sampled for one night per month in June, July, and August using purse seines. In 2015, YOY were sampled in June (2 nights), July (1 night), August (2 nights), and October (1 night). In 2015, YOY were sampled in June (2 nights), July (1 night), August (2 nights), and October (1 night) using purse seines concurrently ($\pm$ 1-2 days) with gill nets. Two gill nets (4 panel, multi-mesh, 75 m x 3 m) were set at two random locations at least 200 m from shoreline at dusk and retrieved at dawn for all sampling dates. On October 3rd, nets were additionally set in the afternoon (15:30 to 17:30) on October 3rd. All collected YOY were counted and measured to the nearest millimeter (total length) and preserved for genetic processing. The majority of YOY samples (993 YOY) were preserved in 95% ethanol. Samples collected by gillnet on October 3rd, 2015 (293 YOY) were frozen for other purposes (Table S2). The timing of sampling was intended to contain the months when juvenile fish were most abundant in the lake prior to emigration. The frequency of sampling and use of different sampling methods in 2015 was justified in a companion study (Devine et al. 2018).

Genetic Analyses

Genetic work was completed at the UMass Amherst Conservation Genetics Laboratory. For adult samples preserved on Whatman paper and YOY preserved in ethanol, DNA was extracted from fin clips. For frozen YOY, DNA was extracted from livers, which were removed from each sample using equipment sterilized in 10% bleach between samples. We amplified 16 published microsatellite markers (*Aa046*, *Aa070*, *Aa074*, *Aa081*, *Aa082*, *Aa082.New*, *Aa091*, *Aa093*, *Aa010*, *Ap033*, *Ap037*, *Ap038*, *Ap047*, *Ap058*, *Ap070*, *Ap071*) (Palkovacs et al. 2008,

A'Hara et al. 2012), using four multiplex polymerase chain reactions (PCRs), which were run in Eppendorf thermal cyclers. PCRs were conducted following methods outlined by Palkovacs et al. (2008) and A'Hara et al. (2012) and contained 5 µL of Qiagen Multiplex Buffer (Qiagen, Inc.), 1 µL of primer mix, 2 µL of RNase-free water, and 2 µL of DNA. PCR product size was determined using an Applied Biosystems 3130xl capillary sequencer. Individual genotypes were scored based on a ROX 500 size standard using Geneious version 7.0.6 (Kearse et al. 2012). During the allele scoring process, we observed that *Aa082* appeared to have two separate and distinguishable loci, one of which was within the size range previously designated by Palkovacs et al (2008) and Palkovacs et al. (2014) as *Aa082*. We retained the name *Aa082* for the locus scored by Palkovacs et al. (2008) and Palkovacs et al. (2014) and we scored the additional locus separately and named it '*Aa082-New*'.

We tested for Hardy-Weinberg (HW) proportions to make inferences about random mating and to test marker performance. Evidence for null alleles in alewife has been reported for four loci we used (*Aa082*, *Ap037*, *Ap047*, and *Ap070*; Palkovacs et al. 2014; McBride et al. 2014). We used exact tests implemented in GENEPOP v. 4.2 to test adult genotypes for departures from HW proportions (Rousset 2008) as we corrected significance values for the false discovery rate using the BY-FDR approach (Benjamini and Yekutieli 2001). We also used MICROCHECKER v.2.2.3 (Van Oosterhout et al. 2004) to test for null alleles. Since samples of single age classes (in this case the offspring samples from each summer) are expected to have departures from HW proportions and an elevated signal of LD due to family structure (Whiteley et al. 2013), we did not conduct tests for deviation from HW proportions nor for LD in the samples of juveniles. We estimated genotyping error by genotyping and scoring 16 individuals multiple times, with a total of 133 replications among all individuals (Table S3). Error rates were

calculated based on Pompanon et al. (2005). Allele mismatches (m_a) and locus mismatches (m_l) were counted and used to calculate allelic (e_a) and locus (e_l) error rates.

Initial tests for deviations from HW proportions led us to test for hybridization between alewife and blueback herring and possible inadvertent inclusion of non-hybridized blueback herring among the translocated adults. Hybridization between these taxa has been previously reported by authors who used the same markers reported here (Hasselman et al. 2014; McBride et al. 2014; McBride et al. 2015). Hybrid swarm formation appears to be restricted to cases where both species are landlocked in sympatry (Hasselman et al. 2014). We tested for hybridization with NEWHYBRIDS v.1.1 Beta 3 (Anderson and Thompson 2002) with 100,000 burn-in cycles, 250,000 iterations, and a Jeffrey's prior. We used genotypes at the same set of loci from 5 known blueback herring and 9 alewife, based on internal inspection of peritoneal coloration (Berlinsky et al. 2015). These individuals were collected by MDMF in nearby Massachusetts coastal waters. Individuals with more than 70% posterior probability of assignment as alewife, blueback, or hybrids (F1 or F2) were assigned to those categories. Putative blueback herring and hybrids were removed from all analyses.

We calculated summary statistics and tested for linkage (gametic) disequilibrium (LD) for the final data set with GENEPOP. We calculated expected (H_e) and observed (H_o) heterozygosity, mean number of alleles (A), and F_{IS} for each set of adult non-hybridized alewife transferred. We also used CERVUS to calculate PI_{av} (the average probability of identity; Waits et al. 2001) and PE (the expected paternity exclusion probability; Jamieson and Taylor 1997) to summarize the power of this marker set to conduct parentage analysis.

197 *Parentage Analyses*

198 We estimated reproductive success using parentage assignments based on pedigree
199 analyses with CERVUS v. 3.0 (Marshall et al. 1998; Kalinowski et al. 2007). Prior to conducting
200 pedigree analyses, we performed empirically-based simulations to estimate accuracy of
201 CERVUS for our data set. Simulations were based on empirical genotypic data from the 2013
202 adults. The settings and details of our simulations are included in the supplementary materials.
203 We used PEDAGOG (Coombs et al. 2010a) to simulate a population of alewife parents and
204 offspring with a known pedigree, generated pedigrees using each of three programs (see next
205 paragraph) and compared generated pedigrees to the true known pedigree using PedAgree
206 (Coombs et al., 2010b). PEDAGOG simulates population genotypes based on empirical
207 genotype data while taking life history traits and sampling probabilities into account. Mating
208 structure, fecundity, and capture probability were included in the simulations (simulation settings
209 are available upon request). Given that most evidence suggests that alewife are batch spawners,
210 simulations assumed polygamous mating (Huber 1978; Ganas et al. 2015). Body length
211 distributions from 2013 were used to assign length for simulated individuals. Fecundity was
212 estimated based on an established body length-fecundity relationship for alewife (Lake and
213 Schmidt 1997). Mortality rate and capture probability were set to reflect existing literature on
214 juvenile mortality and our sampling methods (Walsh et al. 2005).

215 Populations were simulated for six cohorts with the fourth and sixth cohort sampled as
216 adults and offspring, respectively. To reflect our sampling methods and sample sizes, all adults
217 were sampled and 1% of offspring were sampled. The simulation was replicated 10 times to
218 produce 10 sets of adults ($N = 350\text{--}600$) and sampled offspring ($N = 1500\text{--}2500$) with known
219 pedigrees. We used CERVUS to assign simulated offspring to simulated adults for each of the 10

replicates. We selected parentage analysis with parent pair (sexes known) and asked for a report of the most-likely parent, we specified assignments at strict (95%) confidence and assumed default (0.01) genotyping error rates, which is similar to our observed multilocus error rate and well above our observed allelic and locus error rates. Based on the comparison of true and estimated pedigrees across 10 replicate simulations, on average 88% of CERVUS parent-offspring assignments were correct. Our simulation approach provided a more realistic and accurate assessment of these pedigree reconstruction approaches for our particular loci and sampling design compared to the relatively simplified simulations performed by CERVUS (Nilesen et al. 2001; Jones and Arden 2003).

For the analysis of empirical data with CERVUS, we included offspring and adults that were genotyped for at least 12 loci (2013: 100 % of offspring, 99.9% of adults; 2014 100% of offspring and adults, 2015; 88% of offspring, 99.7% of adults). We conducted a separate parentage analysis for each year of data to avoid incorrect assignments across years. We included putative blueback herring and hybrids in the empirical estimation of pedigree relationships because we wanted to include all possible parents in the analysis; however, blueback herring and hybrids were excluded from subsequent analyses.

Statistical Analyses

We used a one-way analysis of variance (ANOVA) to compare total length across study years for all fish and a two-way ANOVA to compare length across study years for males and females. Additionally, we used linear regression to assess the relationship between total length and arrival date.

We used generalized linear models to assess the relationships between reproductive success (number of offspring and number of mates per individual) and three predictor variables (arrival date, length, and sex). We examined four different error structures: Poisson, zero-inflated Poisson (ZIP), negative binomial (NB), and zero-inflated negative binomial (ZINB), and used AIC to compare among these structures. We included zero-inflated versions of the NB and Poisson error structures to account for the additional source of zeros from adult alewife that enter the pond but did not reproduce due to possible pre-spawning mortality, although their genotypes would still be included in our parentage analyses. Previous analyses of reproductive success in fishes have found that models with NB error structure have performed better than models with Poisson error structure (Araki et al. 2007; Naish et al. 2013; Robinson et al. 2017). We ran separate models for each sampling year. For each year, arrival date was standardized such that the first arrival date was “1” and the subsequent days were numbered accordingly. Length was centered around the mean separately for males and females in all three years. Relationships between variables including length and arrival date, were included as interactions during model selection. We fitted these models using the R packages pscl v. 1.4.9 (Jackman 2015; Zeileis et al. 2008) and MASS v. 7.3.-49 (Venables and Ripley 2002). We used log likelihood and AIC values to select the best fitting model for each response variable. We calculated partial pseudo- R^2 for each predictor variable using Zhang’s coefficient of determination for generalized linear models (R^2_v) (Zhang 2016) using the R package rsq v. 1.0.1 (Zhang 2018) to provide an indication of relative effect sizes of each predictor variable. All statistical analyses were conducted using R (R Development Core Team 2014).

Results

Adult translocations

We collected 1029 adults that were classified as non-hybridized alewife (2013: $N = 419$, 2014: $N = 220$, 2015: $N = 390$; Table 1; Table S1). Adult alewife length ranged from 241 to 336 mm across all years (Figure 1; Table S1). Mean length for adult alewife was 275.6 in 2013, 275.8 in 2014, and 274.2 in 2015 and did not differ significantly among years ($F_{1(1,1027)} = 1.27$, $P = 0.190$). For alewife, female length (mean = 284.3 mm) was greater than male length (mean = 271.6 mm) ($F_{1(1,1027)} = 169.37$, $P < 0.001$), regardless of year ($F_{1(1,1027)} = 2.01$, $P = 0.157$). In all three years, adult length was greatest earlier in the season and arrival date was weakly, but significantly, negatively correlated with total length ($R = -0.14$, $P < 0.001$).

We found evidence that we unintentionally translocated 39 adult blueback herring and 30 adult hybrids in the three years, with the most in 2014 (Table 1). Size distributions of putative blueback herring and hybrids are provided in the supplemental material (Table S8). Blueback herring and hybrids were otherwise excluded from additional analysis.

Marker testing and summary of genetic variation

We excluded several loci based on results from exact tests for HW proportions (Tables S5 – S7). Six out of 47 possible tests (13%) were statistically significant following BY-FDR (Benjamini and Yekutieli 2001) correction ($\alpha = 0.05$). Three significant tests included *Aa082*, one of the loci excluded by Palkovacs et al. (2014) based on evidence for a null allele. We excluded *Aa082* from all additional analyses. The other tests were associated with *Aa046* ($F_{IS} = -0.05$) and *Aa039* ($F_{IS} = 0.06$) in 2014 and *Ap071* ($F_{IS} = 0.11$) in 2015. We chose to conservatively exclude *Ap071* from the 2015 data set due to the relatively large positive F_{IS} value (evidence for a deficit of heterozygotes and therefore the presence of potential null alleles).

Subsequent analyses were therefore conducted with 15 loci for 2013 and 2014 and 14 loci for 2015.

Genotyping error rates were low. With *Aa082* excluded, allelic mismatch rates ranged from 0 to 11, allelic error rates ranged from 0 to 0.0026, locus mismatch rates ranged from 0 to 11, and locus error rates ranged from 0 to 0.0052 (Table S4). Genotyping mismatches (m_g) and error rates e_{obs} were 21 (m_g) = 21 and 0.0099 (e_{obs} ; Table S4).

Based on filtered marker sets, mean H_e for adult alewife ranged from 0.516 to 0.540 and mean A ranged from 5.4 to 6.4 for each of the years of adults translocated (Tables S5 – S7). Mean PI_{av} (average probability of identity) for the three years was 4.66^{-10} . The mean expected paternity exclusion probability (PE) across the three years was 0.028. We interpreted LD significance using BY-FDR correction and $\alpha = 0.05$. For 2013, zero of 105 tests were significant (Table S9). In 2014, four out of 105 tests were significant (Table S10). In 2015, 10 out of 105 tests were significant (Table S11).

Pedigree-based inferences

We collected 1,317 YOY alewife, with the largest number sampled in 2015 (2013: $N = 117$, 2014: $N = 242$, and 2015: $N = 958$; Table S2). All YOY that were included in parentage analyses (i.e. those that were genotyped at 12 or more loci 2013: $N = 117$, 2014: $N = 242$, 2015: $N = 843$) were assigned to parents in each year at a specified 95% confidence interval. Nearly all possible parents (99.8%) were genotyped each year since we stocked a pond where the species had been extirpated. Of these possible parents, two adult males (one in 2013 and one in 2015) were removed from analyses because they were genotyped at fewer than 12 loci. The proportion of adult alewife to which at least one offspring was assigned (hereafter, “assigned parents”) varied across years, from 36% in 2013 (151 of 419 adult alewife) to 84% in 2015 (328 of 390

adult alewife) (Table 2). For these assigned parents, the mean number of offspring assigned to each parent varied across years from 0.6 in 2013 to 4.3 in 2015 (Figure 2, Table S12). Females were assigned more offspring (mean = 4.1, coefficient of variation (CV) = 1.51) than males (mean = 1.6, CV = 1.32) across all three years (Figure 2, Table S12). Similarly, the average number of mates assigned per individual was higher for females (3.6, CV = 1.38) than males (1.4, CV = 1.19; Table 3). Additionally, in all three years a higher proportion of females were assigned offspring, with 46-95% of females being assigned offspring across years compared to 31-84% of males (Table 2).

Small families with many half-sibling (i.e., offspring that share one parent) were prevalent in all three years. Full-sibling (i.e., offspring share both parents) family size tended to be small and mean full-sibling family size remained relatively constant across all three years ranging from 1.0 in 2013 to 1.2 in 2015. In 2013, 117 YOY were assigned to 114 unique full-sibling families, in 2014, 266 YOY were assigned to 224 unique full-sibling families, and in 2015, 846 YOY were assigned to 713 unique full-sibling families. Assigned parents generally had multiple assigned full-sibling families with multiple mates (Table 3).

In addition to having multiple mates, individuals spawned with fish arriving on different transfer dates (Figure 3, Figures S1- S5). Specifically, 63% (121 of 193) of female alewife, 47% of male alewife (212 of 449), and 52% of all assigned parents spawned with fish from multiple transfer dates (Figure 3). Similarly, individuals with many offspring assigned were usually assigned YOY collected during different sampling events. In 2015, the average female was assigned offspring collected across 3.3 of the 4 juvenile sampling rounds. The most prolific female alewife in 2015 was assigned 52 offspring collected across all four sampling events

during the summer. Additionally, this 310 mm female had 32 different families and mated with individuals from all four transfer dates.

Predictors of reproductive success

NB models had the lowest AIC values in comparison to models with other error distributions (Poisson, ZIP, and ZINB; see Tables S13-S15), so we used an NB error structure. Over all three study years, sex, and arrival date were significant predictors of alewife reproductive success (offspring assignment and the number of mates; Table 4). Sex had strongest effect on offspring assignment (2013: $R^2_v = 0.111$; 2014: $R^2_v = 0.246$; 2015: $R^2_v = 0.341$; Table 4), with females being assigned more offspring than males in all three years (Figure 2, Table S12). Arrival date explained the second most amount of variation in assigned offspring ($R^2_v = 0.045$ – 0.146 ; Table 4), with the number of offspring assigned declining as arrival date became later. Larger body size (total length) was positively related to assignment of offspring in 2013 ($R^2_v = 0.039$) and 2015 ($R^2_v = 0.119$, Table 4). Given that females were larger and were stocked earlier in relation to their arrival in our study, we included an interaction term for sex, arrival date, and total length; however, these terms were eliminated during model selection because they were neither significant nor beneficial to model fit. With number of mates assigned to an individual as the response variable, separate models for each year indicated that sex explained the most variation ($R^2_v = 0.107$ – 0.470 across years) followed by arrival date ($R^2_v = 0.018$ – 0.139), and body size ($R^2_v = 0.003$ – 0.138 , Table 5).

Discussion

This study provides novel understanding about aspects of fitness and reproductive patterns in a wild population of alewife. Specifically, we demonstrated protracted spawning that included mating events among translocated adults who arrived at the beginning of the season and others who arrived at the end. The mating system in this population is characterized by many small half-sibling families and widespread within-season polygamy, consistent with the observation of asynchronous batch spawning. Individuals can therefore reproduce multiple times over longer periods within each spawning season. Earlier stocking or arrival in the system may provide for more spawning opportunities that maximizes reproductive success, however allowing different components of the run to gain access to spawning grounds may be important for population resiliency in the face of environmental variability in flows and temperatures that alter spawning run dynamics. Phenology and body size also influenced reproductive success, highlighting the importance of maintaining older, larger alewife within populations.

River herring reproductive biology and mating patterns

Based on our pedigree assignments, alewife mated at multiple times throughout the breeding season, confirming that adults can remain in fresh water well after initial spawning. Extended residence in fresh water with multiple spawning events is consistent with findings from three non-genetic studies (Iafrate and Oliviera 2008; Gahagan et al 2010; Rosset et al. 2017), which reported multiple week delays between adult arrival and spawning based on juvenile otolith analysis. Analysis of oocyte development has also identified alewife as asynchronous spawners (Ganias et al. 2015). These studies contradict the general understanding that adult river herring leave spawning grounds almost immediately after initial spawning (Collette and Klein-MacPhee 2002). Instead, alewife can remain in fresh water and spawn multiple batches of

offspring over extended periods. However, we cannot pinpoint specific spawning dates or the length delay between adult arrival and spawning for specific individuals. A comparison of juvenile ages and arrival dates from pedigree assigned parents would further clarify how long adult river herring remain in fresh water, detail patterns in spawning over time, and allow assessment of relationships between duration of stay in fresh water and reproductive success. Still, it is clear that alewife reproduce over substantially longer periods, among different components of the spawning run, and spend more time in fresh water than previously assumed.

Our study provides the first spawning success estimates for alewife and suggests that females have more mates, offspring, and spawning events as well as more variation in mating and offspring assignment than males. This pattern could reflect the stocking of more males than females. Alternatively, given the lack of correlation between the proportion of males and females assigned offspring, high competition among males during mating could explain the discrepancies among sexes. Higher variation in mating and success rates among females could be related to greater egg production and different mating habits between the sexes. Female spawning success rates from our study ranged from 46% to 91%, similar on the high end to one previously reported female spawning success rate of 93% for alewife based on the number of eggs retained by females during their migration to the ocean (Cole et al. 1980). Cole et al. (1980) conducted their study in the same watershed as our study site; however, they did not consider actual YOY production and counted eggs to produce estimates. In our study, the mean number of offspring assigned to each female ranged from 0.8 to 10.5 and was higher in two of three study years than those reported by the only prior study reporting alewife reproductive success where females produced between 1.5 and 3 offspring each season (Huber 1978). This discrepancy is likely because Huber (1978) reported and measured success in terms of emigrating offspring, thus

including juvenile mortality in fresh water with reproduction estimates. Mortality for river herring YOY is very high during the first few months of life, with survival estimates from 0.0001% (Kissil 1974) to 1.0% (Havey 1973). Since our study design did not incorporate juvenile mortality, we cannot directly compare number of offspring the study by Huber (1978). Finally, both Huber (1978) and Cole et al. (1980) assumed determinate spawning in alewife and therefore their estimates of offspring assignment are likely to be biased low, since alewife have been recently identified as indeterminate batch spawners (Ganias et al. 2015).

Factors associated with reproductive success

Earlier arrival was associated with higher reproductive success and more mating events in all three sampling years. This pattern is consistent with trends in other anadromous fishes, including salmonids (Trippel et al. 1997; McPhee and Quinn 1998; Smoker et al. 2000, Dickerson et al. 2002; Abadia-Cardoso et al. 2013), although underlying causes likely differ for alewife. Early arriving salmonids are likely more successful because they are larger and live longer (Trippel et al. 1997; Smoker et al. 2000; Abadia-Cardoso et al. 2013), which allows them to have more mating events and more effectively guard nests for a longer period of time (McPhee and Quinn 1998; Dickerson et al. 2002; Hruska et al. 2011), although they risk nest destruction by later arriving females (redd superimposition) (Hendry et al. 2004; Quinn 2011). Similar to salmonids, early arriving alewife have more time to spawn. Alewife are batch spawners—they spawn multiple times during a spawning season (Huber 1978; Ganias et al. 2015)—which means that earlier arrivers may have more opportunity to mate during the spawning season. Our results support this hypothesis since early arrival was also positively associated with the number of mates. Further, arrival date was a strong predictor of the assignment of multiple mates in our statistical models. Since alewife do not build nests, later

arriving alewife do not have a similar superimposition advantage, although some work suggests adults feed upon eggs (Simonin et al. 2007). Earlier arriving alewife may also have an advantage with respect to survival and growth of offspring in fresh water, as per the match mis-match hypothesis (*sensu* Cushing 1969). The environmental window available for successful spawning and early life history survival has not been studied in detail for alewives, but recent work provides evidence that migrations and offspring survival are not synchronized (Rosset et al. 2017), and thus some optimal window exists. In high-density systems, juvenile and adult alewife predation pressure on large-bodied zooplankton in late spring and early summer produces small-bodied zooplankton community composition in later summer months (Brooks and Dodson 1965; Crowder et al. 1987; Post et al. 2008). Thus, earlier spawned juvenile alewife may have access to more plentiful larger-bodied zooplankton than juveniles spawned later in the summer, which may influence access to forage for fast growth (Kosa and Mather 2001) and affect their emigration timing (Yako 1998). While the influence of juvenile alewife predation pressure on the zooplankton composition in our low-density system may not result in dramatic changes in zooplankton community composition, the trend toward earlier arrival may still serve an advantage for juvenile feeding by allowing for flexibility in the duration of residence in the freshwater nursery environment before emigration. Additionally, early arrival and growth in fresh water may have implications for successful emigration into estuaries and movement into the ocean for overwintering, where strong selection on body size has been observed (Munch et al. 2003).

Body size was correlated with higher reproductive success for both males and females in our study. Larger female body size is often positively correlated with fecundity, egg size, and viability of eggs in fishes (Trippel et al. 1997). Larger males may also have a competitive

advantage during spawning (Fleming 1996; Trippel et al. 1997). There is no published description of spawning behavior for alewife specifically, but it is likely that they exhibit similar behavior to blueback herring that spawn in groups composed of one female and several males (Loesch and Lund 1977). Blueback herring swim around in circles for a few minutes while the males nudge the female. Eventually the group swims faster, and all members dive to the bottom to deposit milt and eggs simultaneously (Loesch and Lund 1977). Larger males might push themselves closer to the female and swim faster when diving to fertilize a larger proportion of eggs. These results add to the limited literature on the importance of male body size in fish species that do not exhibit nest guarding and to the mating system and behaviors of alewife.

Study limitations

Several caveats of our study are worth mentioning. First, sample sizes and sampling gear varied substantially across years and year was the strongest predictor of reproductive success. Estimates of spawning success are higher in 2014 and 2015 when using the purse seine and gill nets, compared to 2013 when we used the boat electroshocker. Additionally, juvenile sampling in 2013 was conducted later in the season than other years. We acknowledge that using different sampling methods within and among years can potentially influence our results. However, observed patterns and factors influencing reproductive success were similar across years. Furthermore, the estimated spawning dates for gill netted fish were similar to purse seined fish, thus it appears that gill nets were not systematically sampling fish spawned at different times when compared to the purse seine. We also used purse seines and gill nets concurrently in 2015 to capture all potential juvenile ages, which further reduced chances of missing fish spawned at different times. Still, larval mortality is extremely high in the first few weeks after hatching (Walsh et al. 2005) and thus earlier spawned cohorts may have been underrepresented, creating a

negative bias for estimates of reproductive success in the earliest spawning individuals. Future studies with larger sample sizes could investigate patterns in initial spawning and hatching success and then track pedigrees through the juvenile stage to determine if patterns are maintained over time.

A second limitation is the relatively low variation explained by arrival date and body size (total length) and that logistical differences and interannual environmental variation could be responsible for patterns in reproductive success. Since alewife were stocked as they initiated upstream travel, variability in oceanic and freshwater climatic conditions among years may have influenced the demography and physiological condition of stocked fish. For example, total length was not significantly related to reproductive success in 2014; likely due to the combination of a lower number of adult fish stocked that year (only 220 pure alewives compared to 419 (2013) and 390 (2015)). Additionally, 46 of the stocked fish that year were removed from analyses because they were identified as blueback herring or hybrids. Temporal overlap in migration of alewives and blueback herring typically occurs later in the season, and thus presence of nearly 17% hybrid or blueback herring may indicate that we sampled too late in the 2014 migration season to capture the entire range of adults, especially the largest and earliest arrivals. A closer examination of these variables among more years and with the same combination of gear will be necessary to understand interannual differences. While the R^2_v values are relatively low for arrival date and total length when compared to sex, they nonetheless explain a significant portion of variation in reproductive success once sex is controlled for, particularly in 2015, the most reliable sampling year.

Another potential concern was the low density of adults translocated into Pentucket Pond. Each year, only 266 to 423 fish were stocked, while adult run size estimates for the study river system (Parker River, MA) ranged from 7,149 to 19,852 during study years (ASMFC 2017). The State of Maine stocks inland spawning habitats with six adult alewife per surface acre as an interim restoration target and require passage (escapement) of a minimum of 35 spawning river herring per surface acre of nursery habitat on harvested runs, except for oligotrophic or higher productivity sites, which have targets of 3-41 fish per surface acre (Maine BRM 2016). Our stocking effort resulted in rates of 4.7, 1.6, and 4.9 adults per surface acre over the three years of the study. At our stocking levels, juvenile density was low and resulted in high growth rates (Rosset 2016) relative to other populations in coastal Massachusetts, although both the run size and juvenile growth rates are similar to historical observations from Pentucket Pond prior to alewife extirpation due to beavers and fishway degradation (Cohen 1976; Jiminez 1978). Thus, the results are particularly relevant for many populations in New England that have recently experienced habitat expansions and recolonizations through similar stocking practices, dam removals, and fish ladder installations. Since our observations represent the low end of variation in density, comparison to studies conducted at higher adult densities would be instructive. Still, alewife populations exist over a broad range of habitats and conditions, so, while unusual for a monitored natural spawning run, adult densities we established represent a point in the range of possible conditions, particularly in stocked systems that are pervasive throughout Maine. However, it is worthwhile to consider how the results may differ in higher density systems. Earlier arriving fish of both sexes and larger males would likely have a more prominent competitive advantage in higher density systems, since both males and females would have a longer time to mate and larger males would be dominant in mating groups. Moreover, larger

female alewife may have an advantage in higher density systems if they produce larger eggs and higher survival rates that can be amplified under increased competition (Perrin 1989; Stearns 1992). Higher densities also result in higher encounter rates and can influence mate choice and the probability of successful mating, particularly among males (Kokko and Rankin 2006), which would more broadly increase reproductive success. However, despite the low density of adults in Pentucket Pond during our study, high rates of offspring assignment suggest that potentially limited spawning access associated with lower rates of encounters was not a problem. Further work will be required to better understand the influence of density and abiotic characteristics on growth, survival and reproductive success in alewife populations at different densities.

Pedigree reconstruction approaches are prone to errors, particularly if many parents are missing (Marshall et al. 1998; Pemberton 2008) or marker sets are prone to genotyping errors (Pompanon et al. 2005; Kalinowski et al. 2007). The controlled stocking and subsequent inclusion of nearly all possible parents in parentage assignments is a strength of our study design. Estimated genotyping error rates demonstrated the settings we used for pedigree reconstruction were reasonable (Morrissey and Wilson 2005; Kalinowski et al. 2007). In addition, we used empirically-based simulations to estimate an 88% rate of accurate assignments for our marker set and sampling design. Erroneous pedigree assignments should not be biased by the year of study or traits examined (body size and arrival time). Thus, it is unlikely that incorrect pedigree assignments systematically biased our temporally replicated inferences regarding the influence of body size and arrival time on reproductive success.

Conservation and Management Implications

Our results provide the first detailed life history information about alewife reproductive success, and while only for one population, our results have important implications for changing environmental conditions that could influence population demographic rates and productivity. Anthropogenically-altered selection pressures including changes in optimal migration timing, size, or age at maturity could influence reproductive success and thus population demographic rates and productivity. Historical data and modelling of projected climate conditions suggests that alewife migrations have already shifted earlier and will continue to do so (Ellis and Vokoun 2009; Lynch et al. 2015). Earlier migration phenology over shorter periods, and particularly if strong selection for earlier arrival time, could reduce population resilience to anomalous years (Alexander et al. 2017). Delays in passing fish ladders or shifting climate patterns can therefore limit the opportunity for multiple mating events and could reduce overall reproductive output. Greater windows for reproduction increase the likelihood that at least one mating event occurs during optimal survival conditions (Cury and Roy 1989; Bollens et al. 1992; Lasker 1981; Wright and Gibb 2005). Thus, a reduced number of mating events may lead to asynchrony and a “mismatch” that negatively affects survival (Cushing 1969, 1975). The most successful alewife in this study? had multiple mating events over different times during the spawning season facilitated by early arrival and larger body size. Conversely, any shift to earlier arrival time but continued spawning over long periods increases the potential for multiple mating events during a season. Similarly, given the positive correlation between alewife size and reproductive success, decreased age and size at maturity (Davis and Schultz 2009; ASMFC 2017) would depress reproductive rates, as observed in other anadromous species (Allendorf et al. 2008; Allendorf and Hard 2009; Audzijonyte et al. 2013). Spawning arrival and migration timing play an

important role in alewife reproductive success and may have broader implications if anadromous fish migrations are shifting temporally in response to climate change (Planque et al. 2010).

Information from our study can be used to make more precise predictions of alewife productivity in fresh water that can be incorporated into models to aid in more effective management of this species of concern. For example, our results can inform widespread stocking and run augmentation. Specifically, efforts could emphasize transferring fish early and throughout seasonal spawning runs to maintain genetic variation in run timing and provide a maximum number of spawning events and opportunity for offspring to encounter suitable growth and survival conditions. Managers could also be attentive of manipulations that would increase selection pressure for early return and maturation.

We have demonstrated how individual reproductive success provides a link among the observed phenotypic variation, population dynamics and reproductive phenology in alewives. Larger and earlier spawning individuals had higher reproductive success, which appears to confer a fitness advantage. Long-term pedigrees would increase the variability in annual environmental differences and, if combined with laboratory studies, could help elucidate these relationships further. This work demonstrated the value of pedigrees to evaluate reproductive patterns in a wild anadromous fish species towards a better understanding of reproductive patterns and the influence of environmental change.

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593 **Data Archiving Statement:** Genotype data for this study will be available at the Dryad Digital
594 Repository: to be completed after manuscript is accepted for publication.

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References

- 597
598 A'Hara, S., Amouroux, P., Argo, E. E., Avand-Faghih, A., Barat, A., Barbieri, L., Bert, T. M.,
599 Blatrix, R., Blin, A., and Bouktila, D. 2012. Permanent genetic resources added to
600 molecular ecology resources database 1 August 2011–30 September 2011. *Mol. Ecol.*
601 *Res.* **12**(1): 185-189. doi: 10.1111/j.1755-0998.2011.03088.
- 602 Abadia-Cardoso, A., Anderson, E. C., Pearse, D. E., and Garza, J. C. 2013. Large-scale
603 parentage analysis reveals reproductive patterns and heritability of spawn timing in a
604 hatchery population of steelhead (*Oncorhynchus mykiss*). *Mol. Ecol.* **22**(18): 4733-4746.
605 doi: 10.1111/mec.12426.
- 606 Allendorf, F. W., England, P. R., Luikart, G., Ritchie, P. A., and Ryman, N. 2008. Genetic
607 effects of harvest on wild animal populations. *Trends Ecol. Evol.* **23**(6): 327-337. doi:
608 10.1016/j.tree.2008.02.008.
- 609 Allendorf, F. W., and Hard, J. J. 2009. Human-induced evolution caused by unnatural selection
610 through harvest of wild animals. *Proc. Natl. Acad. Sci. U.S.A* **106**(Suppl 1): 9987-9994.
611 doi: 10.1073/pnas.0901069106.
- 612 Alexander, K.E., Willis, T.V., Leavenworth, W.B., Hall, C., Mattocks, S., Bittner, S.M., Klein,
613 E., Staudinger, M., Bryan, A., Rosset, J., Carr, B.H. and Jordaan, A. 2017. Tambora and
614 the mackerel year: phenology and fisheries during an extreme climate event. *Sci. Adv.*
615 **3**(1): e1601635. doi: 10.1126/sciadv.1601635.
- 616 Anderson, E., and Thompson, E. 2002. A model-based method for identifying species hybrids
617 using multilocus genetic data. *Genetics*, **160**(3): 1217-1229.

- 618 Araki, H., Waples, R. S., Arden, W. R., Cooper, B., and Blouin, M. S. 2007. Effective population
619 size of steelhead trout: influence of variance in reproductive success, hatchery programs,
620 and genetic compensation between life-history forms. *Mol. Ecol.* **16**(5): 953-966.
621 <https://doi.org/10.1111/j.1365-294X.2006.03206.x>
- 622 ASMFC. 2012. River herring benchmark stock assessment volume 1. Stock Assessment Report
623 No. 12-02. Atlantic States Marine Fisheries Commission, Arlington, VA.
- 624 ASMFC. 2017. River herring stock assessment update volume 1. Atlantic States Marine
625 Fisheries Commission, Arlington, VA.
- 626 Audzijonyte, A., Kuparinen, A., and Fulton, E. A. 2013. How fast is fisheries-induced evolution?
627 Quantitative analysis of modelling and empirical studies. *Evol. Appl.* **6**(4): 585-595. doi:
628 [10.1111/eva.12044](https://doi.org/10.1111/eva.12044).
- 629 Benjamini, Y., and Yekutieli, D. 2001. The control of the false discovery rate in multiple testing
630 under dependency. *Ann. Statist.* **29**(4): 1165-1188. doi:[10.1214/aos/1013699998](https://doi.org/10.1214/aos/1013699998).
- 631 Berlinsky, D. L., M. A. DiMaggio, T. S. Breton, J. Walsh, and Kovach, A. I. 2015. Peritoneal
632 pigmentation in purebred and hybrid river herring. *Trans. Am. Fish. Soc.* **144**(4): 717-
633 723. doi: [10.1080/00028487.2015.1037017](https://doi.org/10.1080/00028487.2015.1037017).
- 634 Bollens, S. M., Frost, B. W., Schwaninger, H. R., Davis, C. S., Way, K. J., and Landsteiner, M.
635 C. 1992. Seasonal plankton cycles in a temperate fjord and comments on the match-
636 mismatch hypothesis. *J. Plankton Res.* **14**(9): 1279-1305. doi: [10.1093/plankt/14.9.1279](https://doi.org/10.1093/plankt/14.9.1279).

- 637 Brooks, J.L., and Dodson, S. I. 1965, Predation, body size, and composition of plankton. Science
638 **150** (3692): 707-714.
- 639 Cargnelli, L.M., and Neff, B. D. 2006. Condition-dependent nesting in bluegill sunfish *Lepomis*
640 *macrochirus*. J. Anim. Ecol. **75**(3): 627-633. doi: 10.1111/j.1365-2656.2006.01083.x.
- 641 Claramunt, G., Serra, R., Castro, L. R., and Cubillos, L. 2007. Is the spawning frequency
642 dependent on female size? Empirical evidence in *Sardinops sagax* and *Engraulis ringens*
643 off northern Chile. Fish. Res. **85**(3): 248 –257. doi: 10.1016/j.fishres.2007.01.009.
- 644 Cohen, D. L. 1976. Food habits of larval and juvenile anadromous alewives, *Alosa*
645 *pseudoharengus* (Wilson), as related to the limnology and zooplankton of Rock and
646 Pentucket Ponds, Georgetown, Massachusetts. M. Sc thesis, Department of
647 Environmental Conservation, University of Massachusetts, Amherst, MA.
- 648 Cole, C. F., Essig, R. J., and Sainelle, O. R. 1980. Biological investigation of the alewife
649 population, Parker River, Massachusetts. U.S. National Marine Fish Wildlife Service
650 Bulletin, **73**(2): 375-396.
- 651 Collette, B. B. and Klein-MacPhee, G. 2002. Bigelow and Schroeder's fishes of the Gulf of
652 Maine, 3rd edition. Smithsonian University Press. Washington, D.C.
- 653 Coombs, J. A., Letcher, B. H., and Nislow, K. H. 2010a. Pedagog: software for simulating eco-
654 evolutionary population dynamics. Mol. Ecol. Res. **10**(3): 558-563. doi: 10.1111/j.1755-
655 0998.2009.02803.x.

- 656 Coombs, J. A., Letcher, B. H., and Nislow, K. H. 2010b. PedAgree: software to quantify error
657 and assess accuracy and congruence for genetically reconstructed pedigree relationships.
658 Conserv. Genet. Resour. **2**(1): 147-150. doi: 10.1007/s12686-010-9202-9.
- 659 Creed, R. P. Jr. 1985. Feeding, diet, and repeat spawning of blueback herring, *Alosa aestivalis*,
660 from the Chowan River, North Carolina. Fish. Bull. **83**(4): 711–716.
661 <http://fishbull.noaa.gov/834/creed.pdf>. [accessed 4 October 2017]
- 662 Crowder, L. B., McDonald, M. E., and Rice, J. A. 1987. Understanding recruitment of Lake
663 Michigan fishes: the importance of size-based interactions between fish and zooplankton.
664 Can. J. Fish. Aquat. Sci. **44**(S2): 141-147. doi: <https://doi.org/10.1139/f87-317>
- 665 Cury, P., and Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success
666 in upwelling areas. Can. J. Fish. Aquat. Sci. **46**(4): 670–680. doi: 10.1139/f89-086
- 667 Cushing, D. H. 1969. The regularity of the spawning season of some fishes. J. Cons. Int. Explor.
668 Mer. **33**(1): 81-97. doi: 10.1093/icesjms/33.1.81
- 669 Cushing, D. H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge,
670 England.
- 671 Dawson, R. D., and Clark, R. G. 2000. Effects of hatching date and egg size on growth,
672 recruitment, and adult size of lesser scaup. Condor. **102**(4): 930-935. doi:
673 10.2307/1370324.

- 674 Davis, J. P., and Schultz, T. 2009. Temporal shifts in demography and life history of an
675 anadromous alewife population in Connecticut. *Mar. Coast. Fish. : Dyn. Manage.*
676 *Ecosyst. Sci. Adv.* **1**(1): 90-106. doi: 10.1577/C08-003.1.
- 677 DeMartini, E.E., and Fountain, R. K. 1981. Ovarian cycling frequency and batch fecundity in
678 the queenfish. *Seriphus politus*: attributes representative of serial spawning fishes. *Fish.*
679 *Bull.* **79**(3): 547-560. <http://fishbull.noaa.gov/79-3/demartini.pdf>. [accessed 4 October
680 2017].
- 681 Devine, M.T., Roy, A. H., Whiteley, A. R., Gahagan, B. I., Armstrong, M. P., and Jordaan,
682 A. 2018. Precision and relative effectiveness of a purse seine for sampling age-0 river
683 herring in lakes. *N. Am. J. of Fish. Manage.* doi: 10.1002/nafm.10065
- 684 Dickerson, B., Quinn, T., and Willson, M. 2002. Body size, arrival date, and reproductive
685 success of pink salmon, *Oncorhynchus gorbuscha*. *Ethol. Ecol. Evol.* **14**(1): 29-44. doi:
686 10.1080/08927014.2002.9522759.
- 687 Ellis, D., and Vokoun, J. C. 2009. Earlier spring warming of coastal streams and implications for
688 alewife migration timing. *N. Am. J. Fish. Manage.* **29**(6): 1584-1589. doi: 10.1577/M08-
689 181.1
- 690 Fleming, I. A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. *Rev.*
691 *Fish Biol. Fish.* **6**(4): 379-416. doi: 10.1007/BF00164323

- 692 Gahagan, B.I., Gherard, K.E., and Schultz, E.T. 2010. Environmental and Endogenous Factors
693 Influencing Emigration in Juvenile Anadromous Alewives. Trans. Am. Fish. Soc. **139**(4):
694 1069-1082. doi: 10.1577/T09-128.1
- 695 Ganas, K., Divino, J. N., Gherard, K. E., Davis, J. P., Mouchlianitis, F., and Schultz, E. T. 2015.
696 A reappraisal of reproduction in anadromous alewives: determinate versus indeterminate
697 fecundity, batch size, and batch number. Trans. Am. Fish. Soc. **144**(6): 1143-1158. doi:
698 10.1080/00028487.2015.1073620.
- 699 Hall, C. J., Jordaan, A., and Frisk, M. G. (2012). Centuries of anadromous forage fish loss:
700 consequences for ecosystem connectivity and productivity. Bioscience, **62**(8): 723-731.
701 doi: 10.1525/bio.2012.62.8.5.
- 702 Hasselman, D. J., Argo, E. E., McBride, M. C., Bentzen, P., Schultz, T. F., Perez-Umphrey, A.
703 A., and Palkovacs, E. P. 2014. Human disturbance causes the formation of a hybrid
704 swarm between two naturally sympatric fish species. Mol. Ecol. **23**(5): 1137-1152. doi:
705 10.1111/mec.12674.
- 706 Hasselman, D.J., Anderson, E.C., Argo, E.E., Bethoney, N.D., Gephard, S.R., Post, D.M.,
707 Schondelmeier, B.P., Schultz, T.F., Willis, T.V. and Palkovacs, E.P. 2015. Genetic stock
708 composition of marine bycatch reveals disproportional impacts on depleted river herring
709 genetic stocks. Can. J. Fish. Aquat. Sci. **73**(6): 951-963. doi: 10.1139/cjfas-2015-0402.
- 710 Havey, K. A. 1973. Production of juvenile alewives, *Alosa pseudoharengus*, at Love Lake,
711 Washington County, Maine. Trans. Am. Fish. Soc. **102**(2): 434-437. doi: 10.1577/1548-
712 8659(1973)102<434:POJAAP>2.0.CO;2.

- 713 Hendry, A. P., Morbey, Y. E., Berg, O. K., and Wenburg, J. K. 2004. Adaptive variation in
714 senescence: reproductive lifespan in a wild salmon population. *Proc. R Soc. Lond. B.*
715 *Biol. Sci.* **271**(1536): 259-266. doi: 10.1098/rspb.2003.2600.
- 716 Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe, viewed in the light of
717 biological research. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer.* **20**(1) : 1-228.
- 718 Hruska, K. A., Hinch, S. G., Patterson, D. A., and Healey, M. C. 2011. Egg retention in relation
719 to arrival timing and reproductive longevity in female sockeye salmon (*Oncorhynchus*
720 *nerka*). *Can. J. Fish. Aquat. Sci.* **68**(2): 250-259. doi: 10.1139/F10-153
- 721 Huber, M. E. 1978. Adult spawning success and emigration of juvenile alewives (*Alosa*
722 *pseudoharengus*) from the Parker River, Massachusetts. M Sc. Thesis, Department of
723 Environmental Conservation, University of Massachusetts, Amherst, MA.
- 724 Iafrate, J., and Oliveira, K. 2008. Factors affecting migration patterns of juvenile river herring in
725 a coastal Massachusetts stream. *Environ. Biol. Fishes*, **81**(4): 101-110. doi: 10.1577/T09-
726 128.1.
- 727 Jackman, S. 2015. *Pscl*: classes and methods for r developed in the political science
728 computational laboratory, Stanford University. R Package Version 1.4.9. Stanford,
729 California: Department of Political Science, Stanford University.
- 730 Jamieson, A., and Taylor, C. S. 1997. Comparisons of three probability formulae for parentage
731 exclusion. *Anim. Genet.* **28**(6): 397-400. doi: 10.1111/j.1365-2052.1997.00186.x

- 732 Jimenez, D. 1978. Growth and size-selective feeding of juvenile anadromous alewives (*Alosa*
733 *pseudoharengus*, Wilson) in Rock and Pentucket Ponds, Georgetown, Massachusetts. M.
734 Sc. thesis, Department of Environmental Conservation, University of Massachusetts,
735 Amherst, MA.
- 736 Jones, A. G., and Arden W. R. 2003. Methods of parentage analysis in natural populations. *Mol.*
737 *Ecol.* **12**(2): 2511-2523. doi: 10.1046/j.1365-294X.2003.01928.x
- 738 Jones, O. R., and Wang. J. 2010. Molecular marker-based pedigrees for animal conservation
739 biologists. *Anim. Conserv.* **13**(1): 26-34. doi: 10.1111/j.1469-1795.2009.00324.x
- 740 Kalinowski, S. T., Taper, M. L., and Marhsall, T. C. 2007. Revising how the computer program
741 CERVUS accommodates genotyping error increases success in paternity assignment.
742 *Mol. Ecol.* **16**(5): 1099-1106. doi: 10.1111/j.1365-294X.2007.03089.x
- 743 Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S.,
744 Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, B., and
745 Drummond, A. 2012. Geneious Basic: an integrated and extendable desktop software
746 platform for the organization and analysis of sequence data. *Bioinformatics* **28**(12): 1647-
747 1649. doi: 10.1093/bioinformatics/bts199.
- 748 Kinnison, M. T., and Hairston, N. G. 2007. Eco-evolutionary conservation biology:
749 contemporary evolution and the dynamics of persistence. *Funct. Ecol.* **21**(3), 444-454.
750 doi: 10.1111/j.1365-2435.2007.01278.x.

- 751 Kissil, G. W. 1974. Spawning of the anadromous alewife, *Alosa pseudoharengus*, in Bride Lake,
752 Connecticut. Trans. Am. Fish. Soc. **103**(2): 312-317. doi: 10.1577/1548-
753 8659(1974)103<312:SOTAAA>2.0.CO;2.
- 754 Kjesbu, O. S., P. Solemdal, P. Bratland, and Fonn., M. 1996. Variation in annual egg production
755 in individual captive Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **53**(3):
756 610–620. doi: 10.1111/j.1095-8649.1996.tb01789.x.
- 757 Kosa, J. T., and Mather, M. E. 2001. Processes contributing to variability in regional patterns of
758 juvenile river herring abundance across small coastal systems. Trans. Am. Fish. Soc.
759 **130**(4): 600-619. doi: 10.1577/1548-8659(2001)130<0600:PCTVIR>2.0.CO;2.
- 760 Kokko, H. and Rankin, D.J., 2006. Lonely hearts or sex in the city? Density-dependent effects in
761 mating systems. Philos. Trans. R. Soc. Lond. B. Biol. Sci. **361**(1466): 319-334. doi:
762 10.1098/rstb.2005.1784.
- 763 Kruuk, L. E. B., and Hill., W. G. 2008. Introduction. Evolutionary dynamics of wild
764 populations: the use of long-term pedigree data. Proc. R. Soc. Lond. B. Biol. Sci.
765 **275**(1635): 593-596. doi: 10.1098/rspb.2007.1689.
- 766 Lake, T. R., and Schmidt, R. E. 1997. The relationship between fecundity of an alewife (*Alosa*
767 *pseudoharengus*) spawning population and egg productivity in Quassaic Creek, a Hudson
768 River tributary (HRM 60) in Orange County, New York. Final Reports of the Tibor T.
769 Polgar Fellowship Program, pp. 1-26.

- 770 Lasker, R. 1981. The role of a stable ocean in larval fish survival and subsequent recruitment. *In*
771 Marine fish larvae: morphology, ecology and relation to fisheries. *Edited by* R. Lasker.
772 University of Washington Press, Seattle, WA. pp. 80–87.
- 773 Lin, J. E., Hard, J. J., Naish, K. A., Peterson, D., Hilborn, R., and Hauser, L., 2016. It's a
774 bear market: evolutionary and ecological effects of predation on two wild sockeye
775 salmon populations. *Heredity*, **116**(5): 447-457. doi: 10.1038/hdy.2016.3.
- 776 Loesch, J. G. 1987. Overview of life history aspects of anadromous Alewife and Blueback
777 Herring in freshwater habitats. *In* Common strategies of anadromous and catadromous
778 fishes. American Fisheries Society, Symposium 1. *Edited by* M. J. Dadswell and R. J.
779 Maryland. pp. 97–103
- 780 Loesch J.G., and Lund, W. A. Jr. 1977. A contribution to the life history of the blueback herring,
781 *Alosa aestivalis*. *Trans. Am. Fish. Soc.* **106**(6): 583-589. doi: 10.1577/1548-
782 8659(1977)106<583:ACTTLH>2.0.CO;2
- 783 Lynch, P. D., Nye, J. A., Hare, J. A., Stock, C. A., Alexander, M. A., Scott, J. D., Curti K. L.,
784 Drew, K. 2015. Projected ocean warming creates a conservation challenge for river
785 herring populations. *ICES J. Mar. Sci.* **72**(1): 374-387. doi:
786 <https://doi.org/10.1093/icesjms/fsu134>.
- 787 Maine BRM 2016. Maine Department of Marine Resources. 2015 Maine River Herring
788 Sustainable Fisheries Plan Update. 103 p.
789 http://www.asmfc.org/files/RiverHerringSFMPs/ME_RiverHerring_SFMP_Dec2016.pdf

- 790 Malvezzi, A. J., Murray, C. S., Feldheim, K. A., DiBattista, J. D., Garant, D., Gobler, C. J.,
791 Chapman, D. D., and Baumann, H. 2015. A quantitative genetic approach to assess the
792 evolutionary potential of a coastal marine fish to ocean acidification. *Evol. Appl.* **8**(4):
793 352-362. doi: 10.1111/eva.12248.
- 794 Marshall, T. C., Slate, J., Kruuk, L.E.B., and Pemberton, J. M. 1998. Statistical confidence for
795 likelihood-based paternity inference in natural populations. *Mol. Ecol.* **7**(5): 639-655. doi:
796 10.1046/j.1365-294x.1998.00374.x.
- 797 Mattocks, S., Hall, C. J., and Jordaan, A. 2017. Damming, lost connectivity, and the historical
798 role of anadromous fish in freshwater ecosystem dynamics. *BioScience* **67**(8):713–728.
799 doi: 10.1093/biosci/bix069.
- 800 McBride, M., Willis, T., Bradford, R., and Bentzen, P. 2014. Genetic diversity and structure of
801 two hybridizing anadromous fishes (*Alosa pseudoharengus*, *Alosa aestivalis*) across the
802 northern portion of their ranges. *Conserv. Genet.* **15**(6): 1281-1298. doi:10.1007/s10592-
803 014-0617-9.
- 804 McBride, M. C., Hasselman, D. J., Willis, T. V., Palkovacs, E. P., and Bentzen, P. 2015.
805 Influence of stocking history on the population genetic structure of anadromous alewife
806 (*Alosa pseudoharengus*) in Maine rivers. *Conserv. Genet.* **16**(5): 1209-1223.
807 doi:10.1007/s10592-015-0733-1
- 808 McPhee, M. V., and Quinn, T. P. 1998. Factors affecting the duration of nest defense and
809 reproductive lifespan of female sockeye salmon, *Oncorhynchus nerka*. *Environ. Biol.*
810 *Fishes* **51**(4): 369-375. doi: 10.1023/A:10074329.

- 811 Milner, J. M., S. D. Albon, A. W. Illius, J. M. Pemberton, and T. H. Clutton-Brock. 1999.
812 Repeated selection of morphometric traits in the Soay sheep on St Kilda. *J. Anim. Ecol.*
813 **68**(3): 472-488. doi: 10.1046/j.1365-2656.1999.00299.x.
- 814 Milner, J. M., Pemberton, J. M., Brotherstone, S., and Albon, S. D., 2000. Estimating variance
815 components and heritabilities in the wild: a case study using the 'animal model'
816 approach. *J. Evol. Biol.* **13**(5): 804-813. doi: 10.1046/j.1420-9101.2000.00222.x.
- 817 Morrissey, M. B., and Wilson, A. J. 2005. The potential costs of accounting for genotypic errors
818 in molecular parentage analyses. *Mol. Ecol.* **14**(13): 4111-4121. doi: 10.1111/j.1365-
819 294X.2005.02708.x.
- 820 Munch, S.B., Mangel, M. and Conover, D.O., 2003. Quantifying natural selection on body size
821 from field data: winter mortality in *Menidia menidia*. *Ecology*, **84**(8): 2168-2177. Doi:
822 10.1890/02-0137.
- 823 Naish, K.A., Seamons, T.R., Dauer, M.B., Hauser, L. and Quinn, T.P., 2013. Relationship
824 between effective population size, inbreeding and adult fitness-related traits in a steelhead
825 (*Oncorhynchus mykiss*) population released in the wild. *Mol. Ecol.* **22**(5):1295-1309. doi:
826 <https://doi.org/10.1111/mec.12185>
- 827 Neves, R. J. 1981. Offshore distribution of alewife, *Alosa pseudoharengus*, and blueback
828 herring, *Alosa aestivalis*, along the Atlantic coast. *Fish. Bull.* **79** (3): 473-485.
829 <http://fishbull.noaa.gov/79-3/neves.pdf> [accessed 10 October 2017].

- 830 Nielsen, R., Mattila, D. K., Clapham, P. J., and Palsbøll, P. J. 2001. Statistical approaches to
831 paternity analysis in natural populations and applications to the North Atlantic Humpback
832 Whale. *Genetics*, **157**(4): 1673-1682. <http://www.genetics.org/content/157/4/1673>
833 [accessed 12 October 2017].
- 834 Nye, J. A., Lynch, P., Alexander, M., Stock, C., and Hare, J. 2012. Results of Preliminary
835 Analyses of the Effect of Climate Change on River Herring. Fisheries and the
836 Environment (FATE) Annual Report 2012.
- 837 Palkovacs, E. P., Dion, K. B., Post, D. M., and Caccone, A. 2008. Independent evolutionary
838 origins of landlocked alewife populations and rapid parallel evolution of phenotypic
839 traits. *Mol. Ecol.* **17**(2): 582-597. doi: 10.1111/j.1365-294X.2007.03593.x.
- 840 Palkovacs, E. P., Hasselman, D. J., Argo, E. E., Gephard, S. R., Limburg, K. E., Post, D. M.,
841 Schultz, T.F., Willis, T. V. 2014. Combining genetic and demographic information to
842 prioritize conservation efforts for anadromous alewife and blueback herring. *Evol. Appl.*
843 **7**(2): 212-226. doi: 10.1111/eva.12111.
- 844 Parrish, R. H., Mallicoate, D. L., and Klingbeil, R. A. 1986. Age dependent fecundity, number
845 of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis*
846 *mordax*. *Fish. Bull.* **84**(3): 503–517.
847 <https://swfsc.noaa.gov/publications/CR/1986/8675.PDF>. [accessed 4 October 2017].
- 848 Pelletier, F., Clutton-Brock, T., Pemberton, J., Tuljapurkar, S., and Coulson, T. 2007. The
849 evolutionary demography of ecological change: linking trait variation and population
850 growth. *Science* **315**(5818): 1571-1574. doi: 10.1126/science.1139024.

- 851 Pemberton, J. M. 2008. Wild pedigrees: the way forward. *Proc. R. Soc. Lond. B Biol. Sci.* .
852 **275**(1635): 613-621. doi: 10.1098/rspb.2007.1531.
- 853 Perrin, N. 1989. Population density and offspring size in the cladoceran *Simocephalus vetulus*
854 (Muller). *Funct. Ecol.* **3**(1): 29-36. <http://www.jstor.org/stable/2389672>. [accessed 4
855 October 2017].
- 856 Perrier, C., Normandeau, É. Dionne, M., Richard, A., and Bernatchez, L. 2014. Alternative
857 reproductive tactics increase effective population size and decrease inbreeding in wild
858 Atlantic salmon. *Evol. Appl.* **7**(9): 1094-1106. oi: 10.1111/eva.12172.
- 859 Peterson, D. A., Hilborn, R., and Hauser, L. 2014. Local adaptation limits lifetime reproductive
860 success of dispersers in a wild salmon metapopulation. *Nat. Commun.* **5**: 3696.
861 doi:10.1038/ncomms4696.
- 862 Planque, B., Fromentin, J. M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., and Kifani,
863 S. 2010. How does fishing alter marine populations and ecosystems sensitivity to
864 climate? *J. Marine Syst.* **79**(3) 403-417. doi: 10.1016/j.jmarsys.2008.12.018.
- 865 Pompanon, F., Bonin, A., Bellemain, E., and Taberlet, P. 2005. Genotyping errors: causes,
866 consequences and solutions. *Nat. Rev. Genet.* **6**(11): 847-859. doi: 10.1038/nrg1707
- 867 Post D.M., Palkovacs E.P., Schielke E.G., and Dodson S.I. 2008. Intraspecific phenotypic
868 variation in a predator affects community structure and cascading trophic interactions.
869 *Ecology.* **89**(7):2019–2032. doi:10.1890/07-1216.

- 870 Quinn, T. P. 2011. The behavior and ecology of Pacific salmon and trout. University of
871 Washington Press, Seattle, WA.
- 872 R Development Core Team. 2014. R: a language and environment for statistical computing.
873 Vienna, Austria : R Foundation for Statistical Computing.
- 874 Regan, C. E., Pilkington, J. G., Pemberton, J. M., and Crawley, M. J. 2016. Sex differences in
875 relationships between habitat use and reproductive performance in Soay sheep (*Ovis*
876 *aries*). Ecol. Lett. **19**(2): 171-179. doi: 10.1111/ele.12550.
- 877 Robinson, Z.L., Coombs, J.A., Hudy, M., Nislow, K.H., Letcher, B.H. and Whiteley, A.R., 2017.
878 Experimental test of genetic rescue in isolated populations of brook trout. Mol. Ecol.
879 **26**(17): 4418-4433. doi: 10.1111/mec.14225
- 880 Rosset, J., Roy, A. H., Gahagan, B. I., Whiteley, A. R., Armstrong, M. P., and Sheppard, J. J.,
881 2017. Temporal patterns of migration and spawning of river herring in coastal
882 Massachusetts. Trans. Am. Fish. Soc. **146**(6): 1101-1114. doi:
883 10.1080/00028487.2017.1341851
- 884 Rosset, J. 2016. The life history characteristics, growth, and mortality of juvenile alewife, *Alosa*
885 *pseudoharengus*, in coastal Massachusetts. M. Sc. thesis, Department of Environmental
886 Conservation, University of Massashusetts, Amherst, MA.
- 887 Rousset, F. 2008. Genepop'007: a complete re-implementation of the genepop software for
888 Windows and Linux. Mol. Ecol. Resour. **8**(1): 103-106. doi: 10.1111/j.1471-
889 8286.2007.01931.x.

- 890 Schoener, T.W. 2011. The newest synthesis: understanding the interplay of evolutionary and
891 ecological dynamics. *Science*, **331**(6016): 426-429. doi: 10.1126/science.1193954.
- 892 Schultz, E. 1993. The effect of birth date on fitness of female dwarf perch, *Micrometrus minimus*
893 (Perciformes: Embiotocidae). *Evolution* **47**(2): 520-539. doi: 10.2307/2410069.
- 894 Secor, D. H. 2000. Spawning in the nick of time? Effect of adult demographics on spawning
895 behaviour and recruitment in Chesapeake Bay striped bass. *ICES J. Mar. Sci.* **57**(2): 403–
896 411. doi: 10.1006/jmsc.1999.0520
- 897 Simonin, P. W., Limburg, K. E., and Machut, L. S. 2007. Bridging the energy gap: anadromous
898 blueback herring feeding in the Hudson and Mohawk Rivers, New York. *Trans. Am.*
899 *Fish. Soc.* **136**(6):1614–1621. doi: 10.1577/T06-161.1.
- 900 Smoker, W. W., Gharrett, A., Stekoll, M. S., and Taylor, S. 2000. Genetic variation of fecundity
901 and egg size in anadromous pink salmon *Oncorhynchus gorbuscha* Walbaum. *Alaska*
902 *Fish. Bull.* **7**: 44-50.
903 <http://www.adfg.alaska.gov/static/home/library/PDFs/afrb/smokerv7.pdf>. [accessed 4
904 October 2017].
- 905 Stearns, S. C. 1992. The evolution of life histories (Vol. 249). Oxford University Press. London,
906 UK.
- 907 Trippel, E. A., Kjesbu, O. S., and Solemdal, P. 1997. Effects of adult age and size structure on
908 reproductive output in marine fishes. *In* Early life history and recruitment in fish

- 909 populations. Edited by R. C. Chambers and E. A. Trippel. Chapman & Hall. New York
910 N.Y. pp. 31-62.
- 911 Turner, S. M., Limburg, K. E., and Palkovacs, E. P. 2015. Can different combinations of natural
912 tags identify river herring natal origin at different levels of stock structure? *Can. J. Fish.*
913 *Aquat. Sci.* **72**(6): 845-854. doi: 10.1139/cjfas-2014-0403.
- 914 Van Oosterhout, C., Hutchinson, W. F., Wills, D. P., and Shipley, P. 2004. MICRO-CHECKER:
915 software for identifying and correcting genotyping errors in microsatellite data. *Mol.*
916 *Ecol. Notes*, **4**(3): 535-538. 10.1111/j.1471-8286.2004.00684.x.
- 917 Venables, W. N. and Ripley, B. D. 2002 *Modern Applied Statistics with S*. 4th ed. New York,
918 NY: Springer.
- 919 Waits, L. P., Luikart, G., and Taberlet, P. 2001. Estimating the probability of identity among
920 genotypes in natural populations: cautions and guidelines. *Mol. Ecol.* **10**(1): 249-256.
921 doi: 10.1046/j.1365-294X.2001.01185.x
- 922 Walsh, H. J., Settle, L. R., and Peters, D. S. 2005. Early life history of blueback herring and
923 alewife in the lower Roanoke River, North Carolina. *Trans. Am. Fish. Soc.* **134**(4): 910-
924 926. doi: 10.1577/T04-060.1.
- 925 Whiteley, A. R., Coombs, J. A., Hudy, M., Robinson, Z., Colton, A. R., Nislow, K. H., and
926 Letcher, B. H. 2013. Fragmentation and patch size shape genetic structure of brook trout
927 populations. *Can. J. Fish. Aquat. Sci.* **70**(5): 678-688. doi: 10.1139/cjfas-2012-0493

- 928 Wilson, A. J., Pemberton, J. M., Pilkington, J. G., Clutton-Brock, T. H., Coltman, D. W., and
929 Kruuk, L. E. B., 2006. Quantitative genetics of growth and cryptic evolution of body size
930 in an island population. *Evol. Ecol.* **21**: 337-356. doi: 10.1007/s10682-006-9106-z.
- 931 Wright, P. J. and Gibb, F. M. 2005. Selection for birth date in North Sea haddock and its relation
932 to maternal age. *J. Anim. Ecol.* **74**(2): 303-312. doi: 10.1111/j.1365-2656.2005.00924.x.
- 933 Wright, P. J. and Trippel, E. A. 2009. Fishery-induced demographic changes in the timing of
934 spawning: consequences for reproductive success. *Fish.* **10**(3): 283-304. doi:
935 10.1111/j.1467-2979.2008.00322.x.
- 936 Yako, L. 1998. Community interactions influencing anadromous herring in freshwater: migration
937 cues and predation. M. Sc. thesis. University of Massachusetts, Amherst, MA.
- 938 Zeileis, A., Kleiber, C., and Jackman, S. 2008. Regression models for count data in R. *J. Stat.*
939 *Softw.* **27**(8): 1-25. doi: 10.18637/jss.v027.i08.
- 940 Zhang, D. 2016. A coefficient of determination for generalized linear models. *Am. Stat.* **71**(4):
941 310-316. doi: 10.1080/00031305.2016.1256839.
- 942 Zhang, D. 2017. rsq: R-squared and Related measures. R Package Version 1.0.1. Purdue
943 University, Indiana.

Table 1. Assigned species identity for transferred adults based on NEWHYBRIDS analysis. Individuals were assigned to categories if they had a posterior probability greater than 70% for one category. Posterior probabilities were generated by NEWHYBRIDS. If individuals did not have a posterior probability greater than 70% for any one category they were listed as Unassigned. Total hybrids indicates a sum of all F1, F2, and Unassigned individuals.

	Number of adults			
	2013	2014	2015	All years
Alewife	419	220	390	1029
Blueback	3	30	6	39
Total hybrids	1	16	13	30
<i>F1</i>	1	10	10	21
<i>F2</i>	0	4	0	4
Unassigned*	0	2	3	5
Total Adults	423	266	409	1098

*Unassigned individuals had a posterior probability less than 70% for all categories.

Table 2. Offspring assignment rates for adult alewife to Pentucket pond in 2013, 2014, and 2015. Number (*n*) is the number of adult alewife (combined and shown for males and females separately) moved to the pond in each year. # and proportion (%) shows the number of offspring (YOY) assigned to these adults for each year.

Year	All adults		Males		Females	
	<i>n</i>	# (%)	<i>n</i>	# (%)	<i>n</i>	# (%)
2013	419	151 (36)	274	85 (31)	145	66 (46)
2014	220	163 (74)	162	110 (68)	58	53 (91)
2015	390	328 (84)	312	254 (81)	78	74 (95)

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Table 3. Number of unique mates per individual (mean, standard deviation (SD), and maximum (Max) for adult alewife 2013, 2014, and 2015.

Year	All adults					Males					Females				
	<i>n</i>	Mean	SD	CV	Max	<i>n</i>	Mean	SD	CV	Max	<i>n</i>	Mean	SD	CV	Max
<i>Total</i>	1029	2	3.12	1.56	32	748	1.4	1.67	1.19	11	281	3.6	4.96	1.38	32
2013	419	1	0.89	0.89	6	274	0.4	0.72	1.80	5	145	0.8	1.12	1.40	6
2014	220	2	1.97	0.99	10	162	1.3	1.28	0.98	5	58	3.6	2.56	0.71	10
2015	390	4	4.22	1.06	32	312	2.3	1.95	0.85	11	78	8.9	6.25	0.70	32

* The minimum number of families is 0 for all adults.

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Table 4. Generalized linear models with negative binomial distributions predicting the number of offspring assigned to an adult alewife for 2013, 2014, and 2015.

2013	Fixed-effects	Estimate	SE	<i>z</i>	<i>P</i> -value	<i>R</i> ² _{<i>V</i>}
	(Intercept)	-0.21093	0.11309	-1.865	0.06216	
	Sex: Male	-0.83802	0.15998	-5.238	<0.001	0.111
	Total Length	0.20362	0.07457	2.73	<0.001	0.042
	Arrival Date	-0.38547	0.07954	-4.847	<0.001	0.090
2014	Fixed-effects	Estimate	SE	<i>z</i>	<i>P</i> -value	
	(Intercept)	1.29244	0.09287	13.917	<0.001	
	Sex: Male	-1.03464	0.11982	-8.635	<0.001	0.246
	Total Length	0.0554	0.0628	0.882	0.377643	0.002
	Arrival Date	-0.26482	0.07157	-3.7	<0.001	0.045
2015	Fixed-effects	Estimate	SE	<i>z</i>	<i>P</i> -value	
	(Intercept)	2.41187	0.08027	30.046	<0.001	
	Sex: Male	-1.52343	0.09739	-15.642	<0.001	0.341
	Total Length	0.161	0.04644	3.467	<0.001	0.119
	Arrival Date	-0.27143	0.0453	-5.992	<0.001	0.146

967 **Table 5.** Generalized linear models with negative binomial distributions predicting the number
 968 of mates assigned to an adult alewife for 2013, 2014, and 2015.

2013	Fixed-effects	Estimate	SE	<i>z</i>	<i>P</i> -value	R^2_V
	(Intercept)	-0.22667	0.11139	-2.035	0.04186	
	Sex: Male	-0.838	0.15764	-5.316	<0.001	0.107
	Total Length	0.01527	0.00516	2.96	<0.05	0.038
	Arrival Date	-0.36277	0.07843	-4.625	<0.001	0.080
2014	Fixed-effects	Estimate	SE	<i>z</i>	<i>P</i> -value	
	(Intercept)	1.275471	0.08787	14.515	<0.001	
	Sex: Male	-1.034926	0.11646	-8.887	<0.001	0.259
	Total Length	0.004839	0.004347	1.113	0.265596	0.003
	Arrival Date	-0.241704	0.064208	-3.764	<0.001	0.053
2015	Fixed-effects	Estimate	SE	<i>z</i>	<i>P</i> -value	
	(Intercept)	2.225956	0.070502	31.573	<0.001	
	Sex: Male	-1.469211	0.087421	-16.806	<0.001	0.470
	Total Length	0.011111	0.003102	3.582	<0.001	0.139
	Arrival Date	-0.229795	0.042197	-5.446	<0.001	0.181

969

970 **Figure Captions**

971 **Figure 1:** Distribution of total length in each study year for all adults, females, and males.

972 **Figure 2:** Number of offspring assigned to all adult, male, and female alewife for 2013, 2014,
973 and 2015. “Count of adults” axis is on a log scale.

974 **Figure 3:** Number of different transfer dates from which mating events occurred per individual
975 for each year. If a fish had mates from all four transfer dates, it was assigned a ‘4’. If it had mates
976 from one transfer date, it was assigned a ‘1’. NA indicates that there was no 4th or 5th transfer
977 date in that year, so mating on those dates would not be possible.

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