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# Response of Estuarine Fish Biomass to Restoration in the Penobscot River, Maine

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**RESPONSE OF ESTUARINE FISH BIOMASS TO RESTORATION**

**IN THE PENOBSCOT RIVER, MAINE**

By

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**ABSTRACT**

Diadromous fish require both freshwater and marine habitat to complete their life cycle. Dams restrict the movement between these habitats and as a result, many populations are historically low across their range. The Penobscot River is the second largest river in Maine and once had large populations of diadromous fish and it has been the focus of mainstem dam removals, dam passage improvements, and stocking with the goal of restoring those populations. Since 2012, NOAA Fisheries has conducted surveys of the Penobscot Estuary using mobile, multi-frequency echosounders (SIMRAD EK60 split-beam 38 and 120 kHz) combined with mid-water trawl surveys to construct a time series of fish distribution to assess this large-scale restoration.

Target strength (TS; dB re $m^2$), the $\log_{10}$ of the backscattering cross section ($\sigma_{bs}$; $m^2$), is an important variable in fisheries acoustics because it is used to compute biological metrics such as biomass and fish density. TS is difficult to characterize due to its stochastic properties from variability in fish physiology, orientation, behavior, depth, and size. When an assemblage consists of multiple species or multiple size classes, assigning TS to the component species or size classes is difficult due to the inability to distinguish individual components in the composite distributions. We addressed these challenges by a unique combination of techniques to characterize TS in the Penobscot River Estuary, Maine.

From trawl data, we determined the estuarine species assemblage was dominated by Clupeids and Osmerids. We used single target detection and echo tracking algorithms to isolate TS values from individual fish. Next, we applied an expectation–maximization algorithm to identify components of the mixed normal TS distribution based on fish total length (TL; cm) data from trawl surveys. Finally, we used ordinary least squares regression to estimate the parameters of $TS = \alpha \log_{10} (TL) + \beta$. Our final parameters, $\alpha = 31.0$ (SE 0.84) and $\beta = -79.5$ (SE 0.90), were similar to published studies from these species. However, our slope and intercept were higher than studies from freshwater and lower than from marine systems. These results suggest that acoustic surveys in estuarine systems with mixed species assemblages and large salinity ranges may need to develop site specific relationships between TS and fish

length. The combination of these methods is an example of a novel technique to derive reproducible TS estimates in mixed pelagic fish assemblages.

We used system-specific parameters to compute biomass from acoustic survey data.  We assessed seasonal estimates of biomass from 2012 to 2017 a period spanning pre-restoration (2012-2014) and post-restoration (2015-2017). Biomass varied with season and year and was generally greater in summer and in post-restoration years. Biomass in pre-restoration years ranged from 9,000 to 114,000 kg per survey and 11 of 45 (23%) surveys had biomass greater than 50,000 kg. Compared to post-restoration years ranged from 23,000 to 316,000 kg per survey and 34 of 43 (76%) surveys had biomass greater than 50,000 kg. Changes in biomass were observed with changes in fish length and density where higher density resulted in higher biomass. This analysis demonstrates the utility of hydroacoustics in monitoring large-system restoration by describing multiple metrics in a complex ecosystem.  The changes observed by increased density and biomass are indications that river restoration is changing the ecology of the estuary.

## DEDICATION

This thesis is dedicated to my loving wife, Melissa whose unwavering support of our life while I was pursuing my education goals. My boys, Brenden and Cameron who won't miss their dad having a "homework" excuse for not playing with them. My parents, Bruce and Cheryl Stevens, for their support in education and instilling a drive to never stop learning. My friends and colleagues that have continually supported my education and career, Randy Spencer for kindling the passion for Atlantic Salmon, the late Ed Hastings for showing me how fun this career can be, Tim Sheehan for exemplifying professionalism and Rory Saunders for always challenging me to be better than I thought I could be.

## ACKNOWLEDGEMENTS

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**CHAPTER ONE**

# 1 ESTIMATING TARGET STRENGTH FOR AN ESTUARINE PELAGIC FISH ASSEMBLAGE

## 1.1 Abstract

Target strength (TS; dB re $m^2$), the $\log_{10}$ of the backscattering cross section ($\sigma_{bs}$; $m^2$), is an important variable in fisheries acoustics because it is used to compute biological metrics such as biomass and fish density. When converting acoustic energy (e.g., volume backscatter) to fish density, representative TSs of the ensonified assemblages are required for valid computations. TS is difficult to characterize due to its stochastic properties from variability in fish physiology, orientation, behavior, depth, and size. When an assemblage consists of multiple species or multiple size classes, assigning TS to the component species or size classes is difficult due to the inability to distinguish individual components in the composite distributions. We addressed these challenges by a unique combination of techniques to characterize TS in the Penobscot River Estuary, Maine, USA which is undergoing extensive dam removal in an effort to increase diadromous fish populations. From trawl data, we determined the species assemblage was dominated by Clupeids and Osmerids. We used single target detection and echo tracking algorithms to isolate TS values from individual fish. Next, we applied an expectation–maximization algorithm to identify components of the mixed normal TS distribution based on fish total length (TL; cm) data from trawl surveys. Finally, we used ordinary least squares regression to estimate the parameters of $TS = \alpha \log_{10}(TL) + \beta$. Our final parameters, $\alpha$ = 31.0 (SE 0.84) and $\beta$ = -79.5 (SE 0.90), were similar to published studies from these species. However, our slope and intercept were higher than studies from freshwater and lower than from marine systems. These results suggest that acoustic surveys in estuarine systems with mixed species assemblages and large salinity ranges may need to develop site specific relationships between TS and fish length. The combination of these methods is an example of a novel technique to derive reproducible TS estimates in mixed pelagic fish assemblages.

## 1.2 Introduction

Active acoustic methods are widely used to monitor density and distribution for a number of freshwater and marine species (Simmonds and MacLennan 2005). Advantages of acoustic methods over traditional survey methods like trawling include the ability to continuously survey large areas, provide vertical detail of nearly the full water column, and the ability to establish repeatable data collection and analysis. These techniques are now used regularly in applications from stock assessments to ecological investigations (Fernandes et al. 2002). Scientific echosounders capable of measuring backscattered sound with precision and repeatability are now readily available. While the field has progressed with advances in equipment and computational processing in the quality and quantity of data as reviewed by Chu (2011), scientists are still challenged to relate observed acoustic properties to the specific biota of interest. Interpretation is accomplished by accepting assumptions such as size distribution and species composition and their relationship to properties of scattering of acoustic pulses.

Acoustic properties of fish have been described for a number of species (review in: Simmonds and MacLennon 2005). Fish morphology strongly affects acoustic backscatter. Acoustically, fish can be generally categorized as species with and without gas-filled swim bladders. Those with gas-filled swim bladders are further separated as having limited swim bladder volume regulation with depth (physostomes) and species that physiologically regulate volume with depth (physoclists). Those without a gas-filled swim bladder may have no functioning swim bladder or a lipid-filled swim bladder (Pelster 1998). Scattering models have been developed for species of various morphologies as well as empirical estimates from laboratory studies (Clay and Heist 1984; Clay 1991; Horne 2000). However, much of the ability to accurately analyze fisheries acoustics results from the careful application of theoretical scattering models or controlled studies of acoustic properties and measurements from representative fish species (e.g. Love 1971; Foote 1987). As a result, researchers are often left to apply generalized parameters (e.g. target strength to fish length regression parameters) and accept unknown uncertainties or applicability. Few researchers have explicitly quantified the degree of uncertainty as Boswell et al. (2008) described for a mid-Atlantic estuary comprised mainly of bay anchovy *Anchoa mitchelli* and Gulf menhaden *Brevoortia patronus*. He found biomass estimates were significantly affected by the choice of target strength to fish length equation as well as the variability of mean volume backscattering strength ($S_v$; dB re 1 $m^{-1}$); MacLennan et al. 2002).

Fisheries acoustics surveys typically rely on monitoring fish aggregations driven by biological events like spawning, feeding, or migrating. The size and acoustic energy of these aggregations can be measured with standardized methods such as $S_v$ to serve as proxies for fish abundance and density (Simmonds and MacLennan 2005). Further translation of these acoustic data to numeric density, abundance, and biomass requires knowledge of the target strength (TS, dB re 1 $m^2$) ($\log_{10}$ conversion of backscattering cross section $\sigma_{bs}$, $m^2$) of the ensonified fish. In most cases, fish capture techniques (e.g. trawls) or other systemic knowledge provides the size distributions and species assemblages necessary to derive fisheries relevant abundance metrics. Measurements of TS are confounded by the variable (bias and stochastic) nature of the acoustic backscatter related to changes in fish behavior and composition (Love 1971; Røttingen 1976). Split-beam echosounders improve TS measurements by correcting for fish's position relative to the beam axis (Soule et al. 1996, 1997). With these data, TS values are related to fish size but vary with tilt angle (relative to the beam), depth, size, and species. TS may also be biased by the density of fish as suggested by Sawada (1993) due to echoes of multiple targets being considered a single target. Measurements of TS have been improved by the application of detection algorithms that group single-target detections into presumed single fish 'tracks' providing added information on tilt angle, direction of movement, and TS deviation (Kieser and Mulligan 1984; Blackman 1986; Dawson et al 2000; Xie 2000). Regardless of the potential biases and challenges, TS can be predictable for individual species and sizes as shown through a number of experiments using empirical and modelling (Foote 1987; Warner et al. 2002; Rudstam et al. 2003).

Characterizing TS measurements *in situ* requires several assumptions be met for defensible comparisons. The most basic assumption is that there is fidelity between the acoustic and capture methods in size and species measured. If this assumption is met, the acoustic properties of the organisms and variability in size and species result in correlated TS measurements whose probability distribution functions have been previously described as Rayleigh (Huang and Clay 1980), Rician (Clay and Heist 1984), or Gaussian (Warner et al. 2002). The mode of TS in these distributions can be compared to lengths observed from fished samples *in situ* and compared statistically by least squares methods (e.g. MacLennan and Menz 1996). However, in systems with mixed species and/or size classes, the expected TS frequency distribution may be a mixed distribution which makes the identification of distinct modes more difficult. One method of describing mixed distributions is the use of maximum-likelihood estimators using expectation–maximization (EM) algorithms (Meng and Rubin 1993). The EM process allows for iterative estimation of parameters and error. These functions have been developed to provide guidance (e.g. number of cases in the mixture, mean and deviation of mixture components) to the fitting procedure when data are available (Benaglia et al. 2009).

Although estuaries are important aquatic habitats for many commercially and ecologically valuable fish, characterizing how many fish these systems are supporting using fisheries monitoring and assessments are time consuming and expensive. Acoustic surveys of estuaries are logistically challenging due to their generally shallow depths and dynamic physical environments but some assessments have been successful (Guillard et al. 2004, 2012; Boswell et al. 2007, 2010; O'Malley et al. 2017). In some cases, estuaries are actually advantageous locations for acoustic surveys due to the limited number of species with life histories involving estuaries (e.g. diadromous fish) or that tolerate the dynamic habitat. This allows for the assumptions of the assemblage being characterized by guild (Able 2005; Elliott et al. 2007; Potter et al. 2015) which provides the ability to describe ecological processes.

National Oceanic and Atmospheric Administration (NOAA) Fisheries has conducted mobile acoustic and trawl surveys of the Penobscot River Estuary, Maine from 2012 to 2017. The Penobscot River has been the site of large-scale river restoration aimed at increasing diadromous species biomass by the removal of mainstem dams (Day 2006). These biweekly and season-long surveys have provided novel insights into the temporal and spatial distribution patterns in the system prior to restoration (O'Malley et al. 2017). They suggested this system appeared to have a mixed but stable assemblage with multi-modal TS distributions, suggesting predictable size and species aggregations. As such, we expect that computing standard metrics, including fish biomass, are possible if precise TS characterization is coupled to these data. Acoustic biomass is a metric that provides a measure of abundance and size inference of fish for fisheries management (Simmonds and MacLennan 2005). Given the restoration goal of increased fish populations, a consistent measure of the magnitude and timing of fish biomass over time would allow assessment and monitoring of the system's response to restoration. A major challenge to unlocking the power of acoustics to predict biomass is to decide which TS-fish length equation is appropriate for this system. For example, Foote (1987) and Warner et al. (2002) showed that the variation in regression parameters can differ by an order of magnitude (~9 dB) for the same sized fish of similar species (Clupeid). Warner et al. (2002) acknowledged this was possibly due to differences in swim bladder volume in different habitats (marine vs. freshwater). Given this, our goals were to utilize the Penobscot survey dataset to: 1) utilize echo tracking algorithms to generate *in situ* TS distributions, 2) utilize EM algorithm to autonomously detect multimodal distribution parameters, and 3) correlate these TS distribution parameters with fish length (TL) distributions to derive empirical relationship and error estimate for this system. These results will provide necessary parameters to allow for interpretation of acoustic survey data from this and systems with similar composition of diadromous species.

## 1.3 Methods

### 1.3.1 Study Area.

The Penobscot River is the second largest in the Northeast US covering an area of 22,000 $km^2$. The Penobscot River discharges 400 $m^3s^{-1}$ on average into an estuary that experiences 3-4 m tides creating a dynamic physical environment with complex patterns of mixing and circulation (Geyer et al. 2018). NOAA Fisheries acoustic and trawl surveys were conducted where the channel depth was generally greater than 6 m and width was less than 2 km, covering an area of approximately 16 $km^2$ (O'Malley et al 2017) (Figure 1.1). A zigzag pattern was used to acoustically survey the estuary where the acoustic "transect" was approximately 50 km long and covered the area of the estuary from near full salinity at Stockton Springs, Maine to tidal freshwater in Bangor, Maine (Figure 1.1). Trawl stations were distributed systematically along the acoustic path, but did not overlap in the northern third of the study area which O'Malley et al. (2017) characterized as generally having consistently low fish density (measured as $s_A$, $m^2$ $m^{-2}$; MacLennan et al. 2002).

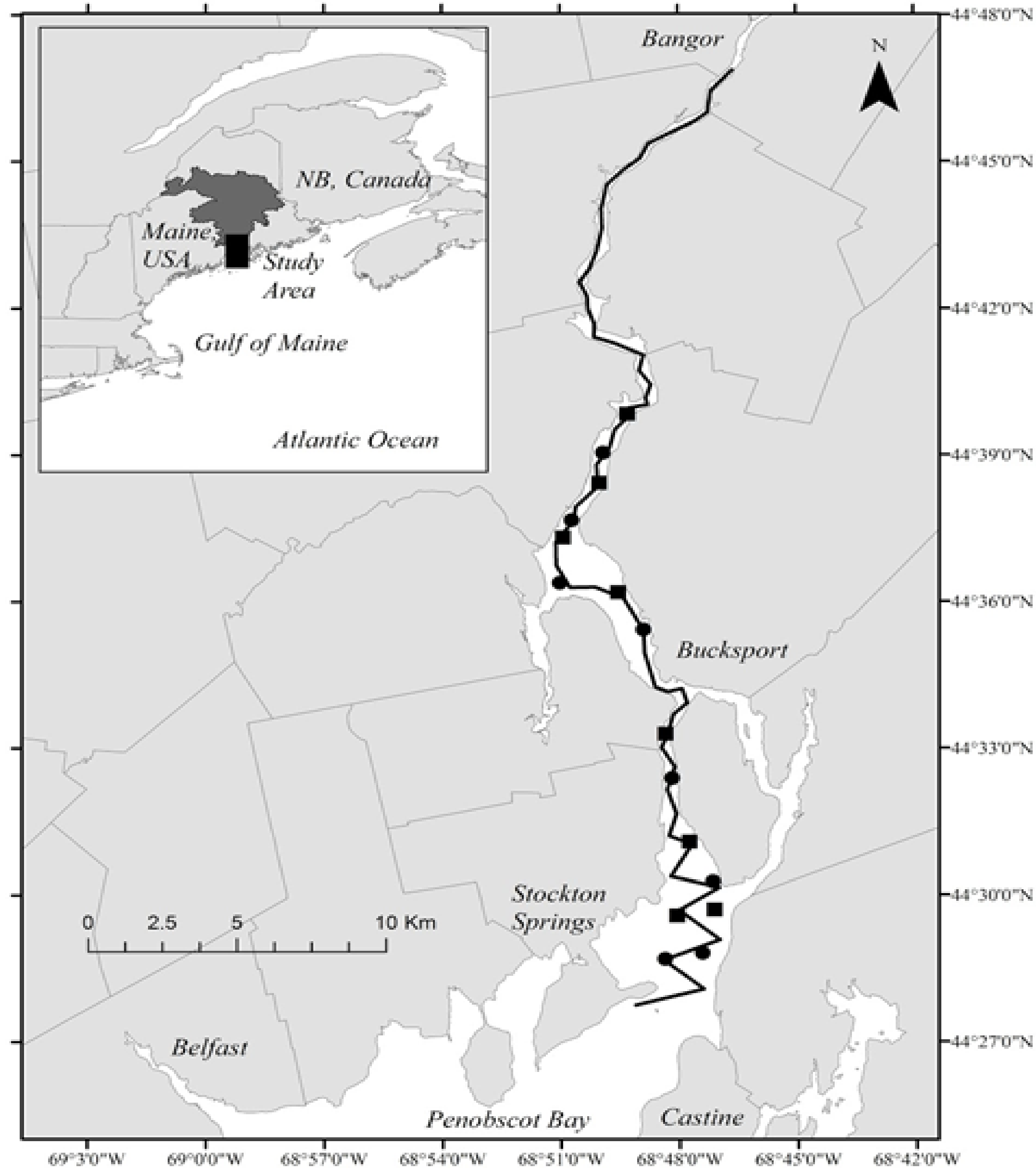


Figure 1.1 Study Area. Penobscot River Estuary study area in regional context (inset) depicting acoustic survey track (line) and trawl stations (circles represent start, squares endpoints).

### 1.3.2 Trawl Survey Data

We analyzed catch and size data collected from mid-water trawl hauls described in Lipsky et al. (2019). Briefly, the trawl sampled 8 fixed locations for 10 minutes at speeds from 3.7-7.4 km $h^{-1}$ using an 11-m wide by 6-m high net with 19 mm diamond mesh. The nest was towed during the flood tide and surveys were conducted the same (2012 and 2013) or subsequent (2014-2017) days as the acoustic survey except for 5/24/2012 and 9/26/2012 when closest acoustic surveys occured 6/1/2012 and 11/05/2012 respectively.  Catch was enumerated by species and a target subsample of 30 individuals was measured for total length (TL, cm) for each tow. Catch per unit effort (CPUE) was standardized as number of fish captured per kilometer traveled recorded by onboard GPS during the tow. We computed the proportion of CPUE by species to determine the most dominant species per sample day. We developed length-frequency distributions for each trawl sample day by pooling the lengths for each species in all tows for the day.

### 1.3.3 Acoustic Survey Data

We analyzed split-beam acoustic data collected from 2012 to 2017 following the survey design described in O'Malley et al. (2017). Briefly, the survey used SIMRAD EK60 120 and 38-kHz split-beam downward-looking transducers located 0.5 m below the water surface via a pole mounted to skiff traveling at approximately 10 km $hr^{-1}$. The acoustic systems were calibrated monthly using a 38.1-mm tungsten carbide with 6% cobalt binder sphere as a standard target. Calibration was conducted within the SIMRAD ER60 Lobe software and echosounder parameters, $s_A$ correction and gain, were updated when the root-mean-square (RMS) error was less than 0.4 following manufacturer recommendations (https://www.simrad.com/ek60#documentation). Surveys were conducted at intervals of 7 to 28 days during ice free months, typically April through October in 2012 to 2017 (Table 1.1). Data were collected along a 50 km continuous transect which zig-zagged across the channel to fixed waypoints. The direction of travel corresponded to the tidal flow and surveys were conducted during daylight hours. Data processing was performed in Echoview version 8.0 (Echoview Software Pty Ltd. 2018). We used

Echoview “method 2” for single target detections (STDs) with settings given in Table 1.2. We utilized the “Fish Track” module of Echoview to determine STDs that were likely from single fish from the 38 kHz transducer (Bertsekas 1990; Echoview Software Pty Ltd. 2018). Track detection properties were set to 4D algorithm with settings given in Table 1.3. The tracking algorithm produced a number of metrics related to the angular position of the grouped pings  however, we extracted mean TS for each fish track with multiple STDs for computations and are hereafter referred to as the target TS.

Table 1.1 Summary of survey timing. Frequency by month, week, and year of 55 paired acoustic and trawl surveys used for this target strength (TS) and fish length (TL) analysis. Surveys were more frequent during May to capture the period of active migration for diadromous fish in the Penobscot River.

| Month | Week | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 |
|---|---|---|---|---|---|---|---|
| April | 17 | 1 | 1 | 0 | 0 | 1 | 1 |
| May | 18-22 | 3 | 5 | 2 | 5 | 4 | 2 |
| June | 23-26 | 1 | 1 | 1 | 1 | 1 | 1 |
| July | 27-30 | 1 | 1 | 1 | 1 | 1 | 1 |
| August | 31-35 | 1 | 1 | 1 | 1 | 1 | 1 |
| September | 36-39 | 1 | 1 | 1 | 1 | 1 | 1 |
| October | 40-43 | 0 | 1 | 1 | 1 | 1 | 1 |
| November | 44-48 | 0 | 1 | 0 | 0 | 0 | 0 |

Table 1.2 Single target detection properties and settings used for acoustic data processing.

| | |
|---|---|
| Beam compensation model | SIMRAD LOBE |
| Compensated TS threshold | -65 dB |
| Maximum compensation | 12 dB |
| Pulse length determination level | 6.0 dB |
| Minimum normalized pulse length | 0.25 |
| Maximum normalized pulse length | 0.50 |
| Exclusion level maximum standard deviation beam angles, major-axis | 1.0 |
| Exclusion level maximum standard deviation beam angles, minor-axis | 1.0 |

Table 1.3 Fish track detection properties and settings used for acoustic data processing.

| **Fish track detection properties** | **Major axis** | **Minor axis** | **Range** |
|---|---|---|---|
| Alpha | 1.0 | 1.0 | 0.25 |
| Beta | 1.0 | 1.0 | 0.25 |
| **Target gates** | | | |
| exclusion distance | 1.0 m | 1.0 m | 0.25 m |
| missed ping expansion | 0% | 0% | 0% |
| Weights | 30 | 30 | 40 |
| Ping gap | 0.0 | | |
| TS | 5.0 | | |
| **Track acceptance properties** | | | |
| minimum number of single targets | 1.0 | | |
| maximum gap between single targets | 0.0 | | |
| minimum number of pings | 1.0 | | |

### 1.3.4 Data Analysis

We analyzed trawl CPUE to determine the most abundant species in trawl catches under the assumption that the catch represented the species and size classes available to the acoustic survey. We determined International Standard Organization (ISO) standard week of year for each sampling date for data analysis and presentation. We visually determined two distinct size classes for each of the dominant species. For Alewife, *Alosa pseudoharengus*, and Blueback Herring, *Alosa aestivalis*, we determined the division at 15 cm, and for Rainbow Smelt [hereafter Smelt], *Osmerus mordax*, and Atlantic Herring, *Clupea harengus*, at 10 cm. These delineations are generally consistent with descriptions of juveniles and adults of each species (Scott and Crossman 1973; Collette and Klein-MacPhee 2002). We calculated mean and standard deviation (SD) for each size class for each of the dominant species for each survey day. The mean and standard deviation for each group was used for subsequent distribution fitting analysis.

To perform a regression analysis of the mean TS and TL values, we assumed the ordered values were associated such that the smallest TS mean was related to the smallest TL mean. This assumption required a threshold be applied to the TS data so that the values approximately aligned with the observations from the trawl. We used a TS threshold following Warner et al. (2002) who applied a lower TS threshold of -61 dB for 1.5–2.0 cm freshwater Alewives. However, given that Foote's (1987) regression predicted an 8 dB difference (higher) TS for 2 cm fish, we determined it was appropriate to also use several incrementally higher thresholds to determine which would provide the best fit for this ecosystem. We estimated the equivalent TS for the smallest fish captured in the trawl (3 cm) using Foote (1987) and Warner et al (2002) regression parameters, -53.7 dB and -62.4 dB respectively. We also set the threshold to an intermediate value of -58.3 dB using Rudstam (2003) for comparison. For the upper threshold, we used the equivalent TS (-33dB) for the largest fish captured in the trawl (32 cm), again using Foote's (1987) regression parameters. This decision was supported our raw TS histograms of numerous targets above -41 dB, the equivalent TS for 32 cm using Warner et al.'s (2002) parameters. We applied the various thresholds to the TS data, ran the EM functions to estimate mixed normal parameters for each survey distribution, and used those mean parameters in the linear regression model in equation 1.1 from Simmons and McLennan (2005).

Equation 1.1 $$\boldsymbol{TS = \alpha \log_{10}(TL) + \beta}$$

Where, TS is mean target strength (dB), TL is mean total length (cm) and α, β are the slope and intercept parameters of the regression line.

We assumed the TL and TS distributions on a given survey for a particular species and size class would follow a normal distribution and that the composite length-frequency distribution would be a mix of normal distributions, similar to methods applied by Warner et al. (2002). They had a similar fish community comprised of multiple size classes of Alewife. We utilized the R (R Core Team 2018) package *mixtools* function *normalmixEM* (Benaglia et al. 2009) to determine the parameters of mixed normal distributions for the frequency histograms for each survey for both TL and TS. This function applies an EM algorithm to iteratively fit mixed normal and estimate mean ($\mu$), standard deviation ($\sigma$), and mixed proportion ($\lambda$) of each case ($k$) using maximum-likelihood maximization method. For TL distributions, we restricted the EM function input parameters, $k$, $\mu$ and $\sigma$, using the mean and SD calculated for each species and size class from the trawl data for each survey. For TS distributions, we restricted the EM function using $k$ determined from the TL analysis but allowed the algorithm to estimate: $\mu$, $\lambda$, and $\sigma$ for each $k$ in each acoustic survey distribution. For both TL and TS fitting procedures, we set the maximum number of iterations to 10,000 but in practice the algorithm rarely used more than 1,000 iterations to meet the convergence criteria of the observed data (i.e., log-likelihood increase by less than epsilon of 0.001).

We used the function *lm* from the R (R Core Team 2018) package *base* to perform linear regression modeling of the relationship of TS to TL assuming that the ordered $\mu$ values of $k$ cases from the EM fitting were related with equation 1.1. We evaluated regression diagnostic plots of residuals, leverage (h), and Cook's distance (D) to determine the homoscedasticity of variance as well as the presence and influence of outliers using a limit of $D > 4/n$ (Neter et al. 1996).

The mid-water trawl hauls sampled approximately the top 6 meters of the water column. We therefore evaluated the assumption that the trawl catch size distribution would represent the acoustic size distribution throughout the water column. We utilized the R function *ks.test* in the R package *stats* to use a two sample Kolmogorov-Smirnov (KS) Test of TS distributions grouped above (sample 1) and below (sample 2) 6 m where a significant p value ($\alpha < 0.05$) would reject the null hypothesis that the groups were from the same empirical cumulative distribution function (ECDF). We determined the bias towards smaller or larger targets in the two samples by comparing the mean of the ECDF for the top and bottom samples.

All statistical and graphical analyses were conducted in RStudio version 1.0.15, R version R version 3.5.1 (2018-07-02) -- "Feather Spray" Platform: x86_64-w64-mingw32/x64 (64-bit) (R Core Team 2018).

## 1.4 Results

### 1.4.1 Fish Length Distributions

We utilized length-frequency distributions for each trawl survey day conducted between 2012 and 2017 (n=55). The trawl catch was dominated by four species with Alewife, Blueback Herring, Smelt, and Atlantic Herring comprising more than 95% of the catch per sampling day throughout the time series (Figure 1.2). Smelt were the least abundant of these species but were very abundant in some surveys (>50% catch) so were included for subsequent analysis of length structure (Figure 1.2).

Trawl TL distributions were comprised of multiple size classes of Alewife, Blueback Herring, Smelt, and Atlantic Herring. Size classes varied inter- and intra-annually allowing for multiple TL to TS comparisons. In surveys during weeks 17 - 26 (spring), the smallest group were Atlantic Herring ( ~ 5 cm) followed by a from near 10 cm juvenile Alewife and/or Blueback Herring, and then multiple groups from 15 cm up to 25 cm from Smelt and adult Blueback and Alewife respectively (Figure 1.3). In surveys during weeks 27-35 (summer) of most years, Atlantic Herring were larger than in spring, with mean ~10 cm and were less distinct from juvenile Alewife and Blueback Herring and the largest groups (20 – 25 cm) from adult Alewife and Blueback Herring. In surveys during weeks 36-48 (fall) of most years, the smallest fish were Smelt with little difference in mean size between juvenile Atlantic, Alewife or Blueback Herring (Figure 1.3; Table S1.5).

The EM fitting procedure efficiently estimated: $\mu$, $\sigma$, and $\lambda$ parameters for each TS and TL distribution and met convergence criteria in all cases (Figure 1.4; Table S1.6, S1.7). TS distributions in most surveys were multinomial with a strong right-hand skew (Figure S1.7). Multiple modes were not readily apparent by visual inspection, rather the distribution was generally broad from -54 dB to -33 dB. The EM fitting for TS were less efficient than the fitting procedure for TL evident by overall higher log-likelihood values and more iterations to reach convergence (Table S1.6, S1.7). The EM algorithm discriminated all TS cases although some of the cases had high standard deviations and final solution log likelihoods were large (Figure 1.4). For example, in week 19 of 2015, the log likelihood was high (-100,699) and 7 cases were estimated but the function appeared to poorly discriminate modes in the distribution.  In contrast, week 22 of 2015, the log likelihood was lower (-7,701) and 8 cases were estimated with most normal components visually aligning with modes in the distribution.  The TL frequency distributions of most surveys were clearly well modeled within modes of composite distributions such as in week 22, 2015 although exceptions were noted as in week 19 when the lowest mode, near 5 cm was not characterized with the calculated mean of any juvenile group (Figure 1.4).

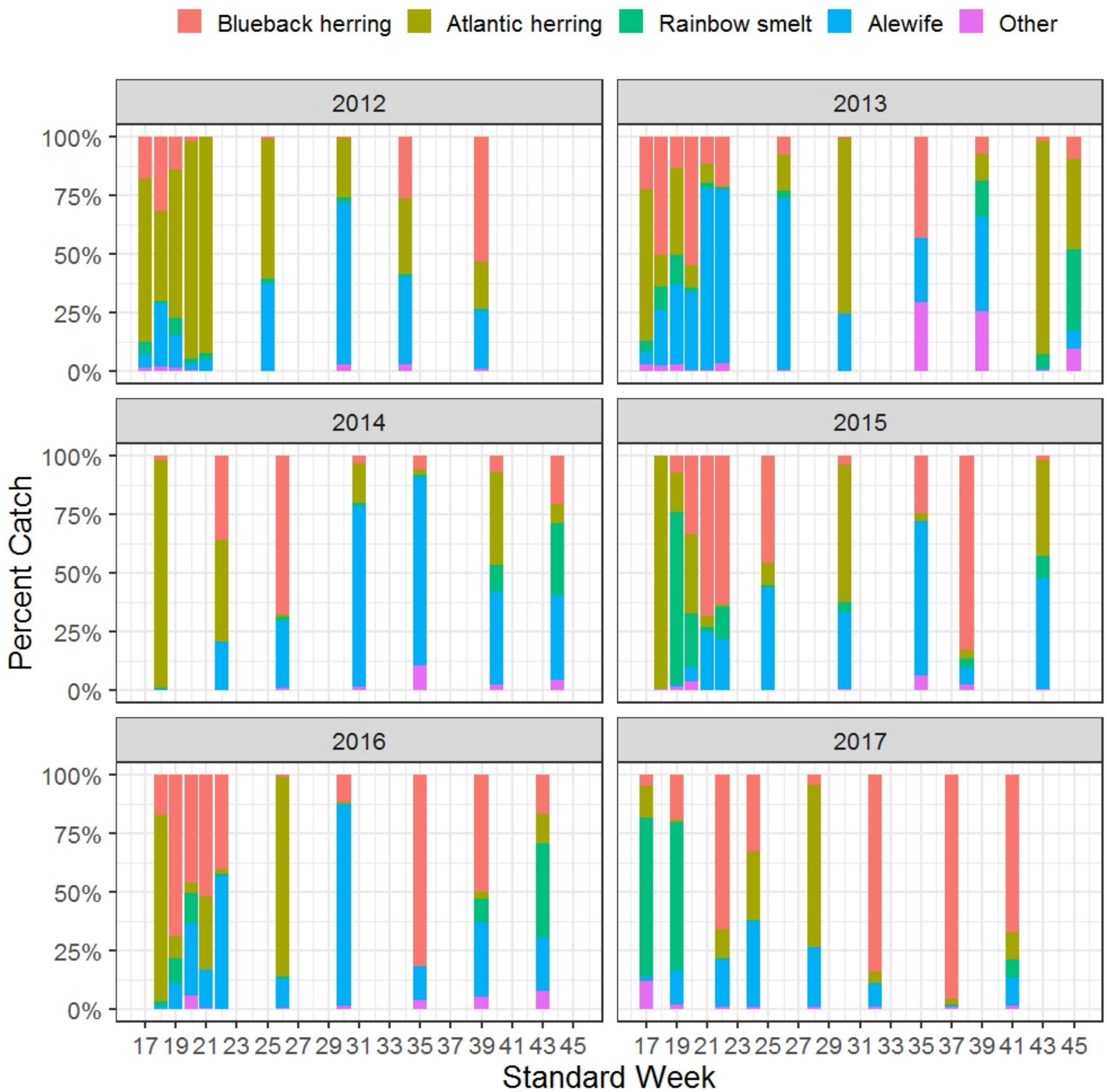


Figure 1.2 Summary of trawl catch. Percent of catch by ISO standard week of year for most common species and remaining 'others' during Penobscot Estuary trawl surveys 2012 to 2017. Together, the four species; Alewife, Blueback Herring, Rainbow Smelt, and Atlantic Herring; represented more than 95% of the catch for the study period.

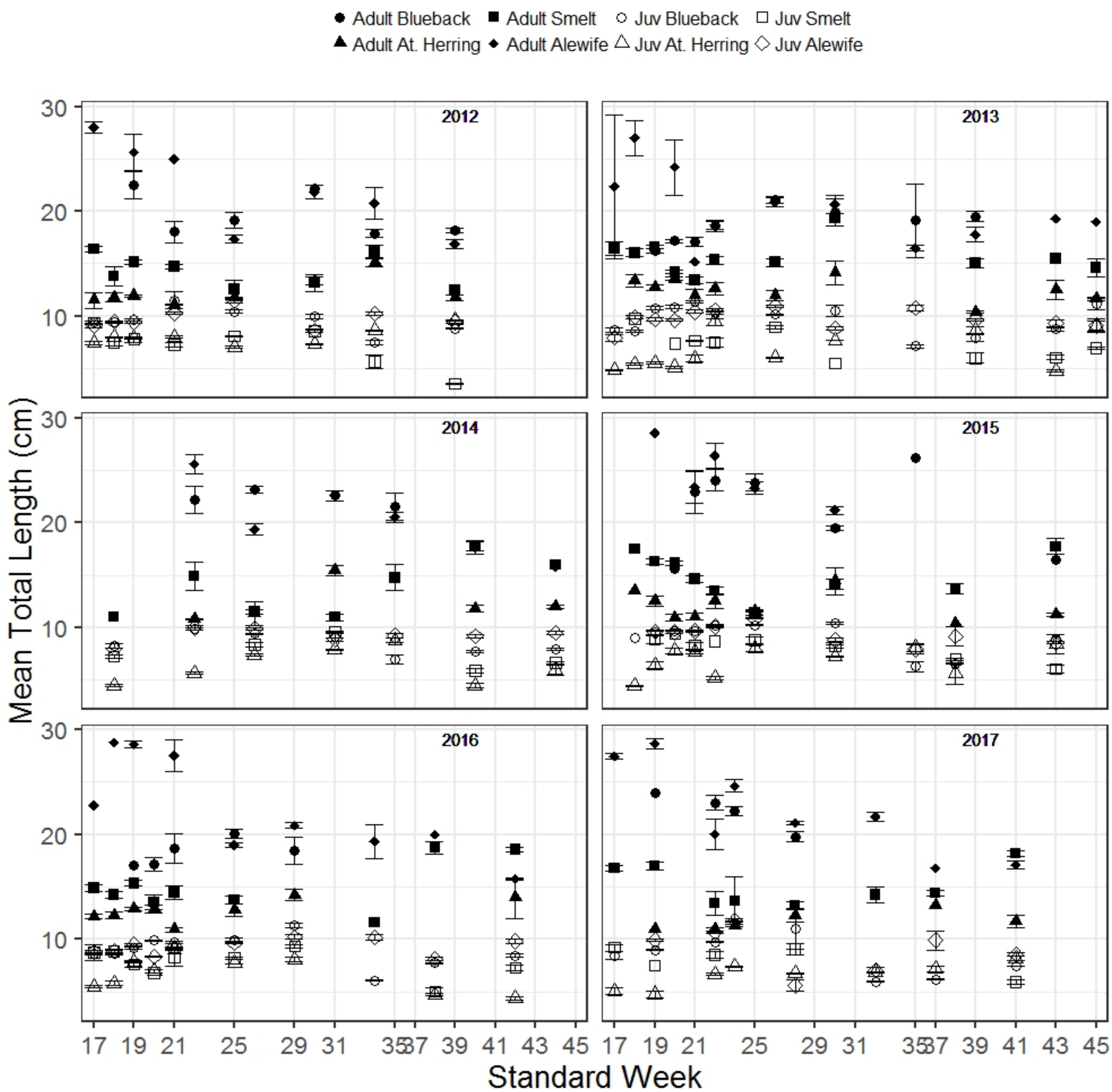


Figure 1.3 Summary of fish length. Mean total length (symbols; cm) +/- standard error (SE; bars) for dominant species; Alewife (diamonds), Blueback Herring (circles), Rainbow Smelt (squares), and Atlantic Herring (triangles); juveniles (open symbols) and adults (solid symbols) for trawl surveys 2012-2017. These parameters (mean, SD, k cases) were used in the EM algorithm function to fit mixed TL and TS distributions.

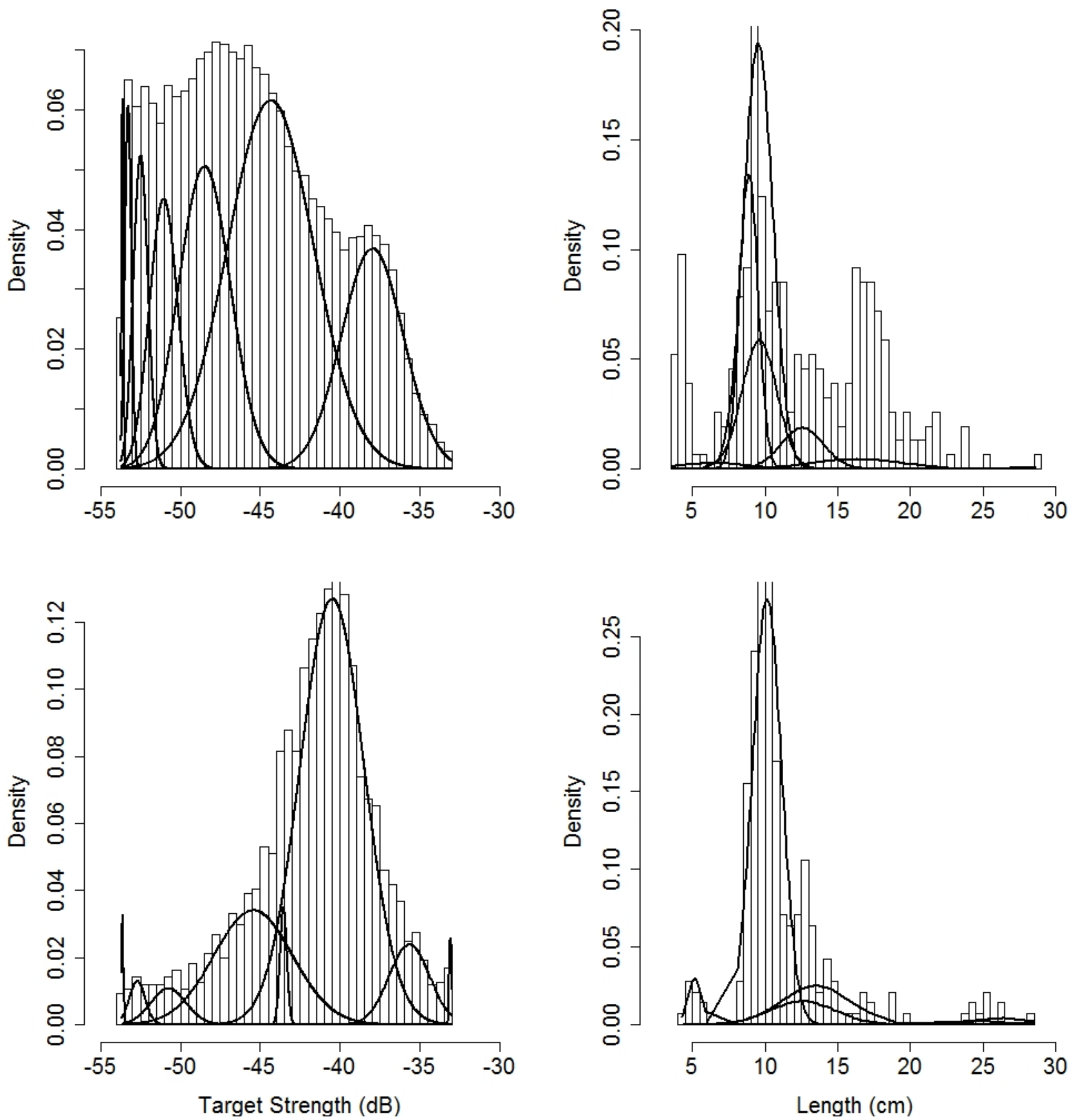


Figure 1.4 Distribution fitting. Frequency histograms (bars) and results of multinomial distribution fitting (lines) of target strength (TS, dB) and total length (TL, cm) frequencies for two surveys, week 19 (top) and week 22 (bottom) of 2015. Top surveys have higher log-likelihood values compared to lower values for bottom, both depict typical patterns for determining modes to relate to acoustic target strength frequency distributions in this analysis.

### 1.4.2 Target Strength to Length Relationship

We used the mean TS and mean TL values (n = 356) of each fitted normal distribution as determined by the EM algorithm to conduct a linear regression analysis and determine the empirical relation of TS to TL. We repeated this process using three lower thresholds (-62.4,-58.3,-53.7 dB) corresponding to the TS for our smallest captured fish (3 cm) from three other studies, Warner et al. (2002), Rudstam (2003), and Foote (1987). We used the model TS = $\alpha \log_{10}$ (TL) + $\beta$ which is the typical model equation used to describe the relationship between TS and TL (Simmonds and MacLennan 2005).The thresholds produced progressively smaller slope, smaller intercept, and better fit ($R^2$) with higher thresholds (Table 1.4; Figure 1.5).

Our best model fit (F-statistic 1356 (1, 382 DF), p-value: < .001) was with the threshold of -53.7 dB which resulted in coefficients of $\alpha$ = 31.0 (SE 0.84) and $\beta$ = -79.5 (SE 0.90) and adjusted R-squared = 0.78 (Table 1.4; Figure 1.5). Our smallest slope parameter was 11, 11.1, and 10.5 dB higher than Foote (1987), Rudstam (2003), and Warner et al. (2002) respectively. Also, our smallest estimated intercept was 7.6, 11.7, 15.2 units greater than aforementioned studies (Table 1.4). The regression diagnostic plots suggest that variance of the residuals was not heteroscedastic, rather the residual variation was greater for small and large TS and TL. Cook's distance values ranged from 0.09 to 0.00 and 23 points were considered for influence to the model prediction (Figure 1.5). Removing the 23 points had little effect on model fit and parameters, F-statistic 1680 (1, 382 DF), p-value: < .001, $\alpha$ = 33.5 (SE 0.82), $\beta$ = -82.3 (SE 0.87) and adjusted R-squared = 0.82 (Figure 1.5).

A common feature in the regression plots were the group of points at lowest TS values with varying TL associated with them.  This feature was present regardless of the dB threshold used prior to the EM algorithm processing. Rather the EM algorithm fitted multiple cases with little difference in mean TS and these were paired with varying mean TL cases (Figure 1.4).

Table 1.4 Regression parameters. Resulting parameters of least-squares regression, intercept (α) and slope (β), error (standard error, SE) and fit (R2) for current and comparative TS-TL studies using the equation: TS = α log10 (TL)– β form.

| Study | Organism (s) | TS threshold (dB) | β (SE) | α (SE) | $R^2$ |
|---|---|---|---|---|---|
| Current | Mixed Clupeid and Smelt | <= -33 & >= -62.4 | 94.0 (1.4) | 37.6 (1.3) | 0.69 |
| | | <= -33 & >= -58.1 | 86.8 (1.1) | 34.1 (1.1) | 0.74 |
| | | <= -33 & >= -53.7 | 79.5 (0.90) | 31.0 (0.84) | 0.78 |
| Foote 1987 | Clupeid | NA | 71.9 | 20 | NA |
| Rudstam 2003 | Smelt | <= -49 & >= -64 | 67.8 | 19.9 | 0.90 |
| Warner et al. 2002 | Alewife | <= -37 & >= -61 | 64.3 | 20.5 | 0.97 |

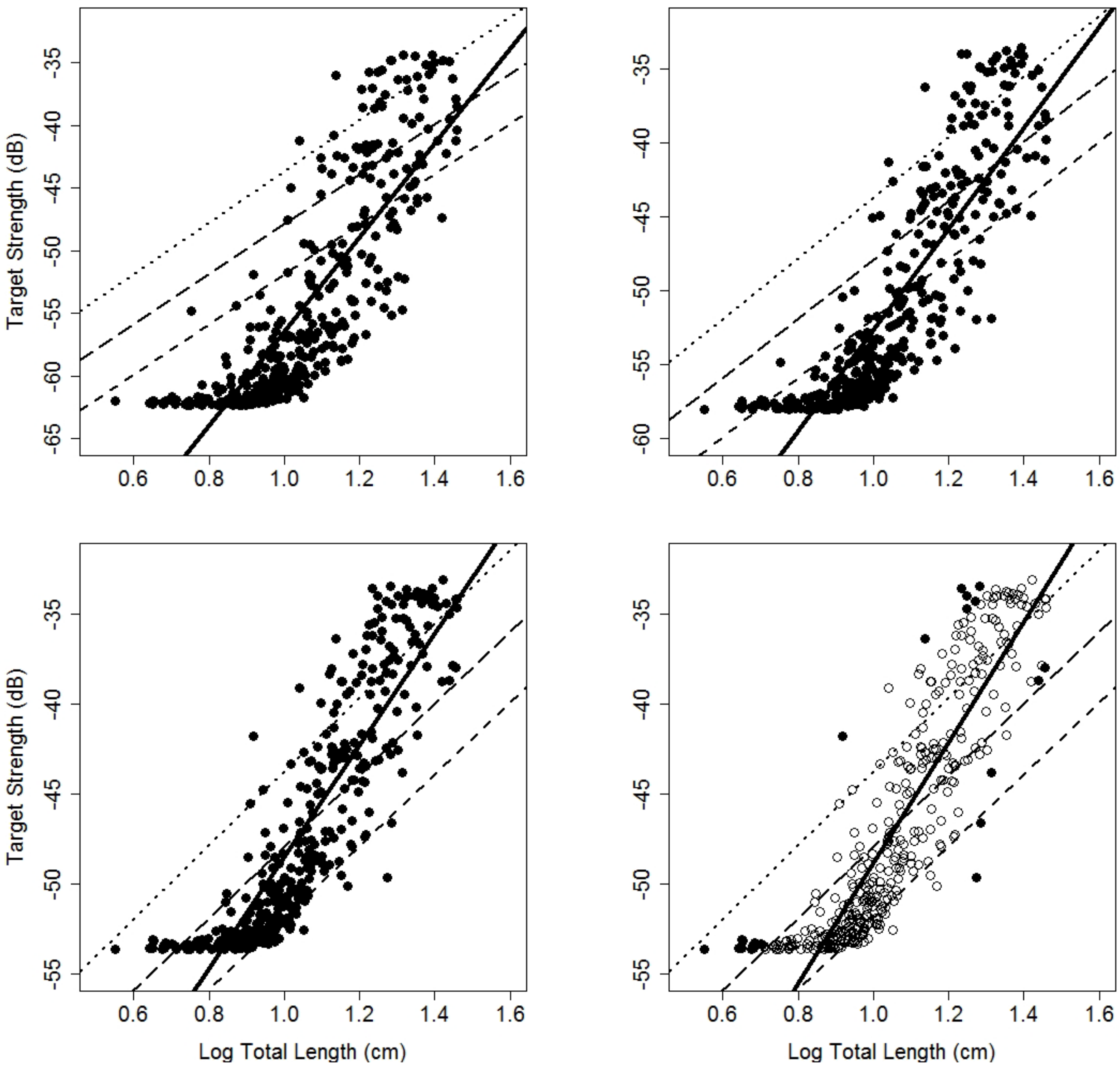


Figure 1.5 Target strength to fish length regressions. Mean fish length ($log_{10}$, cm) versus mean acoustic target strength (dB) estimated from expectation–maximization (EM) algorithm for mixed normal distributions of trawl total length and 38kHz Target Strength data with lower thresholds of -61 dB (top left), -58 dB (top right), -54 dB (bottom left), and with influential points (solid) removed (lower right); collected in 55 surveys 2012 to 2017. Resulting linear regression line with fitted intercept (bold). Regression lines from Foote 1987 (dotted), Rudstam (long dash), and Warner et al. 2002 (short dash) included for comparison. Note y-axis scale varies according to threshold used for each regression.

### 1.4.3 Target Strength to Depth Relationship

The KS tests of the ECDF from above and below 6 m resulted in 49 of 55 (89%) surveys rejecting the null hypothesis ($\alpha < 0.05$) that the upper and lower water column had the same ECFD of TS (Figure 1.6). The KS statistic (D) ranged from 0.02 to 0.39 with a median of 0.14. The layer with larger mean TS was variable with 29 (52%) surveys having the upper layer larger than the lower layer indicating an inconsistent bias for target size versus depth (Figure 1.6). The shape of the ECDF from surveys with highest D appeared to differ mostly at the lower portion of the distribution near TS measurements of ~ -47 dB (Figure 1.6).

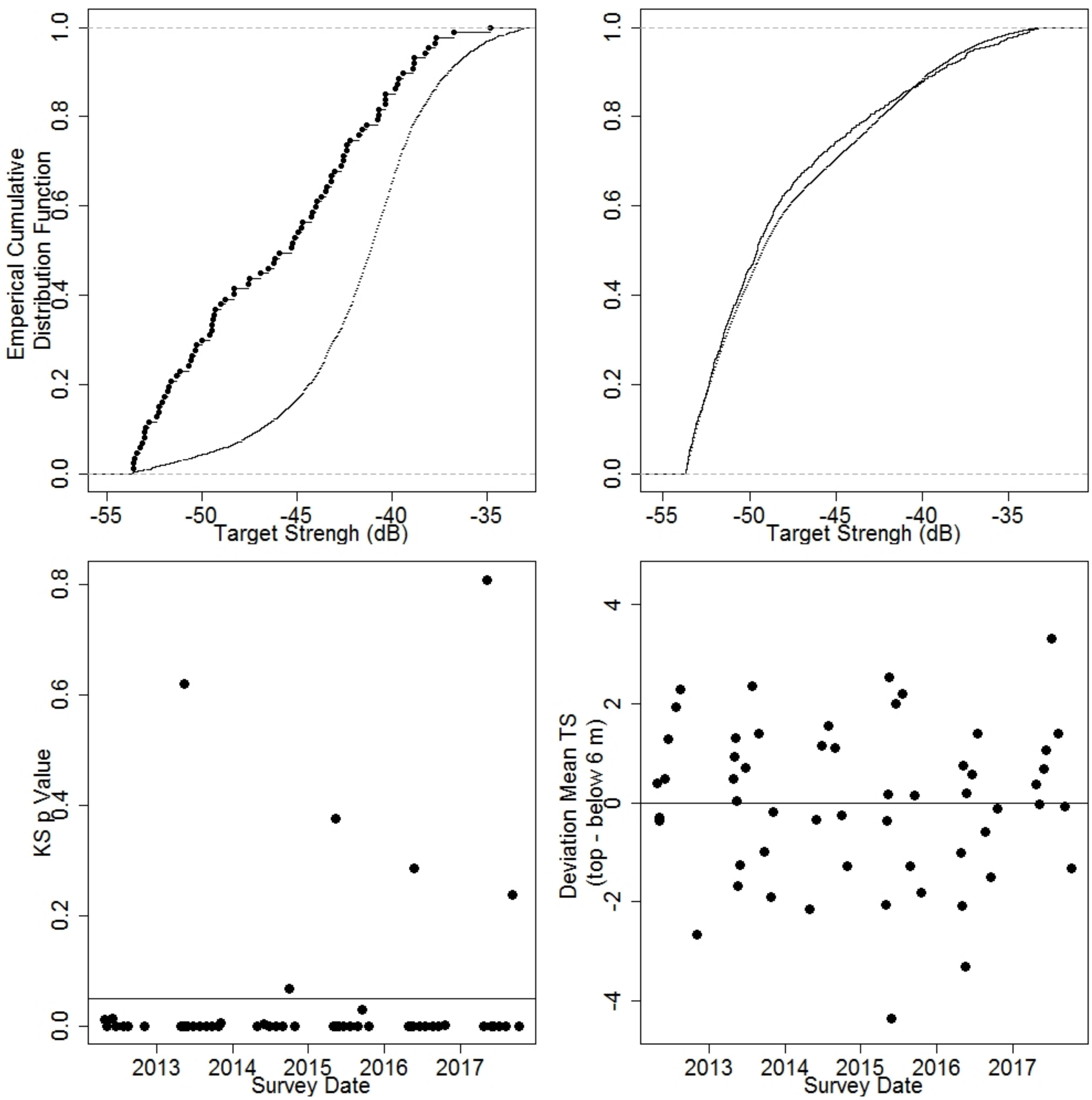


Figure 1.6 Target strength to depth relation. Results of analysis of target strength (TS) relation to water column depth for 6 m surface layer distinction using two sample (top [<6 m] and bottom [>6 m]) KS tests; ECDF for TS with a highly significant p-value (upper left), ECDF for top and bottom TS of a not significant p-value (upper left), KS p-values by survey date with horizontal line depicting alpha = 0.05 (bottom left), deviation (surface - bottom) of mean TS by survey date (bottom right).

## 1.5 Discussion

Our primary goal was to characterize the size and species composition of the fish community by characterizing TS from split-beam acoustic surveys. Our first step was to utilize the trawl data to describe the size (length) and species distributions. The species complex captured by trawling was consistent over the time series and mainly consisted of Clupeid species and occasionally Smelt. The proportions of individual species varied seasonally with surveys during spring 2012 and 2014 dominated by Atlantic Herring. During spring surveys in 2013 and 2015- 2017 catches were dominated by Alewife and Blueback Herring. Smelt catches were the most variable with surveys in spring 2015 and 2017 having over 75% Smelt but in most other surveys Smelt made up less than 5% of the catch. The sizes of the various species also remained consistent with generally two size classes for each species, most likely a juvenile and adult size class respectively. The variation in species and size classes produced multi-modal size frequencies making *in situ* comparisons of TS frequencies possible. These results support O'Malley et al.'s (2017) contention that TS distributions they reported for this estuary were comprised of consistently sized and small (<30 cm) fish.

We combined multiple steps to isolate and then model the distribution of TS measurements to provide a repeatable method to detect TS modes in mixed composite distributions. First, we utilized echo tracking algorithms to combine multiple single target detections into single observations (Soule et al. 1996, 1997; Ona 1999; Dawson et al. 2000; Xie 2000). This technique produced a collection of TS measurements with reduced variation from off-axis pings as also observed in Dawson and Karp (1990). Unfiltered TS values, of unimodal fish sizes could produce wide or bimodal TS distributions that make accurate characterization difficult (e.g. Brooking and Rudstam 2009; Horne 2003). Our echo tracking techniques produced composite TS frequencies that were still broad with weakly apparent modes. As a result, we implemented an EM curve fitting function to iteratively and autonomously detect modes. This technique was successful in producing modes with estimates of error (deviation), however some of the mixture components had very high standard deviation and very small distribution component proportions.

For our objectives, highly variable mixture components are potential sources of error and may have impacted the fit of the TS-TL regression. TS frequency distributions can provide wide standard deviation depending on the scattering properties of the individuals being sampled (Dawson and Karp 1990). Some fish species have shown bimodal TS distribution in surveys attributed to differences in behavior rather than size (Dawson and Karp 1990; Hammond 1997). This impact is unlikely in our shallow system as vertical movements should be less during the portions of the flood tide when velocities in this system have been measured over 7 m $s^{-1}$ (Geyer et al. 2018). Hence, since our TL frequency distributions did not have large variation, we feel the survey data are valid in describing the overall TS distribution. We acknowledge that our regression diagnostics indicated some non-constant variance at the extreme values of the data. Regardless, this patterns is likely a result of the skewed samples sizes, many at small TS-TL and few at large TS-TL and not due to component fitting methods.

We used TS distributions from echo tracking, fit these distributions with an EM algorithm assuming mixed normal structure, and extracted the estimated parameters to fit an empirical relationship for TS and TL. This technique produced regression parameters that were similar compared to previous studies (e.g. Foote 1987, Warner et al. 2002, and Rudstam 2003) but, varied for both slope and intercept. These deviations may be due to variation in the size and species complex, our analytical methods, or both. Warner et al. (2002) and Rudstam (2003) studied Alewives and Smelt respectively, in the Laurentian Great Lakes but with size ranges more similar to the juveniles studied in our study and not the larger adults. Our size and species complex was fairly consistent across the various surveys however, this was reliant on a single capture gear. Since each previous study tunes their acoustic results to concomitant trawl surveys, each new TL-TS relationship may also be influenced by biases in trawl catchability and survey design (e.g. Williams et al. 2010; Kotwicki et al. 2012). Also important is the interpretation of our results is that Warner et al. (2002) and Rudstam (2003) were working in freshwater and Foote (1987) in marine. These authors noted their differences in their equations to other studies and hypothesized differences in morphology or maturity between groups of the same species could affect the TS measurements. In our system, juveniles would be assumed immature but acclimated to the intermediate salinity of the estuary. Adults would be in advanced maturity or post-spawn given their occupation in the estuary during and after spawning. These factors could also contribute to differences in TS – TL regression parameters as compared to the aforementioned studies.

We acknowledge that trawl catchability and selectivity may create important differences between the fish assemblage we observe in the trawl survey and the actual fish assemblage available to the acoustic survey. A potential source for the error in the TL-TS regression is the size-bias of trawl catch. In these data, no fish over ~30 cm were caught but if these fish were represented in the TS data, they would be paired with a lower than appropriate TL value. Similarly, if more smaller sized targets were detected than were captured in the trawl, the TL value would be regressed with larger TS values. We attempted to accommodate this by applying thresholds to the TS data. Trawl catchability has been related to density (Kotwicki, et al. 2012) and light (Williams et al. 2010) both which could be an impact in this estuary. The evaluation of several TS threshold values strongly suggests this is the case. In the lowest threshold, all TS values over ~-30 dB are above the best-fit prediction line and most values less than ~-50 dB are below. In contrast, the highest threshold resulted in parameters more close to previous studies of Foote (1987), Warner et al (2002) and Rudstam (2003). Future studies could implement additional validation techniques (e.g. cameras, imaging SONAR) to quantify capture bias.

Comparability in fish size between trawls and acoustics was a principle assumption that we used to derive TS-TL regression parameters. Our analysis of vertical structure of TS distribution suggests that size distribution is not consistently biased with depth. Rather, the KS statistics indicated smaller fish dominated the upper layer in some surveys and larger fish in other surveys but in most surveys they were significantly different. The KS test is not meant to determine the cause of the difference in ECFDs; however, the difference in mean for the two groups does provide more insight into the shape of the two distributions. These contrary results may be due to the KS-test being too sensitive given the large number of samples (n>10,000) in each comparison or may be due to the relatively shallow nature of the system with fewer targets sampled in the smaller beam volume near the surface as compared to the near the bottom. Both of which would invalidate the usefulness of the test to detect differences. The conclusion however, is that the trawl data may not be representing the entire insonified water column and further investigation is necessary. Geyer et al. (2018) reported that the Penobscot River estuary can become strongly vertically stratified with respect to salinity and we hypothesized this could influence the vertical distribution of fish as seen in other systems (Blaber and Blaber 1980; Martino and Able 2003). Regardless, our regression parameters were similar to other TS – TL studies and our parameters error can be incorporated into future analysis to determine the impact in computations of density and biomass.

### 1.5.1 Conclusion

There have been significant technological advances in fisheries acoustics, particularly in equipment sensitivity (precision) and data processing with increased analytical computational power. The challenge remains how these advances can improve the accuracy of surveys to estimate biological parameters such as abundance and density. Our analysis utilized a unique dataset with concurrent acoustic and trawl samples from a mixed, but consistent estuarine species assemblage. We evaluated several methods of statistical modelling to characterize TS and develop an empirical relationship of TS to fish length for this system. Our results were intermediate to previous estimates using marine and freshwater systems with similar species. These estimates provide parameters unique for this system but methods that may be applied more broadly to researchers working in estuary environments.

## 1.6 Supplemental Material: Target Strength to Fish Length

Table S1.5 Fish length summary statistics. Summary statistics (number [n], mean [μ], standard deviation [σ]) of total length (TL; cm) for juvenile (JUV) and adult (ADU) size classes of Blueback Herring (BBH), Atlantic Herring (SHG), Rainbow Smelt (SLT) and Alewife (SRA) from trawl data from Penobscot River Estuary Surveys 2012-2017.

| Survey | ADU BBH | | | ADU SHG | | | ADU SLT | | | ADU SRA | | | JUV BBH | | | JUV SHG | | | JUV SLT | | | JUV SRA | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Year** week | n | μ | σ | n | μ | σ | n | μ | σ | n | μ | σ | n | μ | σ | n | μ | σ | n | μ | σ | n | μ | σ |
| **2012** | | | | | | | | | | | | | | | | | | | | | | | | |
| 17 | 1 | 16.50 | 0.00 | 4 | 11.50 | 1.46 | 82 | 16.40 | 2.63 | 9 | 28.01 | 1.68 | 173 | 9.44 | 1.02 | 85 | 7.42 | 1.14 | 13 | 9.35 | 0.62 | 88 | 9.08 | 1.33 |
| 18 | | | | 15 | 11.80 | 1.61 | 9 | 13.78 | 2.67 | | | | 124 | 9.40 | 1.13 | 157 | 7.97 | 1.31 | 5 | 7.50 | 0.85 | 115 | 9.46 | 0.86 |
| 19 | 12 | 22.53 | 4.54 | 192 | 11.93 | 1.51 | 157 | 15.16 | 2.59 | 5 | 25.60 | 3.81 | 268 | 9.66 | 1.31 | 274 | 7.88 | 1.24 | 25 | 7.80 | 1.35 | 187 | 9.41 | 1.05 |
| 21 | 6 | 18.02 | 2.51 | 82 | 11.11 | 0.70 | 90 | 14.71 | 1.83 | 1 | 25.00 | 0.00 | 6 | 11.52 | 1.92 | 190 | 8.00 | 1.17 | 23 | 7.27 | 1.05 | 84 | 10.27 | 1.15 |
| 25 | 22 | 19.18 | 3.47 | 104 | 11.73 | 1.26 | 7 | 12.54 | 2.22 | 23 | 17.34 | 1.68 | 101 | 10.45 | 1.88 | 116 | 7.06 | 1.15 | 59 | 8.09 | 0.71 | 99 | 11.49 | 1.78 |
| 30 | 1 | 22.20 | 0.00 | 12 | 13.33 | 1.29 | 17 | 13.19 | 3.32 | 19 | 21.83 | 2.75 | 30 | 9.98 | 1.07 | 182 | 7.36 | 0.58 | 58 | 8.58 | 0.80 | 267 | 8.63 | 2.48 |
| 34 | 15 | 17.89 | 1.58 | 11 | 15.14 | 1.55 | 36 | 16.10 | 3.91 | 8 | 20.76 | 4.32 | 91 | 7.44 | 2.09 | 101 | 8.61 | 0.49 | 20 | 5.65 | 2.88 | 186 | 10.24 | 2.16 |
| 39 | 11 | 18.19 | 0.71 | 86 | 11.76 | 2.34 | 1 | 12.50 | 0.00 | 17 | 16.91 | 1.69 | 222 | 8.80 | 0.69 | 91 | 9.60 | 0.46 | 19 | 3.56 | 0.36 | 195 | 9.41 | 1.71 |
| **2013** | | | | | | | | | | | | | | | | | | | | | | | | |
| 17 | | | | | | | 17 | 16.46 | 2.52 | 2 | 22.35 | 9.69 | 58 | 8.69 | 1.56 | 128 | 4.83 | 0.53 | | | | 18 | 7.96 | 1.36 |
| 18 | | | | 11 | 13.36 | 1.83 | 67 | 16.04 | 2.95 | 7 | 27.00 | 4.43 | 115 | 8.58 | 1.33 | 65 | 5.44 | 1.12 | 2 | 9.75 | 0.07 | 95 | 9.94 | 1.41 |
| 19 | 4 | 16.23 | 0.49 | 43 | 12.75 | 1.63 | 119 | 16.60 | 1.90 | | | | 70 | 10.78 | 1.37 | 130 | 5.54 | 1.45 | | | | 65 | 9.67 | 1.45 |
| 20 | 25 | 17.18 | 0.88 | 44 | 13.55 | 1.00 | 105 | 14.21 | 1.68 | 4 | 24.18 | 5.34 | 124 | 10.88 | 1.36 | 106 | 5.12 | 1.45 | 1 | 7.40 | 0.00 | 117 | 9.61 | 1.29 |
| 21 | 2 | 17.10 | 0.57 | 13 | 11.99 | 1.90 | 24 | 13.43 | 1.52 | 1 | 15.20 | 0.00 | 86 | 11.36 | 1.10 | 56 | 5.96 | 2.19 | 5 | 7.64 | 0.22 | 80 | 10.42 | 1.52 |
| 22 | 20 | 18.63 | 2.36 | 7 | 12.63 | 1.60 | 28 | 15.36 | 2.03 | 89 | 18.69 | 3.62 | 129 | 10.32 | 1.43 | 5 | 9.46 | 0.74 | 5 | 7.48 | 0.92 | 212 | 10.58 | 1.70 |
| 26 | 5 | 21.10 | 0.65 | 2 | 12.00 | 0.71 | 41 | 15.13 | 2.34 | 56 | 20.88 | 2.98 | 134 | 10.16 | 0.63 | 91 | 6.04 | 0.74 | 28 | 8.94 | 0.75 | 241 | 10.92 | 1.27 |
| 30 | 6 | 19.90 | 3.10 | 3 | 14.17 | 1.99 | 1 | 19.30 | 0.00 | 28 | 20.66 | 4.30 | 25 | 10.53 | 2.84 | 343 | 7.70 | 0.50 | 1 | 5.50 | 0.00 | 301 | 8.82 | 2.73 |
| 35 | 2 | 19.10 | 4.95 | | | | | | | 10 | 16.49 | 0.84 | 44 | 7.13 | 1.15 | | | | | | | 54 | 10.75 | 1.91 |
| 39 | 2 | 19.50 | 0.71 | 19 | 10.41 | 0.33 | 39 | 15.04 | 2.78 | 13 | 17.79 | 2.36 | 28 | 7.89 | 1.75 | 28 | 8.68 | 1.62 | 5 | 5.98 | 1.09 | 150 | 9.65 | 1.68 |
| 43 | | | | 5 | 12.48 | 1.99 | 1 | 15.50 | 0.00 | 1 | 19.30 | 0.00 | 77 | 8.75 | 1.18 | 103 | 4.79 | 1.08 | 42 | 6.03 | 1.39 | 37 | 9.31 | 2.08 |
| 45 | | | | 40 | 11.66 | 0.96 | 11 | 14.61 | 2.96 | 1 | 19.00 | 0.00 | 13 | 11.18 | 1.95 | 7 | 9.04 | 1.26 | 51 | 6.93 | 0.97 | 12 | 9.08 | 2.29 |
| **2014** | | | | | | | | | | | | | | | | | | | | | | | | |
| 18 | | | | | | | 1 | 11.00 | 0.00 | | | | 21 | 8.27 | 0.94 | 30 | 4.49 | 0.39 | 7 | 7.23 | 0.52 | 1 | 8.00 | 0.00 |
| 22 | 8 | 22.21 | 3.54 | 21 | 10.81 | 0.46 | 4 | 14.93 | 2.67 | 15 | 25.63 | 3.49 | 167 | 9.92 | 1.55 | 106 | 5.67 | 1.50 | | | | 34 | 10.00 | 1.15 |
| 26 | 32 | 23.15 | 1.71 | 2 | 11.35 | 1.63 | 10 | 11.52 | 0.81 | 23 | 19.37 | 2.56 | 266 | 9.44 | 0.87 | 14 | 7.41 | 0.49 | 20 | 8.39 | 1.02 | 241 | 9.88 | 1.65 |
| 31 | 9 | 22.60 | 1.48 | 4 | 15.45 | 0.95 | 8 | 11.01 | 0.92 | 60 | 22.59 | 3.57 | 53 | 9.12 | 3.32 | 68 | 7.91 | 0.73 | 7 | 9.54 | 0.34 | 315 | 8.88 | 2.78 |
| 35 | 5 | 21.56 | 2.86 | | | | 7 | 14.76 | 3.29 | 52 | 20.53 | 3.39 | 18 | 6.94 | 1.79 | 10 | 8.82 | 0.54 | | | | 159 | 9.22 | 3.06 |

Table S1.5 Fish length summary statistics. *Continued*

| Survey **Year** week | ADU BBH | | | ADU SHG | | | ADU SLT | | | ADU SRA | | | JUV BBH | | | JUV SHG | | | JUV SLT | | | JUV SRA | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | n | μ | σ | n | μ | σ | n | μ | σ | n | μ | σ | n | μ | σ | n | μ | σ | n | μ | σ | n | μ | σ |
| **2014** | | | | | | | | | | | | | | | | | | | | | | | | |
| 40 | | | | 5 | 11.84 | 0.81 | 57 | 17.76 | 3.30 | 22 | 17.68 | 2.93 | 76 | 7.74 | 0.82 | 34 | 4.48 | 1.38 | 39 | 5.89 | 1.35 | 111 | 9.20 | 2.08 |
| 44 | | | | 8 | 11.99 | 0.56 | 1 | 16.00 | 0.00 | 1 | 15.80 | 0.00 | 67 | 7.93 | 0.88 | 15 | 5.98 | 1.83 | 71 | 6.65 | 1.01 | 120 | 9.51 | 1.77 |
| **2015** | | | | | | | | | | | | | | | | | | | | | | | | |
| 18 | | | | 1 | 13.50 | 0.00 | 1 | 17.50 | 0.00 | | | | 1 | 9.00 | 0.00 | 79 | 4.46 | 0.57 | | | | | | |
| 19 | | | | 8 | 12.55 | 1.46 | 143 | 16.34 | 3.12 | 1 | 28.60 | 0.00 | 64 | 9.52 | 1.00 | 57 | 6.42 | 2.34 | 3 | 8.87 | 0.64 | 30 | 9.60 | 1.21 |
| 20 | 1 | 15.60 | 0.00 | 14 | 10.97 | 1.14 | 114 | 16.15 | 2.20 | | | | 65 | 9.72 | 0.78 | 91 | 7.78 | 2.19 | 1 | 9.40 | 0.00 | 67 | 9.56 | 0.94 |
| 21 | 5 | 22.92 | 4.39 | 11 | 11.07 | 1.05 | 54 | 14.63 | 2.64 | 10 | 23.42 | 4.90 | 287 | 9.68 | 0.70 | 115 | 7.67 | 1.87 | 5 | 8.26 | 0.69 | 131 | 9.67 | 1.09 |
| 22 | 8 | 24.09 | 2.97 | 11 | 12.58 | 2.30 | 46 | 13.50 | 2.40 | 3 | 26.43 | 2.10 | 129 | 10.23 | 1.29 | 10 | 5.17 | 0.46 | 1 | 8.70 | 0.00 | 75 | 10.12 | 1.00 |
| 25 | 17 | 23.84 | 3.30 | 86 | 11.62 | 0.81 | 48 | 11.42 | 1.43 | 56 | 23.32 | 4.32 | 344 | 10.24 | 0.83 | 10 | 8.06 | 1.17 | 14 | 8.81 | 1.31 | 231 | 10.91 | 1.34 |
| 30 | 5 | 19.48 | 0.47 | 5 | 14.46 | 2.92 | 33 | 14.15 | 2.91 | 52 | 21.21 | 2.58 | 67 | 10.40 | 0.86 | 119 | 7.29 | 0.65 | 20 | 8.24 | 0.67 | 244 | 8.79 | 2.97 |
| 35 | 1 | 26.20 | 0.00 | | | | | | | | | | 16 | 6.28 | 1.86 | 4 | 8.13 | 0.73 | | | | 43 | 7.92 | 2.72 |
| 38 | | | | 1 | 10.40 | 0.00 | 10 | 13.75 | 1.63 | | | | 62 | 6.57 | 0.56 | 8 | 5.60 | 2.71 | 3 | 6.97 | 0.21 | 12 | 9.18 | 3.08 |
| 43 | 1 | 16.50 | 0.00 | 44 | 11.25 | 1.30 | 12 | 17.75 | 2.57 | | | | 5 | 8.90 | 0.91 | 8 | 8.41 | 2.59 | 12 | 6.07 | 1.38 | 108 | 8.60 | 1.40 |
| **2016** | | | | | | | | | | | | | | | | | | | | | | | | |
| 17 | | | | 20 | 12.18 | 0.86 | 43 | 14.90 | 2.03 | 1 | 22.80 | 0.00 | 104 | 8.58 | 0.81 | 104 | 5.51 | 0.95 | 2 | 8.75 | 1.06 | 51 | 8.80 | 0.74 |
| 18 | | | | 12 | 12.29 | 0.97 | 84 | 14.24 | 2.73 | 1 | 28.80 | 0.00 | 104 | 8.64 | 0.92 | 77 | 5.83 | 1.51 | 13 | 8.85 | 0.69 | 67 | 8.87 | 1.03 |
| 19 | 1 | 17.00 | 0.00 | 33 | 12.87 | 0.96 | 168 | 15.35 | 3.43 | 6 | 28.58 | 0.80 | 139 | 9.20 | 1.15 | 28 | 7.87 | 0.52 | 22 | 7.60 | 1.41 | 89 | 9.53 | 0.98 |
| 20 | 2 | 17.15 | 0.92 | 7 | 12.91 | 1.09 | 3 | 13.57 | 1.25 | | | | 367 | 9.91 | 1.17 | 119 | 6.98 | 1.99 | 1 | 6.80 | 0.00 | 192 | 8.34 | 0.84 |
| 21 | 5 | 18.68 | 3.15 | 24 | 10.92 | 1.13 | 23 | 14.46 | 3.32 | 3 | 27.53 | 2.61 | 198 | 9.72 | 0.86 | 205 | 9.04 | 0.53 | 5 | 8.24 | 1.76 | 241 | 9.23 | 0.95 |
| 25 | 61 | 20.08 | 3.14 | 17 | 12.82 | 2.46 | 44 | 13.77 | 2.72 | 143 | 19.02 | 2.57 | 86 | 9.95 | 1.59 | 549 | 7.68 | 0.71 | 75 | 8.18 | 0.83 | 361 | 9.64 | 1.47 |
| 29 | 3 | 18.47 | 2.19 | 4 | 14.23 | 1.11 | | | | 107 | 20.88 | 2.60 | 88 | 11.35 | 1.92 | 7 | 8.06 | 0.62 | 3 | 9.33 | 0.29 | 245 | 10.21 | 3.43 |
| 34 | | | | | | | 1 | 11.60 | 0.00 | 7 | 19.37 | 4.28 | 236 | 6.05 | 0.73 | | | | | | | 110 | 10.18 | 2.96 |
| 38 | | | | | | | 25 | 18.73 | 3.15 | 1 | 20.00 | 0.00 | 125 | 7.73 | 0.75 | 6 | 4.73 | 0.30 | 9 | 5.01 | 1.04 | 111 | 8.12 | 1.49 |
| 42 | | | | 2 | 13.95 | 2.76 | 103 | 18.59 | 1.96 | 2 | 15.75 | 0.07 | 73 | 8.42 | 1.38 | 46 | 4.38 | 1.13 | 38 | 7.31 | 1.69 | 96 | 9.83 | 1.78 |
| **2017** | | | | | | | | | | | | | | | | | | | | | | | | |
| 17 | | | | | | | 104 | 16.78 | 2.42 | 4 | 27.48 | 0.46 | 11 | 8.46 | 1.09 | 17 | 5.06 | 1.35 | 11 | 9.21 | 1.07 | | | |
| 19 | 1 | 24.00 | 0.00 | 1 | 11.00 | 0.00 | 77 | 17.02 | 3.07 | 4 | 28.68 | 1.06 | 180 | 8.99 | 1.18 | 19 | 4.76 | 1.25 | 1 | 7.50 | 0.00 | 131 | 9.91 | 1.20 |
| 22 | 14 | 23.00 | 2.62 | 7 | 10.93 | 0.41 | 5 | 13.42 | 2.53 | 12 | 20.05 | 5.08 | 281 | 9.76 | 1.36 | 59 | 6.68 | 1.15 | 12 | 8.53 | 1.18 | 136 | 10.69 | 1.61 |
| 24 | 56 | 22.24 | 3.29 | 36 | 11.29 | 0.69 | 3 | 13.67 | 3.93 | 60 | 24.66 | 4.72 | 154 | 11.59 | 1.65 | 93 | 7.38 | 0.52 | | | | 100 | 11.79 | 1.73 |
| 28 | 24 | 19.78 | 2.47 | 2 | 12.30 | 0.99 | 7 | 13.21 | 1.06 | 132 | 21.10 | 1.57 | 3 | 11.00 | 3.35 | 177 | 6.77 | 0.73 | 3 | 9.07 | 0.95 | 34 | 5.61 | 2.88 |
| 32 | | | | | | | 2 | 14.25 | 1.06 | 37 | 21.71 | 2.75 | 194 | 5.96 | 1.15 | 101 | 6.84 | 0.48 | | | | 89 | 7.04 | 2.40 |
| 37 | | | | 1 | 13.20 | 0.00 | 6 | 14.40 | 0.63 | 1 | 16.80 | 0.00 | 270 | 6.19 | 0.83 | 49 | 7.19 | 1.68 | | | | 10 | 9.91 | 2.86 |

Table S1.6 Target strength distribution fitting. Model parameters, mean (mu), standard deviation (sig), and proportion (lam) and final log likelihood (loglik) results of mixed (up to 8 cases) normal fitting procedure on target strength (TS; dB) with lower threshold of -54 dB applied from acoustic survey data from Penobscot River Estuary 2012-2017. Survey is labeled with standard week and Year (WW.YY) format.

| Survey | loglik | Case 1 | | | Case 2 | | | Case 3 | | | Case 4 | | | Case 5 | | | Case 6 | | | Case 7 | | | Case 8 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam |
| 17.12 | -26483.2 | -53.6 | 0.0 | 0.0 | -53.3 | 0.2 | 0.0 | -52.8 | 0.3 | 0.1 | -51.9 | 0.6 | 0.1 | -37.8 | 2.2 | 0.0 | -50.3 | 1.0 | 0.1 | -43.4 | 2.0 | 0.5 | -47.4 | 1.7 | 0.3 |
| 17.13 | -19490.6 | -53.2 | 0.3 | 0.0 | -43.5 | 3.2 | 0.7 | -52.0 | 0.7 | 0.1 | -49.4 | 1.6 | 0.2 | -40.2 | 0.9 | 0.0 | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 17.16 | -42211.2 | -53.4 | 0.2 | 0.0 | -52.4 | 0.6 | 0.0 | -44.7 | 0.2 | 0.0 | -33.8 | 0.5 | 0.0 | -50.0 | 1.4 | 0.1 | -39.3 | 2.0 | 0.5 | -44.4 | 2.8 | 0.3 | NA | NA | NA |
| 17.17 | -33211.9 | -53.4 | 0.2 | 0.1 | -50.5 | 1.3 | 0.2 | -52.5 | 0.5 | 0.1 | -38.7 | 2.3 | 0.3 | -46.0 | 2.7 | 0.4 | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 18.12 | -25349.6 | -53.4 | 0.2 | 0.0 | -52.5 | 0.5 | 0.1 | -50.9 | 1.0 | 0.1 | -48.5 | 1.7 | 0.2 | -40.0 | 1.1 | 0.1 | -43.1 | 3.2 | 0.5 | NA | NA | NA | NA | NA | NA |
| 18.13 | -17279.9 | -53.5 | 0.2 | 0.0 | -52.5 | 0.5 | 0.0 | -50.9 | 1.0 | 0.1 | -46.9 | 2.1 | 0.3 | -42.8 | 0.0 | 0.0 | -41.6 | 2.2 | 0.5 | -34.4 | 0.7 | 0.0 | NA | NA | NA |
| 18.14 | -18752.1 | -48.5 | 1.9 | 0.2 | -53.1 | 0.4 | 0.1 | -51.6 | 0.9 | 0.1 | -41.8 | 3.4 | 0.5 | -39.1 | 1.0 | 0.0 | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 18.15 | -59901.3 | -53.1 | 0.4 | 0.1 | -51.0 | 1.2 | 0.2 | -47.4 | 2.3 | 0.4 | -43.1 | 3.5 | 0.3 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 18.16 | -33902.6 | -53.2 | 0.3 | 0.0 | -52.0 | 0.7 | 0.1 | -50.1 | 1.2 | 0.1 | -47.1 | 1.8 | 0.2 | -42.3 | 2.4 | 0.4 | -38.8 | 1.9 | 0.3 | -34.2 | 0.7 | 0.0 | NA | NA | NA |
| 19.12 | -47039.0 | -53.5 | 0.1 | 0.0 | -50.7 | 0.9 | 0.1 | -46.5 | 1.7 | 0.2 | -53.0 | 0.3 | 0.0 | -52.1 | 0.5 | 0.1 | -48.7 | 0.8 | 0.1 | -41.7 | 2.3 | 0.5 | -34.6 | 0.6 | 0.0 |
| 19.13 | -22040.6 | -53.6 | 0.1 | 0.0 | -49.3 | 1.5 | 0.2 | -51.7 | 0.8 | 0.1 | -53.0 | 0.3 | 0.1 | -43.2 | 2.9 | 0.7 | -36.2 | 1.5 | 0.0 | NA | NA | NA | NA | NA | NA |
| 19.15 | -100699.3 | -48.5 | 1.6 | 0.2 | -53.6 | 0.1 | 0.0 | -52.5 | 0.5 | 0.1 | -53.2 | 0.2 | 0.0 | -51.0 | 0.9 | 0.1 | -44.3 | 2.7 | 0.4 | -38.0 | 1.9 | 0.2 | NA | NA | NA |
| 19.16 | -34386.5 | -53.1 | 0.3 | 0.0 | -53.6 | 0.1 | 0.0 | -52.1 | 0.6 | 0.1 | -50.2 | 1.2 | 0.2 | -47.1 | 1.8 | 0.2 | -42.1 | 2.2 | 0.3 | -38.7 | 1.7 | 0.1 | -34.2 | 0.7 | 0.0 |
| 19.17 | -30288.2 | -53.4 | 0.2 | 0.0 | -49.9 | 1.2 | 0.1 | -52.8 | 0.4 | 0.1 | -51.7 | 0.6 | 0.1 | -41.5 | 2.3 | 0.3 | -37.9 | 1.6 | 0.2 | -46.5 | 2.0 | 0.2 | -34.6 | 0.9 | 0.0 |
| 20.13 | -24080.5 | -53.5 | 0.1 | 0.0 | -52.9 | 0.4 | 0.0 | -51.3 | 0.9 | 0.1 | -48.3 | 1.7 | 0.2 | -43.3 | 2.3 | 0.6 | -36.2 | 1.1 | 0.0 | -38.7 | 1.4 | 0.1 | -33.9 | 0.5 | 0.0 |
| 20.15 | -67905.2 | -47.6 | 1.7 | 0.2 | -53.5 | 0.1 | 0.0 | -52.8 | 0.4 | 0.1 | -50.0 | 1.1 | 0.1 | -51.7 | 0.7 | 0.1 | -42.9 | 2.8 | 0.3 | -37.8 | 2.0 | 0.2 | NA | NA | NA |
| 20.16 | -26101.0 | -52.8 | 0.4 | 0.0 | -53.5 | 0.1 | 0.0 | -51.2 | 1.0 | 0.1 | -48.3 | 1.8 | 0.1 | -41.3 | 0.6 | 0.0 | -41.7 | 3.3 | 0.7 | -38.0 | 0.0 | 0.0 | NA | NA | NA |
| 21.12 | -34638.7 | -53.5 | 0.1 | 0.0 | -52.9 | 0.3 | 0.0 | -52.0 | 0.6 | 0.1 | -49.9 | 1.2 | 0.2 | -43.0 | 2.8 | 0.4 | -46.9 | 2.0 | 0.3 | -36.4 | 1.4 | 0.0 | -34.1 | 0.6 | 0.0 |
| 21.13 | -27634.3 | -53.5 | 0.1 | 0.0 | -53.0 | 0.3 | 0.0 | -52.2 | 0.4 | 0.0 | -51.0 | 0.8 | 0.1 | -48.6 | 1.5 | 0.2 | -43.5 | 2.5 | 0.6 | -33.5 | 0.3 | 0.0 | -37.2 | 1.7 | 0.1 |
| 21.15 | -81061.5 | -53.4 | 0.2 | 0.0 | -52.6 | 0.4 | 0.1 | -39.5 | 1.9 | 0.2 | -51.2 | 0.9 | 0.1 | -48.9 | 1.5 | 0.2 | -44.5 | 2.5 | 0.3 | -36.6 | 1.4 | 0.1 | -33.9 | 0.5 | 0.0 |
| 21.16 | -25743.2 | -53.5 | 0.1 | 0.0 | -52.9 | 0.3 | 0.0 | -52.1 | 0.6 | 0.1 | -50.4 | 1.1 | 0.1 | -44.7 | 0.1 | 0.0 | -47.7 | 1.7 | 0.1 | -42.5 | 2.8 | 0.6 | -35.0 | 1.0 | 0.0 |
| 22.13 | -17454.2 | -53.6 | 0.1 | 0.0 | -53.2 | 0.2 | 0.0 | -52.5 | 0.4 | 0.1 | -51.3 | 0.8 | 0.1 | -48.9 | 1.5 | 0.2 | -44.2 | 2.7 | 0.5 | -38.3 | 1.8 | 0.1 | -34.3 | 0.7 | 0.0 |
| 22.14 | -24414.5 | -53.4 | 0.2 | 0.0 | -52.9 | 0.3 | 0.0 | -51.6 | 0.8 | 0.1 | -34.4 | 0.9 | 0.0 | -49.1 | 1.5 | 0.2 | -43.4 | 2.9 | 0.6 | -38.0 | 1.9 | 0.0 | NA | NA | NA |

Table S1.6 Target strength distribution fitting. *Continued*

| Survey | loglik | Case 1 | | | Case 2 | | | Case 3 | | | Case 4 | | | Case 5 | | | Case 6 | | | Case 7 | | | Case 8 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam |
| 22.15 | -7701.3 | -53.6 | 0.0 | 0.0 | -52.7 | 0.5 | 0.0 | -45.4 | 2.5 | 0.2 | -35.7 | 1.3 | 0.1 | -33.1 | 0.1 | 0.0 | -40.5 | 2.0 | 0.6 | -50.7 | 1.1 | 0.0 | -43.5 | 0.2 | 0.0 |
| 22.17 | -32812.0 | -53.6 | 0.1 | 0.0 | -53.1 | 0.3 | 0.0 | -42.5 | 2.3 | 0.4 | -52.2 | 0.6 | 0.1 | -50.5 | 1.0 | 0.1 | -47.5 | 1.7 | 0.2 | -37.5 | 1.6 | 0.1 | -34.2 | 0.7 | 0.0 |
| 24.17 | -24984.1 | -52.6 | 0.5 | 0.1 | -53.5 | 0.2 | 0.0 | -50.7 | 1.1 | 0.1 | -47.5 | 1.9 | 0.2 | -42.7 | 3.0 | 0.5 | -36.1 | 1.4 | 0.1 | -33.5 | 0.3 | 0.0 | NA | NA | NA |
| 25.12 | -32548.2 | -49.1 | 1.4 | 0.3 | -53.4 | 0.2 | 0.0 | -52.7 | 0.4 | 0.1 | -51.4 | 0.8 | 0.1 | -45.6 | 2.3 | 0.3 | -39.9 | 2.2 | 0.1 | -35.5 | 0.9 | 0.0 | -33.4 | 0.3 | 0.0 |
| 25.15 | -30488.9 | -53.6 | 0.1 | 0.0 | -53.1 | 0.3 | 0.0 | -52.2 | 0.5 | 0.1 | -50.8 | 0.9 | 0.1 | -48.5 | 1.5 | 0.2 | -34.2 | 0.7 | 0.0 | -37.2 | 1.6 | 0.1 | -43.2 | 2.9 | 0.5 |
| 25.16 | -41308.4 | -53.6 | 0.1 | 0.0 | -53.1 | 0.3 | 0.0 | -52.3 | 0.5 | 0.1 | -47.6 | 1.9 | 0.4 | -36.8 | 1.5 | 0.1 | -50.9 | 0.9 | 0.1 | -43.1 | 2.8 | 0.3 | -34.0 | 0.6 | 0.0 |
| 26.13 | -17508.9 | -53.4 | 0.2 | 0.0 | -52.9 | 0.3 | 0.1 | -39.4 | 2.0 | 0.1 | -51.9 | 0.6 | 0.1 | -50.2 | 1.0 | 0.2 | -47.8 | 1.3 | 0.2 | -44.2 | 2.0 | 0.2 | -35.3 | 1.3 | 0.0 |
| 26.14 | -21456.6 | -53.6 | 0.1 | 0.0 | -53.3 | 0.2 | 0.0 | -52.4 | 0.5 | 0.1 | -51.0 | 0.9 | 0.1 | -48.7 | 1.6 | 0.2 | -38.3 | 1.9 | 0.1 | -34.4 | 0.7 | 0.0 | -44.7 | 2.6 | 0.4 |
| 28.17 | -39037.6 | -53.6 | 0.1 | 0.0 | -53.1 | 0.3 | 0.1 | -51.9 | 0.7 | 0.1 | -45.0 | 2.7 | 0.4 | -49.3 | 1.6 | 0.3 | -38.3 | 1.9 | 0.1 | -35.2 | 0.9 | 0.0 | -33.6 | 0.3 | 0.0 |
| 29.16 | -30019.0 | -53.5 | 0.2 | 0.0 | -47.6 | 2.0 | 0.3 | -52.7 | 0.4 | 0.1 | -51.0 | 1.0 | 0.2 | -43.0 | 2.8 | 0.3 | -37.8 | 1.8 | 0.1 | -34.1 | 0.7 | 0.0 | NA | NA | NA |
| 30.12 | -42687.5 | -53.5 | 0.1 | 0.0 | -52.9 | 0.3 | 0.1 | -51.7 | 0.7 | 0.1 | -49.6 | 1.3 | 0.3 | -47.1 | 1.9 | 0.3 | -42.3 | 2.9 | 0.2 | -36.5 | 1.5 | 0.0 | -33.9 | 0.6 | 0.0 |
| 30.13 | -22012.5 | -53.6 | 0.0 | 0.0 | -53.3 | 0.2 | 0.0 | -52.7 | 0.4 | 0.1 | -49.5 | 1.3 | 0.2 | -40.4 | 2.5 | 0.2 | -51.6 | 0.7 | 0.1 | -46.6 | 2.0 | 0.3 | -35.2 | 1.1 | 0.0 |
| 30.15 | -34282.3 | -53.5 | 0.1 | 0.0 | -52.8 | 0.4 | 0.1 | -49.9 | 1.1 | 0.1 | -34.0 | 0.5 | 0.0 | -51.7 | 0.7 | 0.1 | -47.0 | 1.9 | 0.3 | -37.0 | 1.6 | 0.1 | -42.5 | 2.8 | 0.3 |
| 31.14 | -40701.1 | -50.7 | 1.0 | 0.1 | -53.6 | 0.1 | 0.0 | -53.2 | 0.2 | 0.0 | -52.4 | 0.5 | 0.1 | -47.1 | 2.1 | 0.3 | -36.6 | 1.5 | 0.1 | -42.7 | 3.0 | 0.4 | -33.7 | 0.4 | 0.0 |
| 32.17 | -42374.2 | -53.4 | 0.2 | 0.1 | -52.5 | 0.5 | 0.1 | -50.5 | 1.3 | 0.2 | -45.8 | 2.9 | 0.4 | -37.9 | 2.6 | 0.1 | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 34.12 | -41072.2 | -53.5 | 0.1 | 0.0 | -53.0 | 0.3 | 0.0 | -52.1 | 0.5 | 0.1 | -50.7 | 0.9 | 0.1 | -47.9 | 1.6 | 0.4 | -44.3 | 2.4 | 0.3 | -38.7 | 2.0 | 0.1 | -34.5 | 0.8 | 0.0 |
| 34.16 | -80268.7 | -53.3 | 0.2 | 0.1 | -52.2 | 0.7 | 0.2 | -42.1 | 4.1 | 0.3 | -49.7 | 1.6 | 0.3 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 35.13 | -21045.9 | -53.1 | 0.4 | 0.1 | -47.2 | 2.4 | 0.3 | -51.3 | 1.1 | 0.3 | -42.8 | 3.6 | 0.3 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 35.14 | -31788.3 | -53.6 | 0.1 | 0.0 | -53.2 | 0.3 | 0.1 | -52.1 | 0.6 | 0.1 | -50.1 | 1.4 | 0.2 | -43.8 | 3.5 | 0.5 | -35.7 | 1.5 | 0.0 | NA | NA | NA | NA | NA | NA |
| 35.15 | -31824.7 | -53.0 | 0.4 | 0.1 | -50.8 | 1.3 | 0.2 | -38.7 | 2.8 | 0.2 | -45.5 | 2.9 | 0.5 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 37.17 | -42478.3 | -53.4 | 0.2 | 0.1 | -52.6 | 0.4 | 0.1 | -51.2 | 0.9 | 0.2 | -48.9 | 1.6 | 0.2 | -42.2 | 3.4 | 0.3 | -35.6 | 1.5 | 0.1 | NA | NA | NA | NA | NA | NA |
| 38.15 | -30663.6 | -53.4 | 0.2 | 0.0 | -52.6 | 0.5 | 0.1 | -51.0 | 1.0 | 0.2 | -47.9 | 1.9 | 0.2 | -43.3 | 3.0 | 0.5 | -36.3 | 1.8 | 0.1 | NA | NA | NA | NA | NA | NA |
| 38.16 | -49766.1 | -53.6 | 0.1 | 0.0 | -53.3 | 0.2 | 0.1 | -52.8 | 0.4 | 0.2 | -51.6 | 0.8 | 0.2 | -49.6 | 1.4 | 0.2 | -42.6 | 4.0 | 0.2 | NA | NA | NA | NA | NA | NA |
| 39.12 | -40300.4 | -53.6 | 0.1 | 0.0 | -53.3 | 0.2 | 0.0 | -52.6 | 0.4 | 0.1 | -51.4 | 0.8 | 0.1 | -49.3 | 1.3 | 0.2 | -44.9 | 2.3 | 0.5 | -39.5 | 2.0 | 0.1 | -35.1 | 1.0 | 0.0 |
| 39.13 | -24565.1 | -53.6 | 0.1 | 0.0 | -53.3 | 0.2 | 0.1 | -51.7 | 0.6 | 0.1 | -52.7 | 0.3 | 0.1 | -50.3 | 1.0 | 0.1 | -47.8 | 1.6 | 0.1 | -43.1 | 2.5 | 0.3 | -37.3 | 1.9 | 0.0 |

Table S1.6 Target strength distribution fitting. *Continued*

| Survey | loglik | Case 1 | | | Case 2 | | | Case 3 | | | Case 4 | | | Case 5 | | | Case 6 | | | Case 7 | | | Case 8 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam | mu | sig | lam |
| 40.14 | -37821.9 | -53.6 | 0.1 | 0.0 | -53.2 | 0.3 | 0.1 | -52.1 | 0.6 | 0.2 | -50.0 | 1.3 | 0.3 | -46.0 | 2.4 | 0.2 | -40.2 | 2.6 | 0.2 | -34.7 | 0.9 | 0.0 | NA | NA | NA |
| 41.17 | -45633.2 | -53.6 | 0.1 | 0.0 | -53.3 | 0.2 | 0.1 | -52.6 | 0.4 | 0.1 | -51.2 | 0.9 | 0.2 | -49.1 | 1.5 | 0.2 | -41.9 | 3.3 | 0.3 | -35.9 | 1.5 | 0.1 | NA | NA | NA |
| 42.16 | -51554.7 | -53.5 | 0.1 | 0.0 | -52.2 | 0.5 | 0.1 | -53.1 | 0.3 | 0.1 | -48.7 | 1.4 | 0.2 | -50.7 | 0.9 | 0.2 | -44.9 | 2.5 | 0.2 | -39.3 | 2.5 | 0.2 | NA | NA | NA |
| 43.13 | -22167.2 | -53.6 | 0.1 | 0.0 | -53.1 | 0.3 | 0.0 | -51.9 | 0.8 | 0.1 | -49.1 | 1.5 | 0.2 | -43.6 | 2.9 | 0.4 | -38.8 | 2.2 | 0.1 | -34.4 | 0.8 | 0.0 | NA | NA | NA |
| 43.15 | -47245.8 | -53.4 | 0.2 | 0.0 | -52.7 | 0.4 | 0.1 | -51.1 | 1.0 | 0.1 | -48.4 | 1.7 | 0.2 | -36.9 | 1.6 | 0.1 | -42.7 | 3.0 | 0.5 | -34.0 | 0.6 | 0.0 | NA | NA | NA |
| 44.14 | -27024.6 | -53.6 | 0.0 | 0.0 | -53.4 | 0.2 | 0.0 | -52.6 | 0.5 | 0.1 | -50.9 | 1.0 | 0.1 | -48.4 | 1.6 | 0.2 | -38.3 | 2.3 | 0.1 | -43.6 | 2.8 | 0.4 | NA | NA | NA |
| 45.13 | -17838.2 | -53.6 | 0.1 | 0.0 | -52.3 | 0.5 | 0.1 | -50.6 | 1.0 | 0.2 | -53.2 | 0.2 | 0.1 | -48.1 | 1.7 | 0.2 | -42.5 | 2.8 | 0.3 | -37.6 | 1.9 | 0.0 | NA | NA | NA |

Table S1.7 Fish length distribution fitting. Model parameters, mean (mu), standard deviation (sig), and proportion (lam) and final log likelihood (loglik) results of mixed (up to 8 cases) normal fitting procedure on total length (TL; mm) from trawl survey data from Penobscot River Estuary 2012-2017. Survey is labeled with standard week and Year (WW.YY) format.

| Survey | loglik | Case 1 | | | Case 2 | | | Case 3 | | | Case 4 | | | Case 5 | | | Case 6 | | | Case 7 | | | Case 8 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | mu1 | sig1 | lam1 | mu2 | sig2 | lam2 | mu3 | sig3 | lam3 | mu4 | sig4 | lam4 | mu5 | sig5 | lam5 | mu6 | sig6 | lam6 | mu7 | sig7 | lam7 | mu8 | sig8 | lam8 |
| 17.12 | -2111.5 | 165.0 | 12.4 | 0.1 | 115.0 | 14.6 | 0.0 | 164.0 | 26.3 | 0.1 | 280.1 | 16.8 | 0.0 | 94.4 | 10.2 | 0.2 | 74.2 | 11.4 | 0.1 | 93.5 | 6.2 | 0.0 | 90.8 | 13.3 | 0.4 |
| 17.13 | -968.7 | 164.6 | 25.2 | 0.1 | 223.5 | 96.9 | 0.0 | 86.9 | 15.6 | 0.2 | 48.3 | 5.3 | 0.6 | 79.6 | 13.6 | 0.1 | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 17.16 | -1571.2 | 121.8 | 8.6 | 0.0 | 149.0 | 20.3 | 0.0 | 228.0 | 24.2 | 0.0 | 85.8 | 8.1 | 0.5 | 55.1 | 9.5 | 0.2 | 87.5 | 10.6 | 0.2 | 88.0 | 7.4 | 0.0 | NA | NA | NA |
| 17.17 | -752.4 | 167.8 | 24.2 | 0.7 | 274.8 | 4.6 | 0.0 | 84.6 | 10.9 | 0.0 | 50.6 | 13.5 | 0.1 | 92.1 | 10.7 | 0.2 | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 18.12 | -1756.1 | 118.0 | 16.1 | 0.0 | 137.8 | 26.7 | 0.0 | 94.0 | 11.3 | 0.3 | 79.7 | 13.1 | 0.3 | 75.0 | 8.5 | 0.0 | 94.6 | 8.6 | 0.3 | NA | NA | NA | NA | NA | NA |
| 18.13 | -1807.7 | 133.6 | 18.3 | 0.0 | 160.4 | 29.5 | 0.2 | 270.0 | 44.3 | 0.0 | 85.8 | 13.3 | 0.3 | 54.4 | 11.2 | 0.2 | 97.5 | 0.7 | 0.0 | 99.4 | 14.1 | 0.3 | NA | NA | NA |
| 18.14 | -308.6 | 110.0 | 12.1 | 0.1 | 82.7 | 9.4 | 0.6 | 44.9 | 3.9 | 0.0 | 72.3 | 5.2 | 0.1 | 80.0 | 5.9 | 0.3 | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 18.15 | -341.7 | 135.0 | 2.8 | 0.0 | 175.0 | 0.0 | 0.0 | 90.0 | 44.5 | 0.8 | 44.6 | 5.7 | 0.2 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 18.16 | -1775.6 | 122.9 | 9.7 | 0.1 | 142.4 | 27.3 | 0.1 | 288.0 | 104.2 | 0.0 | 86.4 | 9.2 | 0.3 | 58.3 | 15.1 | 0.1 | 88.5 | 6.9 | 0.3 | 88.7 | 10.3 | 0.1 | NA | NA | NA |
| 19.12 | -5270.8 | 225.2 | 45.4 | 0.0 | 119.3 | 15.1 | 0.1 | 151.6 | 25.9 | 0.1 | 256.0 | 38.1 | 0.0 | 96.6 | 13.1 | 0.3 | 78.8 | 12.4 | 0.3 | 78.0 | 13.5 | 0.0 | 94.1 | 10.5 | 0.1 |
| 19.13 | -2206.8 | 162.2 | 4.9 | 0.0 | 127.5 | 16.3 | 0.1 | 166.0 | 19.0 | 0.2 | 107.8 | 13.7 | 0.2 | 55.4 | 14.5 | 0.3 | 96.7 | 14.5 | 0.1 | NA | NA | NA | NA | NA | NA |
| 19.15 | -1654.1 | 125.5 | 14.6 | 0.2 | 163.4 | 31.2 | 0.1 | 286.0 | 1.5 | 0.0 | 95.2 | 10.0 | 0.2 | 64.2 | 23.4 | 0.3 | 88.7 | 6.4 | 0.1 | 96.0 | 12.1 | 0.0 | NA | NA | NA |
| 19.16 | -2369.8 | 170.0 | 4.3 | 0.0 | 128.7 | 9.6 | 0.1 | 153.5 | 34.3 | 0.3 | 285.8 | 8.0 | 0.0 | 92.0 | 11.5 | 0.0 | 78.7 | 5.2 | 0.1 | 76.0 | 14.1 | 0.1 | 95.3 | 9.8 | 0.4 |
| 19.17 | -2117.5 | 240.0 | 19.4 | 0.0 | 110.0 | 1.6 | 0.1 | 170.2 | 30.7 | 0.0 | 286.8 | 10.6 | 0.0 | 89.9 | 11.8 | 0.2 | 47.6 | 12.5 | 0.3 | 75.0 | 8.3 | 0.1 | 99.1 | 12.0 | 0.3 |
| 20.13 | -2605.4 | 171.8 | 8.8 | 0.1 | 135.5 | 10.0 | 0.3 | 142.1 | 16.8 | 0.0 | 241.8 | 53.4 | 0.0 | 108.8 | 13.6 | 0.2 | 51.2 | 14.5 | 0.2 | 74.0 | 24.5 | 0.0 | 96.1 | 12.9 | 0.3 |
| 20.15 | -1672.5 | 156.0 | 22.6 | 0.0 | 109.7 | 11.4 | 0.0 | 161.5 | 22.0 | 0.3 | 97.2 | 7.8 | 0.5 | 77.8 | 21.9 | 0.1 | 94.0 | 39.1 | 0.1 | 95.6 | 9.4 | 0.0 | NA | NA | NA |
| 20.16 | -3108.5 | 171.5 | 9.2 | 0.0 | 129.1 | 10.9 | 0.1 | 135.7 | 12.5 | 0.1 | 99.1 | 11.7 | 0.1 | 69.8 | 19.9 | 0.0 | 68.0 | 15.1 | 0.2 | 83.4 | 8.4 | 0.5 | NA | NA | NA |
| 21.12 | -2310.7 | 180.2 | 25.1 | 0.0 | 111.1 | 7.0 | 0.3 | 147.1 | 18.3 | 0.2 | 250.0 | 48.8 | 0.0 | 115.2 | 19.2 | 0.1 | 80.0 | 11.7 | 0.1 | 72.7 | 10.5 | 0.3 | 102.7 | 11.5 | 0.0 |
| 21.13 | -1388.1 | 171.0 | 5.7 | 0.0 | 119.9 | 19.0 | 0.0 | 134.2 | 15.2 | 0.2 | 152.0 | 54.3 | 0.3 | 113.6 | 11.0 | 0.2 | 59.6 | 21.9 | 0.0 | 76.4 | 2.2 | 0.2 | 104.2 | 15.2 | 0.1 |
| 21.15 | -3109.7 | 229.2 | 43.9 | 0.0 | 110.7 | 10.5 | 0.0 | 146.3 | 26.4 | 0.0 | 234.2 | 49.0 | 0.0 | 96.8 | 7.0 | 0.0 | 76.7 | 18.7 | 0.0 | 82.6 | 6.9 | 0.8 | 96.7 | 10.9 | 0.0 |
| 21.16 | -2677.4 | 186.8 | 31.5 | 0.0 | 109.2 | 11.3 | 0.0 | 144.6 | 33.2 | 0.0 | 275.3 | 26.1 | 0.0 | 97.2 | 8.6 | 0.3 | 90.4 | 5.3 | 0.3 | 82.4 | 17.6 | 0.0 | 92.3 | 9.5 | 0.3 |
| 22.13 | -2410.3 | 186.3 | 23.6 | 0.0 | 126.3 | 16.0 | 0.0 | 153.6 | 20.3 | 0.2 | 186.9 | 36.2 | 0.1 | 103.2 | 14.3 | 0.6 | 94.6 | 7.4 | 0.1 | 74.8 | 9.2 | 0.0 | 105.8 | 17.0 | 0.0 |
| 22.14 | -1652.7 | 51.1 | 6.3 | 0.3 | 133.3 | 16.6 | 0.1 | 79.7 | 3.5 | 0.0 | 89.6 | 4.0 | 0.3 | 123.3 | 4.1 | 0.0 | 104.3 | 6.2 | 0.3 | 246.6 | 34.4 | 0.1 | NA | NA | NA |
| 22.15 | -1256.0 | 240.9 | 29.7 | 0.0 | 125.8 | 23.0 | 0.1 | 135.0 | 24.0 | 0.2 | 264.3 | 21.0 | 0.0 | 102.3 | 12.9 | 0.0 | 51.7 | 4.6 | 0.0 | 87.0 | 27.9 | 0.0 | 101.2 | 10.0 | 0.7 |

Table S1.7 Fish length distribution fitting. *Continued*

| Survey | loglik | Case 1 | | | Case 2 | | | Case 3 | | | Case 4 | | | Case 5 | | | Case 6 | | | Case 7 | | | Case 8 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | mu1 | sig1 | lam1 | mu2 | sig2 | lam2 | mu3 | sig3 | lam3 | mu4 | sig4 | lam4 | mu5 | sig5 | lam5 | mu6 | sig6 | lam6 | mu7 | sig7 | lam7 | mu8 | sig8 | lam8 |
| 22.17 | -2396.4 | 230.0 | 26.2 | 0.0 | 109.3 | 4.1 | 0.0 | 134.2 | 25.3 | 0.1 | 200.5 | 50.8 | 0.0 | 97.6 | 13.6 | 0.7 | 66.8 | 11.5 | 0.1 | 85.3 | 11.8 | 0.0 | 106.9 | 16.1 | 0.1 |
| 24.17 | -2549.0 | 222.4 | 32.9 | 0.0 | 112.9 | 6.9 | 0.0 | 136.7 | 39.3 | 0.0 | 246.6 | 47.2 | 0.2 | 115.9 | 16.5 | 0.4 | 73.8 | 5.2 | 0.2 | 117.9 | 17.3 | 0.1 | NA | NA | NA |
| 25.12 | -2561.5 | 191.8 | 34.7 | 0.1 | 117.3 | 12.6 | 0.0 | 125.4 | 22.2 | 0.2 | 173.4 | 16.8 | 0.0 | 104.5 | 18.8 | 0.5 | 70.6 | 11.5 | 0.2 | 80.9 | 7.1 | 0.0 | 114.9 | 17.8 | 0.0 |
| 25.15 | -3462.4 | 238.4 | 33.0 | 0.0 | 116.2 | 8.1 | 0.1 | 114.2 | 14.3 | 0.2 | 233.2 | 43.2 | 0.1 | 102.4 | 8.3 | 0.6 | 80.6 | 11.7 | 0.0 | 88.1 | 13.1 | 0.0 | 109.1 | 13.4 | 0.0 |
| 25.16 | -6141.2 | 200.8 | 31.4 | 0.0 | 128.2 | 24.6 | 0.0 | 137.7 | 27.2 | 0.0 | 190.2 | 25.7 | 0.1 | 99.5 | 15.9 | 0.2 | 76.8 | 7.1 | 0.2 | 81.8 | 8.3 | 0.4 | 96.4 | 14.7 | 0.0 |
| 26.13 | -2822.5 | 211.0 | 6.5 | 0.0 | 120.0 | 7.1 | 0.0 | 151.3 | 23.4 | 0.1 | 208.8 | 29.8 | 0.1 | 101.6 | 6.3 | 0.4 | 60.4 | 7.4 | 0.1 | 89.4 | 7.5 | 0.0 | 109.2 | 12.7 | 0.2 |
| 26.14 | -2560.4 | 231.5 | 17.1 | 0.1 | 113.5 | 16.3 | 0.1 | 115.2 | 8.1 | 0.0 | 193.7 | 25.6 | 0.0 | 94.4 | 8.7 | 0.7 | 74.1 | 4.9 | 0.0 | 83.9 | 10.2 | 0.1 | 98.8 | 16.5 | 0.0 |
| 28.17 | -1846.9 | 197.8 | 24.7 | 0.1 | 123.0 | 9.9 | 0.0 | 132.1 | 10.6 | 0.0 | 211.0 | 15.7 | 0.3 | 110.0 | 33.5 | 0.0 | 67.7 | 7.3 | 0.4 | 90.7 | 9.5 | 0.0 | 56.1 | 28.8 | 0.1 |
| 29.16 | -2753.1 | 184.7 | 21.9 | 0.0 | 142.2 | 11.1 | 0.2 | 208.8 | 26.0 | 0.1 | 113.5 | 19.2 | 0.1 | 80.6 | 6.2 | 0.0 | 93.3 | 2.9 | 0.5 | 102.1 | 34.3 | 0.1 | NA | NA | NA |
| 30.12 | -2666.0 | 222.0 | 16.1 | 0.0 | 133.2 | 12.9 | 0.0 | 131.9 | 33.2 | 0.0 | 218.3 | 27.5 | 0.0 | 99.8 | 10.7 | 0.2 | 73.6 | 5.8 | 0.4 | 85.8 | 8.0 | 0.0 | 86.3 | 24.8 | 0.4 |
| 30.13 | -3072.6 | 199.0 | 31.0 | 0.0 | 141.7 | 19.9 | 0.0 | 193.0 | 51.0 | 0.0 | 206.6 | 43.0 | 0.0 | 105.3 | 28.4 | 0.3 | 77.0 | 5.0 | 0.6 | 55.0 | 8.0 | 0.1 | 88.2 | 27.3 | 0.0 |
| 30.15 | -2904.0 | 194.8 | 4.7 | 0.0 | 144.6 | 29.2 | 0.1 | 141.5 | 29.1 | 0.0 | 212.1 | 25.8 | 0.1 | 104.0 | 8.6 | 0.1 | 72.9 | 6.5 | 0.2 | 82.3 | 6.7 | 0.3 | 87.9 | 29.7 | 0.2 |
| 31.14 | -2671.3 | 226.0 | 14.8 | 0.0 | 154.5 | 9.5 | 0.0 | 110.1 | 9.2 | 0.1 | 225.9 | 35.7 | 0.1 | 91.2 | 33.2 | 0.0 | 79.1 | 7.3 | 0.0 | 95.4 | 3.4 | 0.0 | 88.8 | 27.8 | 0.8 |
| 32.17 | -1774.5 | 142.5 | 10.6 | 0.0 | 217.1 | 27.5 | 0.1 | 59.6 | 11.5 | 0.8 | 68.4 | 4.8 | 0.0 | 70.4 | 24.0 | 0.1 | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 34.12 | -2248.4 | 178.9 | 15.8 | 0.0 | 151.4 | 15.5 | 0.0 | 161.0 | 39.1 | 0.2 | 207.6 | 43.2 | 0.0 | 74.4 | 20.9 | 0.3 | 86.1 | 4.9 | 0.3 | 56.5 | 28.8 | 0.0 | 102.4 | 21.6 | 0.3 |
| 34.16 | -1472.9 | 116.0 | 23.2 | 0.2 | 193.7 | 42.8 | 0.0 | 60.5 | 7.3 | 0.8 | 101.8 | 29.6 | 0.0 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 35.13 | -527.0 | 191.0 | 49.5 | 0.0 | 164.9 | 8.4 | 0.1 | 71.3 | 11.5 | 0.4 | 107.5 | 19.1 | 0.5 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 35.14 | -1312.6 | 215.6 | 28.6 | 0.1 | 147.6 | 32.9 | 0.4 | 205.3 | 33.9 | 0.0 | 69.4 | 17.9 | 0.5 | 88.2 | 5.4 | 0.0 | 92.2 | 30.6 | 0.0 | NA | NA | NA | NA | NA | NA |
| 35.15 | -298.7 | 262.0 | 22.7 | 0.0 | 62.8 | 18.6 | 0.6 | 81.2 | 7.3 | 0.1 | 79.2 | 27.2 | 0.3 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 37.17 | -1497.3 | 132.0 | 32.4 | 0.0 | 144.0 | 6.3 | 0.0 | 168.0 | 81.0 | 0.0 | 61.9 | 8.3 | 0.1 | 71.9 | 16.8 | 0.3 | 99.1 | 28.6 | 0.5 | NA | NA | NA | NA | NA | NA |
| 38.15 | -394.5 | 104.0 | 24.6 | 0.0 | 137.5 | 16.3 | 0.1 | 65.7 | 5.6 | 0.6 | 56.0 | 27.1 | 0.1 | 69.7 | 2.1 | 0.1 | 91.8 | 30.8 | 0.0 | NA | NA | NA | NA | NA | NA |
| 38.16 | -1174.2 | 187.3 | 31.5 | 0.1 | 200.0 | 11.1 | 0.0 | 77.3 | 7.5 | 0.6 | 47.3 | 3.0 | 0.0 | 50.1 | 10.4 | 0.0 | 81.2 | 14.9 | 0.2 | NA | NA | NA | NA | NA | NA |
| 39.12 | -2686.6 | 181.9 | 7.1 | 0.0 | 117.6 | 23.4 | 0.1 | 125.0 | 22.8 | 0.0 | 169.1 | 16.9 | 0.1 | 88.0 | 6.9 | 0.5 | 96.0 | 4.6 | 0.2 | 35.6 | 3.6 | 0.0 | 94.1 | 17.1 | 0.1 |
| 39.13 | -1461.4 | 195.0 | 7.1 | 0.0 | 104.1 | 3.3 | 0.5 | 150.4 | 27.8 | 0.0 | 177.9 | 23.6 | 0.1 | 78.9 | 17.5 | 0.2 | 86.8 | 16.2 | 0.0 | 59.8 | 10.9 | 0.2 | 96.5 | 16.8 | 0.1 |
| 40.14 | -1697.3 | 118.4 | 8.1 | 0.1 | 177.6 | 33.0 | 0.3 | 176.8 | 29.3 | 0.0 | 77.4 | 8.2 | 0.5 | 44.8 | 13.8 | 0.2 | 58.9 | 13.5 | 0.0 | 92.0 | 20.8 | 0.0 | NA | NA | NA |

Table S1.7 Fish length distribution fitting. *Continued*

| Survey | loglik | Case 1 | | | Case 2 | | | Case 3 | | | Case 4 | | | Case 5 | | | Case 6 | | | Case 7 | | | Case 8 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | mu1 | sig1 | lam1 | mu2 | sig2 | lam2 | mu3 | sig3 | lam3 | mu4 | sig4 | lam4 | mu5 | sig5 | lam5 | mu6 | sig6 | lam6 | mu7 | sig7 | lam7 | mu8 | sig8 | lam8 |
| 41.17 | -2279.7 | 117.0 | 11.3 | 0.0 | 182.1 | 26.6 | 0.2 | 171.0 | 6.9 | 0.0 | 74.4 | 6.1 | 0.2 | 81.8 | 19.9 | 0.0 | 59.5 | 13.2 | 0.1 | 85.7 | 12.7 | 0.4 | NA | NA | NA |
| 42.16 | -1836.9 | 139.5 | 27.6 | 0.0 | 185.9 | 19.6 | 0.3 | 157.5 | 0.7 | 0.0 | 84.2 | 13.8 | 0.1 | 43.8 | 11.3 | 0.1 | 73.1 | 16.9 | 0.1 | 98.3 | 17.8 | 0.3 | NA | NA | NA |
| 43.13 | -1257.2 | 124.8 | 19.9 | 0.2 | 155.0 | 4.3 | 0.0 | 193.0 | 0.0 | 0.0 | 87.5 | 11.8 | 0.2 | 47.9 | 10.8 | 0.2 | 60.3 | 13.9 | 0.1 | 93.1 | 20.8 | 0.4 | NA | NA | NA |
| 43.15 | -872.1 | 165.0 | 27.7 | 0.0 | 112.5 | 13.0 | 0.2 | 177.5 | 25.7 | 0.1 | 89.0 | 9.1 | 0.0 | 84.1 | 25.9 | 0.1 | 60.7 | 13.8 | 0.0 | 86.0 | 14.0 | 0.6 | NA | NA | NA |
| 44.14 | -1236.2 | 119.9 | 5.6 | 0.1 | 160.0 | 59.5 | 0.0 | 158.0 | 1.4 | 0.0 | 79.3 | 8.8 | 0.4 | 59.8 | 18.3 | 0.1 | 66.5 | 10.1 | 0.2 | 95.1 | 17.7 | 0.2 | NA | NA | NA |
| 45.13 | -642.0 | 116.6 | 9.6 | 0.1 | 146.1 | 29.6 | 0.0 | 190.0 | 9.3 | 0.0 | 111.8 | 19.5 | 0.0 | 90.4 | 12.6 | 0.3 | 69.3 | 9.7 | 0.2 | 90.8 | 22.9 | 0.3 | NA | NA | NA |

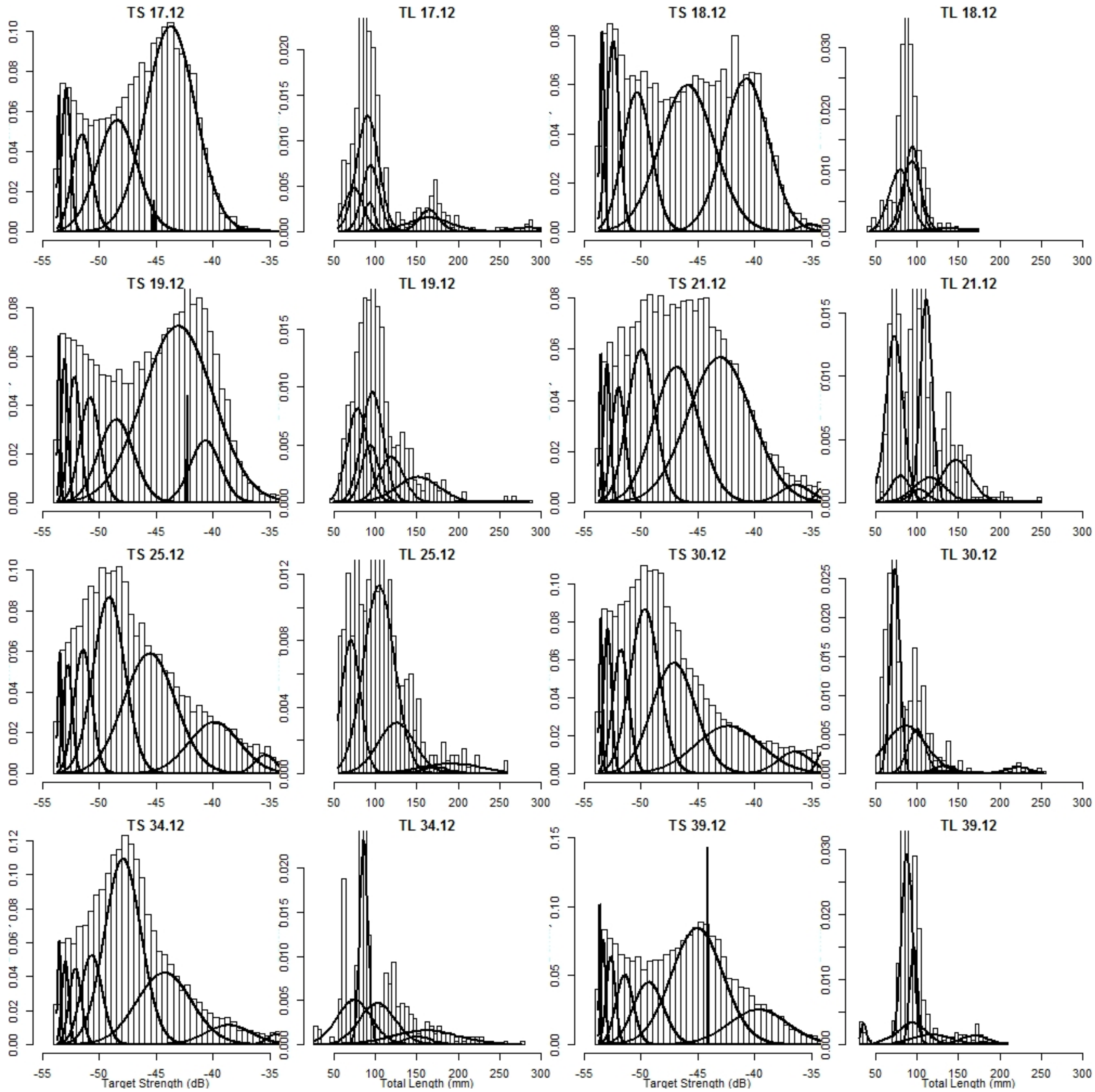


Figure S1.7 Acoustic and trawl survey size frequencies. Target strength (TS, dB) and fish length (TL, mm) density histograms (bars) with fitted normal functions (lines) from expectation maximization fitting algorithm for each species-size case for each survey in the Penobscot Estuary. Note each plot is labeled with TS or TL and the week and year in WW.YY format.

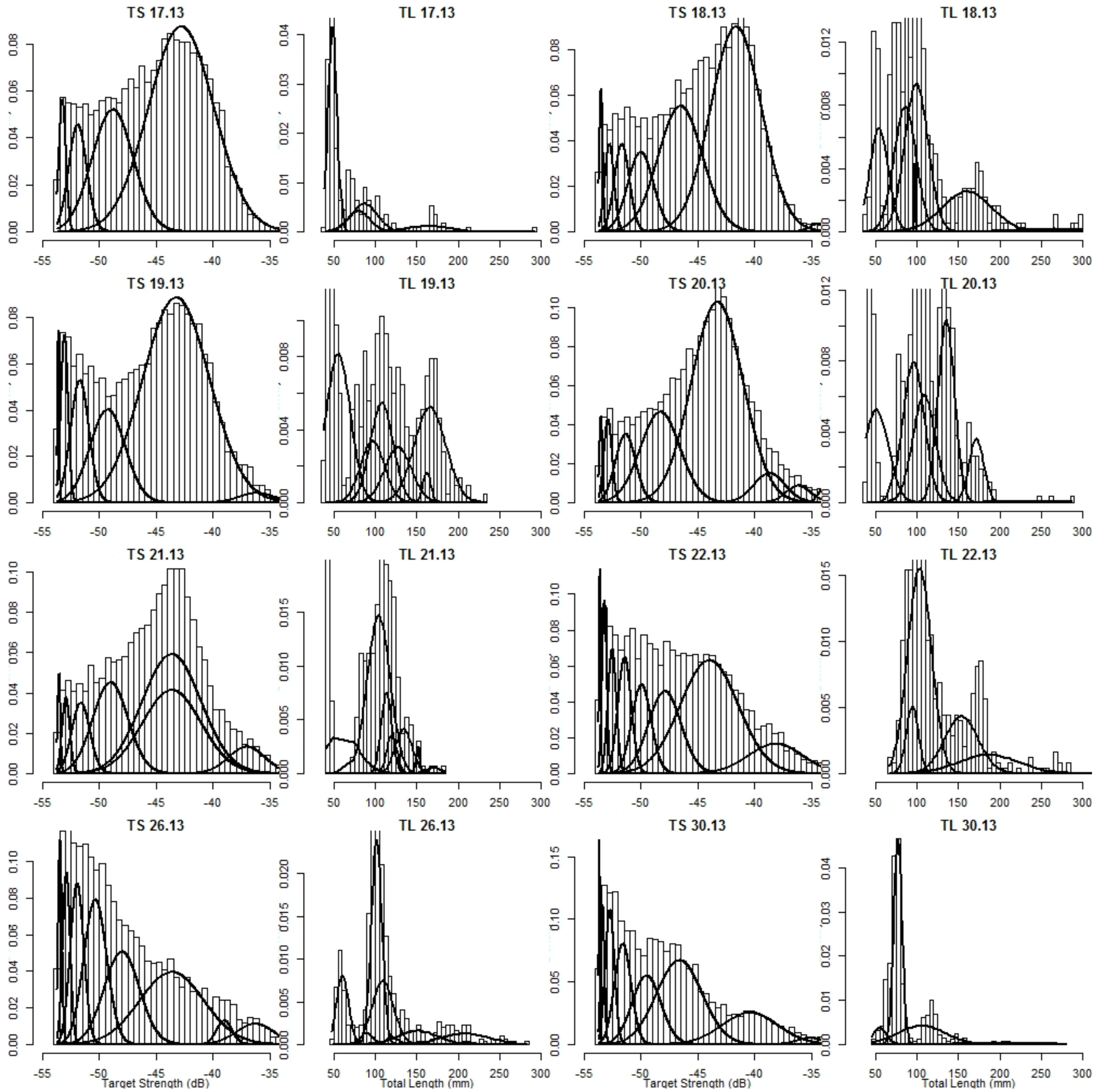


Figure S1.7 Acoustic and trawl survey size frequencies. *Continued*

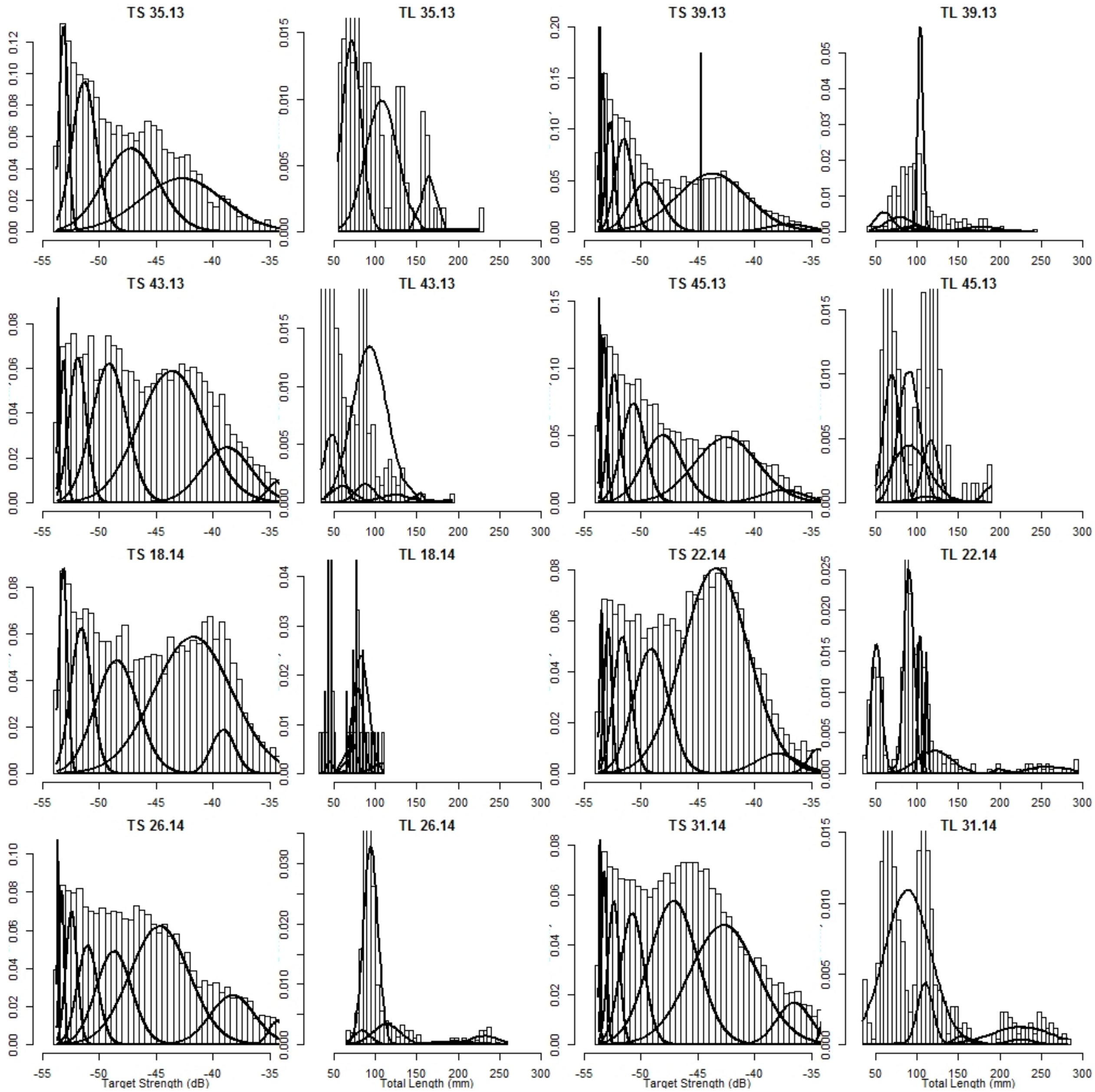


Figure S1.7 Acoustic and trawl survey size frequencies. *Continued*

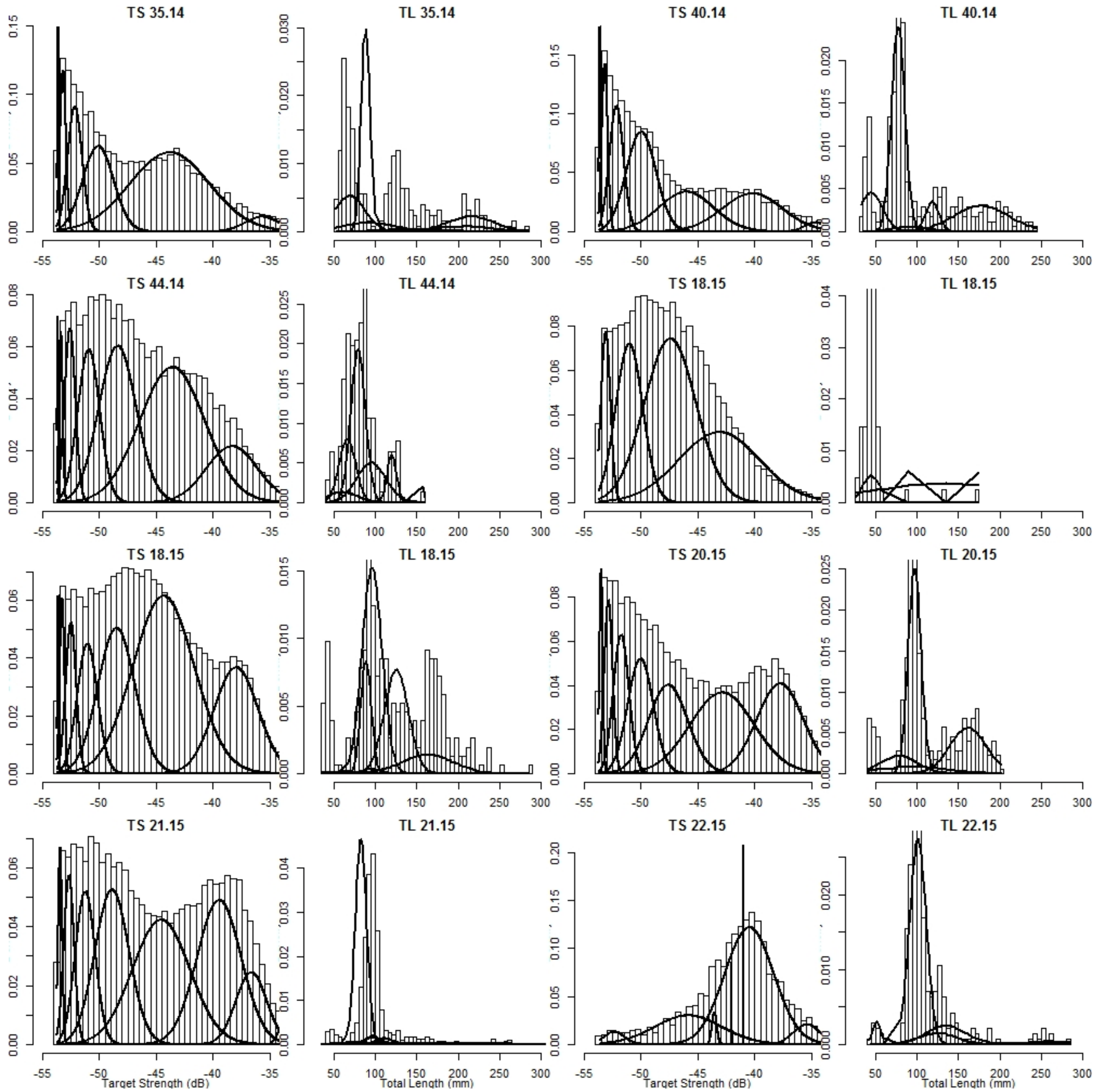


Figure S1.7 Acoustic and trawl survey size frequencies. *Continued*

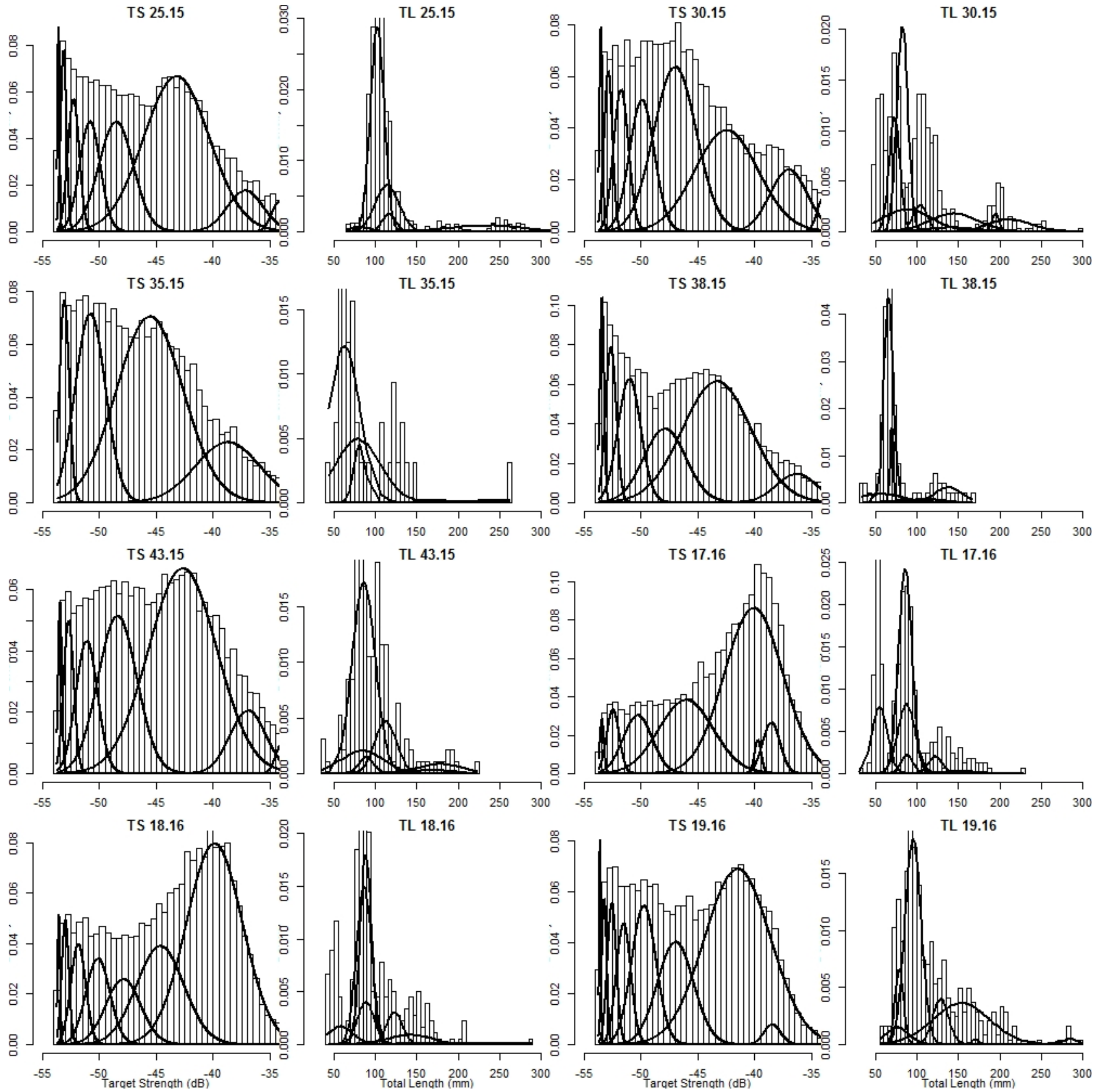


Figure S1.7 Acoustic and trawl survey size frequencies. *Continued*

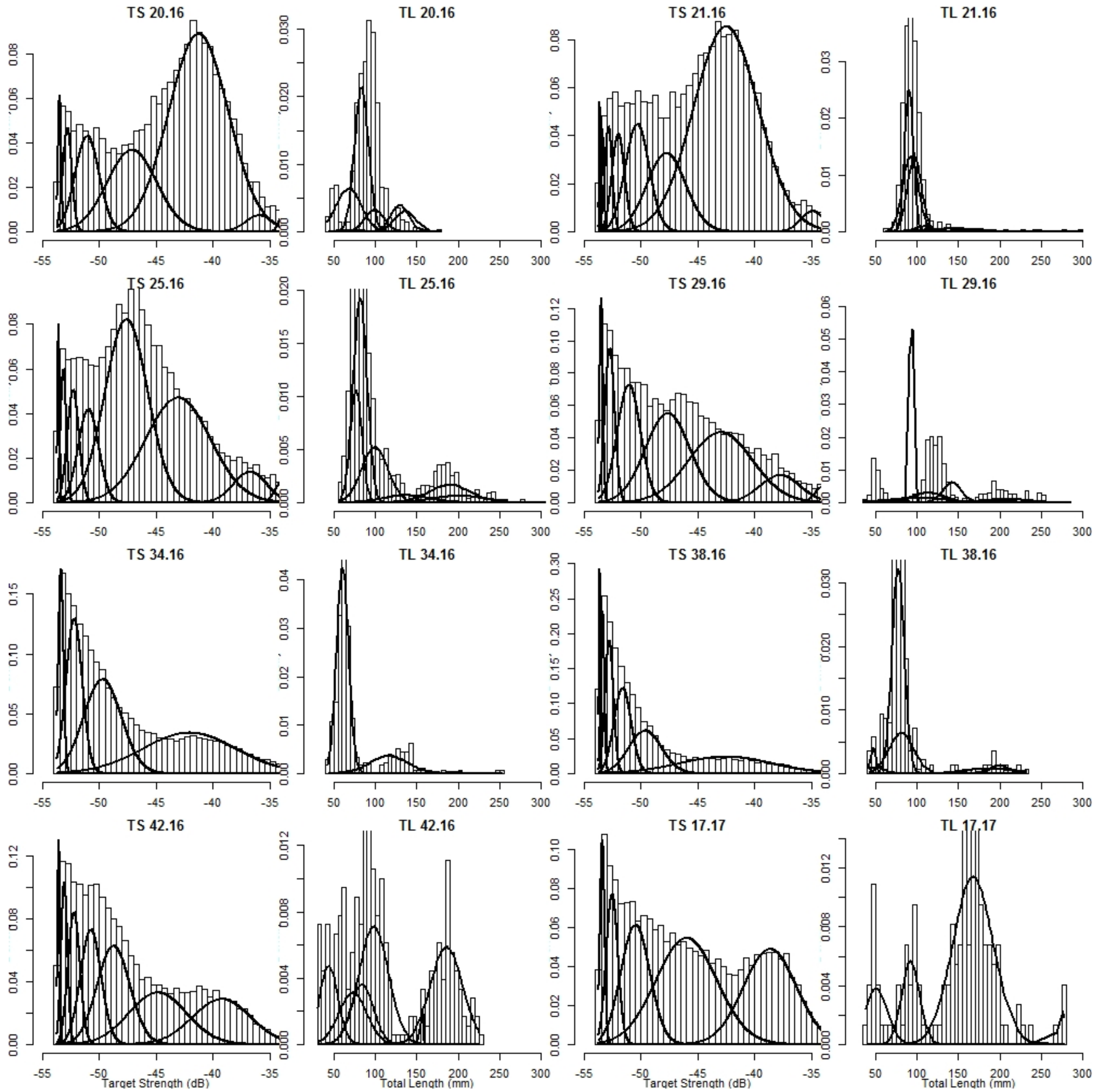


Figure S1.7 Acoustic and trawl survey size frequencies. *Continued*

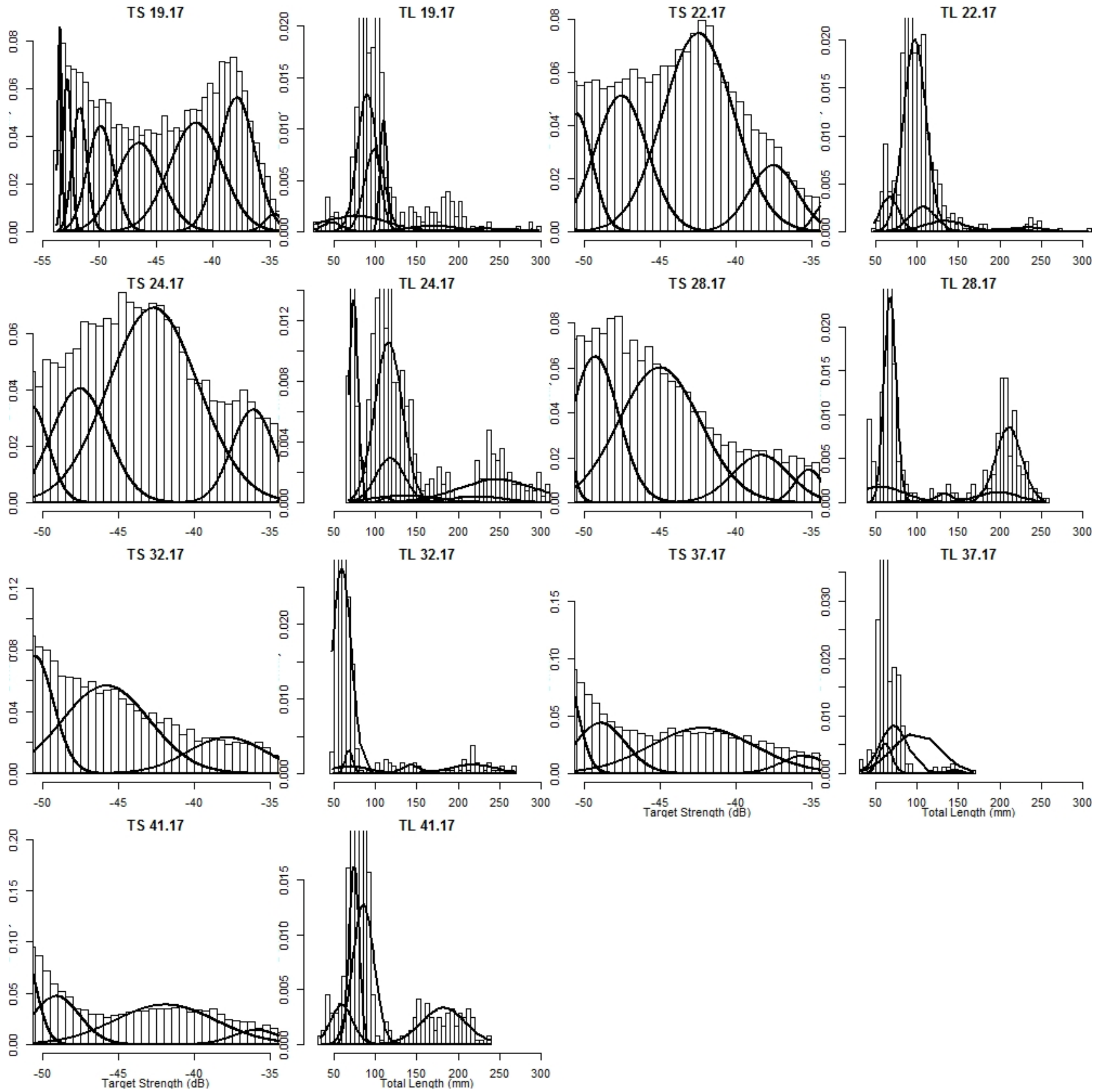


Figure S1.7 Acoustic and trawl survey size frequencies. *Continued*

## CHAPTER TWO

# 2 RESPONSE OF ESTUARINE FISH BIOMASS TO RESTORATION IN THE PENOBSCOT RIVER, MAINE

## 2.1 Abstract

Diadromous fish require both freshwater and marine habitat to complete their life cycle. Dams restrict the movement between these habitats and as a result, many populations are historically low across their range. The Penobscot River is the second largest river in Maine and once had large populations of diadromous fish and it has been the focus of mainstem dam removals, dam passage improvements, and stocking with the goal of restoring those populations. Since 2012, NOAA Fisheries has conducted surveys of the Penobscot Estuary using mobile, multi-frequency echosounders (SIMRAD EK60 split-beam 38 and 120 kHz) combined with mid-water trawl surveys to construct a time series of fish distribution to assess this large-scale restoration. We used system-specific parameters to compute biomass from acoustic survey data. We assessed seasonal estimates of biomass from 2012 to 2017 a period spanning pre-restoration (2012-2014) and post-restoration (2015-2017). Biomass varied with season and year and was generally greater in summer and in post-restoration years. Biomass in pre-restoration years ranged from 9,000 to 114,000 kg per survey and 11 of 45 (23%) surveys had biomass greater than 50,000 kg. Compared to post-restoration years ranged from 23,000 to 316,000 kg per survey and 34 of 43 (76%) surveys had biomass greater than 50,000 kg. Changes in biomass were observed with changes in fish length and density where higher density resulted in higher biomass. During pre-restoration, fish density was high in relatively less area of the estuary when compared to the large area of moderate to high density during post-restoration. Similarly, fish size was generally larger post-restoration than pre-restoration in spring and summer and smaller in fall. This analysis demonstrates the utility of hydroacoustics in monitoring large-system restoration by describing multiple metrics in a complex ecosystem. The changes observed by increased density and biomass are indications that river restoration is changing the ecology of the estuary.

## 2.2 Introduction

Diadromous fish provide a number of ecological processes due to their abundant, seasonal migrations to complete their life cycle and the resulting transport of nutrients among freshwater and marine ecosystems (Hall et al. 2012). For example, Alewife *Alosa pseudoharengus* and Blueback Herring *Alosa aestivalis* (collectively “river herring”) spawning migrations from the sea to inland lakes and streams provided large pulses of marine-derived nutrients before dams were widespread (Hall et al. 2011). Sea Lamprey *Petromyzon marinus* provide two-way transport of energy during their semelparous lifecycle (Weaver et al 2018). Juvenile migrations from freshwater to the ocean may have provided forage for nearshore groundfish (Ames 2004; Ames and Lichter 2013, McDermott et al. 2015) and Striped Bass *Morone saxatilis* (Hartman 2003). Some species physically alter habitat by moving substrate to build nests (Hogg et al. 2014). Finally, the suite of diadromous fish species co-evolved and may provide inter-specific synergy necessary for successful populations. For example, adult river herring buffering predation of Atlantic Salmon *Salmo salar* smolts (Saunders et al 2006) or Sea Lamprey carcasses subsidizing nutrients available to juvenile Atlantic Salmon (Guyette et al. 2014). Unfortunately, dams restrict or prevent the natural movement between habitats and have contributed to historically low diadromous fish populations across their ranges (Limburg and Waldman 2009).

The Penobscot River is the second largest river in New England (USA) and is the focus of large-scale habitat improvements due to its large fisheries production potential and relatively low habitat fragmentation (Martin and Apse 2011). The goal of the restoration is to increase diadromous fish populations to naturally sustainable levels near what existed in “pre-dam” eras through dam removal and passage improvements (Day 2006). Diadromous fish populations numbered in the 10’s of millions for River Herring to 10’s of thousands for Atlantic Salmon in the 1880’s (Saunders et al. 2006). The restoration began with the removal of two lower-mainstream dams in 2012 and 2013, a new fish-lift type fishway at the lowermost dam in 2014, and a nature-like bypass of a third mainstem dam in 2016. In addition, the implementation of the State of Maine sea-run fisheries management plan included stocking river herring into various lakes to “seed” the population and jumpstart restoration began in 2010 (MDMR and MDIFW 2009).

Palmer et al. (2005) suggested that assessment and dissemination of results is a necessary component of determining ecological success for restoration projects. The success and assessment of outcomes of river restoration projects can be difficult to calculate due to disparity of data and reporting, lack of monitoring, or poorly defined objectives (Bernhardt et al. 2005). In contrast, the Penobscot restoration had a monitoring plan that was implemented prior to restoration beginning in 2010 (T. Sheehan, NOAA Fisheries, Pers. comm.). Monitoring results have demonstrated some early successes of the restoration with catches of diadromous fish at dams with fish-ways. River Herring counted at these dams have increased from less than 200,000 annually in 2012 to 2014 to nearly 2 million annually in 2015 to 2017 (MEDMR 2018; M. Simpson, Maine Department of Marine Resources, Pers. comm.). Watson et al. (2018) found fish assemblage dynamics have changed in the mainstem river post-dam removal with less abundant slow-water specialist species and more access for anadromous species. Changes were also detected in smaller tributaries with native freshwater and diadromous species recolonizing habitat shortly after barrier removal (Gardner et al. 2013; Hogg et al. 2015).

Most of the Penobscot River restoration monitoring is focused on conditions in freshwater, however the estuary is an important habitat and data collected there may provide evidence of unique responses to upriver restoration. The Penobscot estuary provides a logical location to monitor changes in diadromous fish populations since it is the common habitat for migrating fish (inland or seaward). Since 2012, NOAA Fisheries has conducted surveys of the Penobscot Estuary using mobile, multi-frequency echosounders (Simrad EK60 split-beam 38 and 120 kHz systems) combined with concurrent mid-water trawl surveys. Scientific echosounders are used to quantify fish over large areas and acoustic/trawl surveys are widely used in fisheries assessments around the world (Simmonds and MacLennan 2005). Data derived from split-beam transducers can also be used to acoustically characterize individual fish targets for example, mean target strength (TS, dB re 1 $m^2$) is used to scale acoustic energy to numeric density and with corresponding biological data can subsequently estimate abundance and biomass

(Simmonds and MacLennan 2005). The NOAA acoustic/trawl surveys provide a baseline of pre-restoration pelagic fish abundance (acoustics) and length distribution (trawl) in the Penobscot River Estuary (O'Malley et al. 2017). In addition, they proposed that the Penobscot River NOAA survey could be used to measure ecological processes by quantifying the timing and magnitude of fish density measured acoustically as volume backscatter ($s_A$ $m^2$ $m^{-2}$, MacLennan et al. 2002).

Acoustic data can be converted to fish length via generalized equations (e.g. Foote 1987). The relationship of TS to fish length (e.g., total length, TL) has been empirically derived from experiments with several fish species and can be described by the equation $TS = \alpha \log_{10} (TL) - \beta$ (Simmonds and MacLennan 2005). TS varies depending on the anatomy and morphology of the fish as well as the angle of the fish relative to the beam (Love 1971). For conventional conversion of acoustic data in voltage units (e.g. dB) to biomass in biological units (e.g. kg), proper characterization of fish length is necessary to extrapolate acoustic volume backscatter to areal fish density (number/$m^2$) and by determining average size to finally calculate biomass (kg of fish) (Simmonds and MacLennan 2005). Fish of the Penobscot estuary have been characterized in terms of species and length composition (O'Malley et al. 2017; Chapter one) and both of these metrics vary seasonally and annually.

In Chapter one, we evaluated several modelling methods to generate a relationship between TS and TL. These models parameters were uniquely derived for this system to allow calculation of total biomass from acoustic survey data. Our goals were to use the parameters derived using the mid-water trawl surveys coupled to acoustic surveys to characterize patterns in the fish distribution (size and density) of the Penobscot River Estuary during the period from 2012 to 2017. This time series spans the dam removals in 2012 and 2013 and observed increases in upriver counts of river herring in 2015 to 2017. Our hypotheses are that increases in diadromous fish populations accomplished through river restoration activities should be evident in the estuary through increases in fish biomass as derived from acoustic data. In addition, our goal was to describe temporal patterns in the components of fish biomass, density and size, for changes coincident to river restoration. For fish density, we evaluated acoustic backscatter in

Nautical Area Scattering Coefficient (NASC; $m^2$ $nmi^{-2}$) and trawl CPUE while for fish size we evaluated TS (dB re 1 $m^2$) and trawl length frequencies.

## 2.3 Methods

### 2.3.1 Study Area.

The Penobscot covers an area of 22,000 $km^2$ and has an annual average discharge of 400 $m^3$ $s^{-1}$. The estuary begins at the head of tide in Bangor, Maine and extends approximately 150 km to the seaward end of Penobscot Bay in Rockland, Maine (NOAA SEAB 1985). The river discharge combined with a 3 - 4 m tidal range creates a dynamic physical environment with complex patterns of mixing and circulation (Haefner 1967; Geyer et al. 2018). For this study, we focused on the approximately 50 km long stretch of river that extends from tidal freshwater in Bangor, Maine to the end of the tidal mixing zone near Stockton Springs, Maine (NOAA SEAB 1985). The acoustic and trawl survey data were collected from the area of the estuary where the channel depth was generally greater than 6 m and width was less than 2 km (Figure 1.1). The acoustic path covered the entire 50 km distance and the trawl stations were distributed systematically along the lower two-thirds of the acoustic transect. The area without overlap was characterized as having generally low fish density (O'Malley et al. 2017).

### 2.3.2 Acoustic Survey Data

We analyzed split-beam acoustic data collected from 2012 to 2017 following the survey design in O'Malley et al. (2017) and Lipsky et al. (2019). Simrad EK60 120 and 38 kHz spit-beam transducers were positioned 0.5 m below the water surface via a pole attached to a skiff. Acoustic data were collected along a 50 km continuous zigzag path crisscrossing the channel with fixed waypoints along the estuary. Each survey was completed in one day during flood tide and daylight hours. Surveys were conducted at 7 to 14 day intervals during ice free months, typically April through October. Survey frequency was increased in spring months to coincide with the timing of most diadromous species spawning migrations. The echo sounders were calibrated monthly using a 38.1-mm tungsten carbide with 6% cobalt binder sphere as a standard target. Calibration was conducted within the Simrad ER60 Lobe software and echosounder parameters, $s_A$ correction and gain, were updated when residual root-mean-square (RMS) between the observed and modeled data were less than 0.4 following manufacturer recommendations (https://www.simrad.com/ek60#documentation). Acoustic data were processed using Echoview version 8.0 (Echoview Software Pty Ltd. 2018). Processing steps are outlined in O'Malley et al. (2017) but in summary, raw signal data were filtered to isolate backscatter ($s_A$) of fish from other biota using dB differencing (38 – 120 kHz) methods (McKelvey and Wilson 2006). The differenced $s_a$ ($m^2$ $m^{-2}$) was scaled to unit area, $s_A$ to Nautical Area Scattering Coefficient [NASC; $m^2$ $nmi^{-2}$] (MacLennan et al. 2002) and was integrated for 500 m which we refer to as our elemental distance sampling units (EDSU) as defined by Simmonds and MacLennan (2005) along the transect for each survey.

We used Echoview 'method 2' for single target detections (STDs) with settings in Table 1.2 (Echoview Software Pty Ltd. 2018). This algorithm utilizes the angular data from the split-beam echosounders to compensate TS with respect to the target position in the acoustic beam combined with other criteria to eliminate overlapping pulses resulting in those expected to be from single targets. We utilized the *Fish Track* module of Echoview to determine STDs that were likely from single fish from the 38 kHz transducer. The tracking algorithm grouped pings into single fish observations (fish tracks) using an alpha-beta filtering method from Blackman (1986) combined with various acceptance criteria in Table 1.3 related to time and physical distance of sequential pings to detect tracks (Bertsekas 1990; Echoview Software Pty Ltd. 2018). From the detected fish tracks, we extracted mean TS for each fish track with multiple STDs for computations and are hereafter simply referred to as the TS. We applied a lower threshold of -65 dB for subsequent TS analysis corresponding to fish ~3 cm which were the smallest individuals caught in the trawl so we were confident that our estimates were of fish and not smaller biota. We applied an upper threshold of -15 dB corresponding to fish ~120 cm to eliminate the potential for erroneous single target measurements to bias biomass estimates as fish this size are infrequent in this system (Watson et al. 2018).

### 2.3.3 Trawl Survey Data

We analyzed catch, length, and weight data collected from midwater trawl hauls as documented in Lipsky et al. (2019). The trawl was a surface-oriented trawl which was used to sample 8 fixed locations for 10 minutes at speeds of 2 - 4 knots. The 11 m wide by 6 m high net was towed during the flood tide and surveys were conducted on the same (2012 and 2013) or subsequent (2014-2017) days as the acoustic survey. Catch was enumerated by species and a subsample was measured for total length (mm) and weight (g). Catch per unit effort was calculated as number of fish captured per km towed. See Lipsky et al. (2019) for more detail of acoustic and trawl sample design and methods.

### 2.3.4 Data Analysis

For seasonal comparisons, we determined International Standard Organization (ISO) standard week of year for each sampling date and defined week 13 to 24 as spring, 25 to 33 as summer, and 34 to 49 as fall. We summarized catch and length data from trawl hauls to characterize species composition, length, and relative abundance in catch-per-unit-effort (CPUE). Length distributions were derived from the length samples from a subset of catch and extrapolated to total catch. Acoustic data were summarized for TS (proxy for length), $s_A$ (proxy for density), and acoustically derived biomass estimates. We derived biomass for each 500 m EDSU by the following set of calculations.

First, we determined the mean backscattering cross section ($\bar{\boldsymbol{\sigma}}_{\boldsymbol{bs_i}}$, m$^2$) by converting the mean TS values (dB scale) to linear scale for each EDSU with equation 2.1.

Equation 2.1 $$\bar{\boldsymbol{\sigma}}_{\boldsymbol{bs_i}} = \frac{\mathbf{1}}{\boldsymbol{n}}\sum \mathbf{10}^{\boldsymbol{TS_{i,}/10}}$$

Where $TS_i$ is n target strength values for a given EDSU, $i$. In cases where $n$ < 10, we substituted a survey specific global mean, $\bar{\boldsymbol{\sigma}}_{bs_g}$, calculated from all targets on that survey ($\bar{\boldsymbol{\sigma}}_{bs_g}$ = 4.079373e-05 m$^2$) to prevent areas with large densities but few targets detected from biasing the system biomass computation as suggested by Horne and Jech (1999).

Next, we converted the acoustic areal density, $s_A$ (m$^2$ nmi$^{-2}$) to fish density, $\rho_a$ (fish m$^{-2}$) with the $\bar{\boldsymbol{\sigma}}_{\boldsymbol{bs_i}}$ from equation 1 for each EDSU with equation 2.2.

Equation 2.2 $$\boldsymbol{\rho_{a,i}} = \left[\boldsymbol{s_{A,i}}/\left(\mathbf{4\pi} \times \bar{\boldsymbol{\sigma}}_{\boldsymbol{bs_i}} \times 1852^2\right)\right]$$

Then, we computed the mean total length ($\bar{L}_i$, cm) per EDSU by converting $\boldsymbol{\bar{\sigma}}_{\boldsymbol{bs_i}}$ from equation 1 to TS and applying the system specific regression parameters for TS to L from Chapter 1 ($TS = 31.0\ \log_{10} L\ -\ 79.5$) with equation 2.3.

Equation 2.3 $$\boldsymbol{\bar{L}_i = 10^{\frac{\left(10(\log_{10}(\overline{\sigma}_{bs_i})\right)+79.5}{31.0}}}$$

Then, we computed the mean weight ($\boldsymbol{\overline{W}_i}$, kg) as determined by equation 2.4.

Equation 2.4 $$\boldsymbol{\overline{W}_i = a\bar{L}_i^b\ \times\ 0.001}$$

Where a = 0.00391 and b = 3.162 from the total length (cm) – weight (g) regression coefficients estimated from trawl data (described below) and estimated from the equation with parameters derived from this system in Chapter 1 and scaled to kilograms.

Finally, total biomass ($B_T$, kg km-2) was calculated using equation 2.5.

Equation 2.5 $$\boldsymbol{B_T = \sum_i \rho_{a,i} \times \bar{w}_i \times A_i}$$

Where density $\boldsymbol{\rho_{a,i}}$ from equation 2, average weight, $\boldsymbol{\bar{w}_i}$ from equation 3, and area, $\boldsymbol{A_i}$ of each of 105 EDSUs (i) in the survey were multiplied and resulting values summed to compute total biomass. We assumed the area representing each EDSU was ~152,000 $m^2$ or 1/105th of the approximately 1.6 e+7 $m^2$ study area (O'Malley et al. 2017).

We used Type III sums of squares ANOVA to determine if significant change had occurred in any of the metrics: biomass, acoustic density, trawl density (CPUE), trawl length means over time using year and season as dependent factors in the linear model. We used post-hoc pairwise comparisons of least-squares (LS) means using Tukey HSD (Honest Significant Difference) to evaluate at the $\alpha = 0.05$ level which groups were statistically different. Because of the variable shaped distributions for TS, we used a cluster analysis of two-sided Kolmogorov–Smirnov test results to evaluate the similarity of distributions over the time series. All statistical and graphical analyses were conducted in R Studio version 1.0.15, R (R Core Team 2018) version 3.5.1 (2018-07-02) -- "Feather Spray" Platform: x86_64-w64-mingw32/x64 (64-bit) (R Core Team 2018).

## 2.4 Results

### 2.4.1 Acoustic Biomass

We used the trawl data to determine length-weight regression parameters needed for computing biomass estimates from acoustic data. We selected 2,046 measurements of individuals with total length (TL; cm) and weight (W; g). We estimated the coefficients in the equation 2.6

Equation 2.6 $$\log_{10}(W) = a\ \log_{10}(TL)^{b}$$

using least-squares linear regression and found strong significant relationship ($p < 0.001$, residual standard error = 0.1314, n = 2,062 degrees of freedom, adjusted R-squared = 0.9035, and F-statistic = 0.00019; Figure 2.1). The regression parameters, a = -5.544 and b = 3.162 were used to estimate weight from length of fish determined by acoustic measurements (TS) by converting from $\log_{10}$ to linear units such that $W = 0.00391 * TL^{3.162}$.

We calculated biomass as the product of average fish density and weight which we then summed for all EDSUs in each transect. Biomass estimates varied by season and year and ranged from 9,000 to 316,000 kg throughout the time series (Figure 2.2; Table 2.1). We observed the highest biomass in summer surveys in all years except 2015 when the highest biomass was seen in early spring. Biomass in pre-restoration years ranged from 9,000 to 114,000 kg per survey and 11 of 45 (23%) surveys had biomass greater than 50,000 kg. Compared to post-restoration years ranged from 23,000 to 316,000 kg per survey and 34 of 43 (76%) surveys had biomass greater than 50,000 kg (Table 2.1). Biomass for a survey followed similar seasonal patterns as acoustic density such that higher biomass surveys also had higher mean NASC. In some cases however, large differences were evident such as surveys during weeks 24 and 26 in 2017 when mean NASC was nearly equal, ~900 $m^2$ $nmi^{-2}$ however biomass was 80,000 kg and 110,000 kg respectively (Figure 2.2; 2.6).

An ANOVA of biomass was significant, $R^2$= 0.61, F (17, 70) = 6.44, p= <.001 with season and year explaining significant variability in fish biomass (Table 2.2). The Tukey analysis revealed the LS means of most groups (season and year) were not significantly different (Figure 2.3; Table S2.3). For spring, 2012 - 2014 and 2016 - 2017 were not significantly different but 2015 was different having the largest LS mean biomass of ~150,000 kg. In summer, 2012 was significantly different than 2017, but the remaining years the LS means were not detectably different. For fall, LS means were not significantly different in 2012 – 2017 except for 2013 which was the lowest mean for the time series.

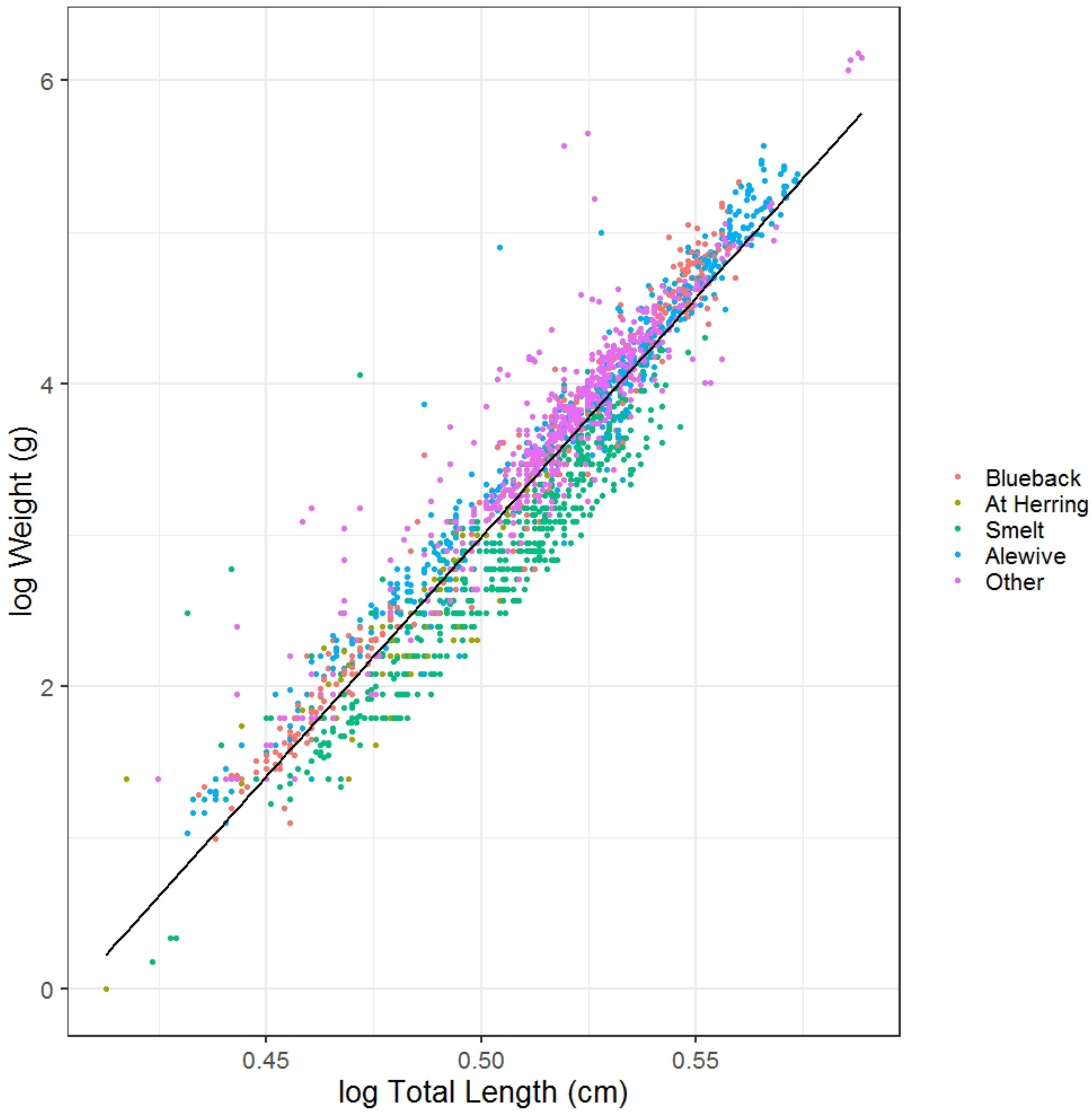


Figure 2.1 Trawl length to weight regression. Log total length plotted as a function of weight (dots) and least squares regression fit (line) for individual fish measured during trawl events 2012-2017 in the Penobscot River Estuary. The Least Squares fit, Log Weight = 3.162* Log TL -2.408, R2 = 0.9035, was used to estimate weight based on length of fish detected in acoustic surveys.

Table 2.1 Acoustic biomass. Acoustically derived biomass (kg) calculated for surveys 2012-2017 in the Penobscot River Estuary.

| Week | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 |
|---|---|---|---|---|---|---|
| 13 | 30,834 | | | | | |
| 14 | | 43,603 | | | | |
| 15 | 35,590 | | | | | |
| 16 | 21,634 | 27,958 | | | | |
| 17 | 23,668 | 12,562 | 34,711 | 277,511 | 23,407 | 51,054 |
| 18 | 11,886 | 15,694 | 38,400 | 152,295 | 77,908 | |
| 19 | 26,495 | 11,796 | | 199,841 | | 70,761 |
| 20 | | 25,386 | 46,131 | 121,329 | 40,951 | 56,415 |
| 21 | | 16,932 | | 159,579 | | |
| 22 | 36,874 | 9,061 | 60,982 | 90,174 | 54,897 | 51,782 |
| 23 | | | | 63,629 | | |
| 24 | | 19,009 | | | | 135,489 |
| 25 | 47,361 | | 55,725 | 68,683 | | |
| 26 | | 14,087 | 50,512 | | 72,498 | 114,236 |
| 27 | 30,418 | | | | | |
| 28 | | 65,804 | | 171,205 | 209,626 | 316,281 |
| 29 | | | 90,202 | | | |
| 30 | 79,347 | 85,188 | | 141,598 | 133,251 | 95,907 |
| 31 | | | 114,950 | | | |
| 32 | | 102,877 | | 76,800 | 104,774 | 110,966 |
| 33 | 42,121 | | 32,173 | | | |
| 35 | | 23,308 | 51,061 | 52,667 | 116,759 | 177,049 |
| 36 | | | | 65,105 | | |
| 37 | | 25,174 | | | 100,990 | 145,296 |
| 38 | | | 33,390 | 37,529 | | |
| 39 | | 18,904 | | | 34,522 | 94,938 |
| 40 | | | 58,601 | | | |
| 41 | | | | | 36,581 | 76,968 |
| 42 | | | 18,536 | | | |
| 43 | | 22,229 | | 48,410 | 36,220 | |
| 44 | | | 28,793 | | | |
| 45 | 22,206 | 15,663 | | 31,958 | | |
| 47 | 19,635 | | | | | |
| 49 | | | | 38,803 | | |

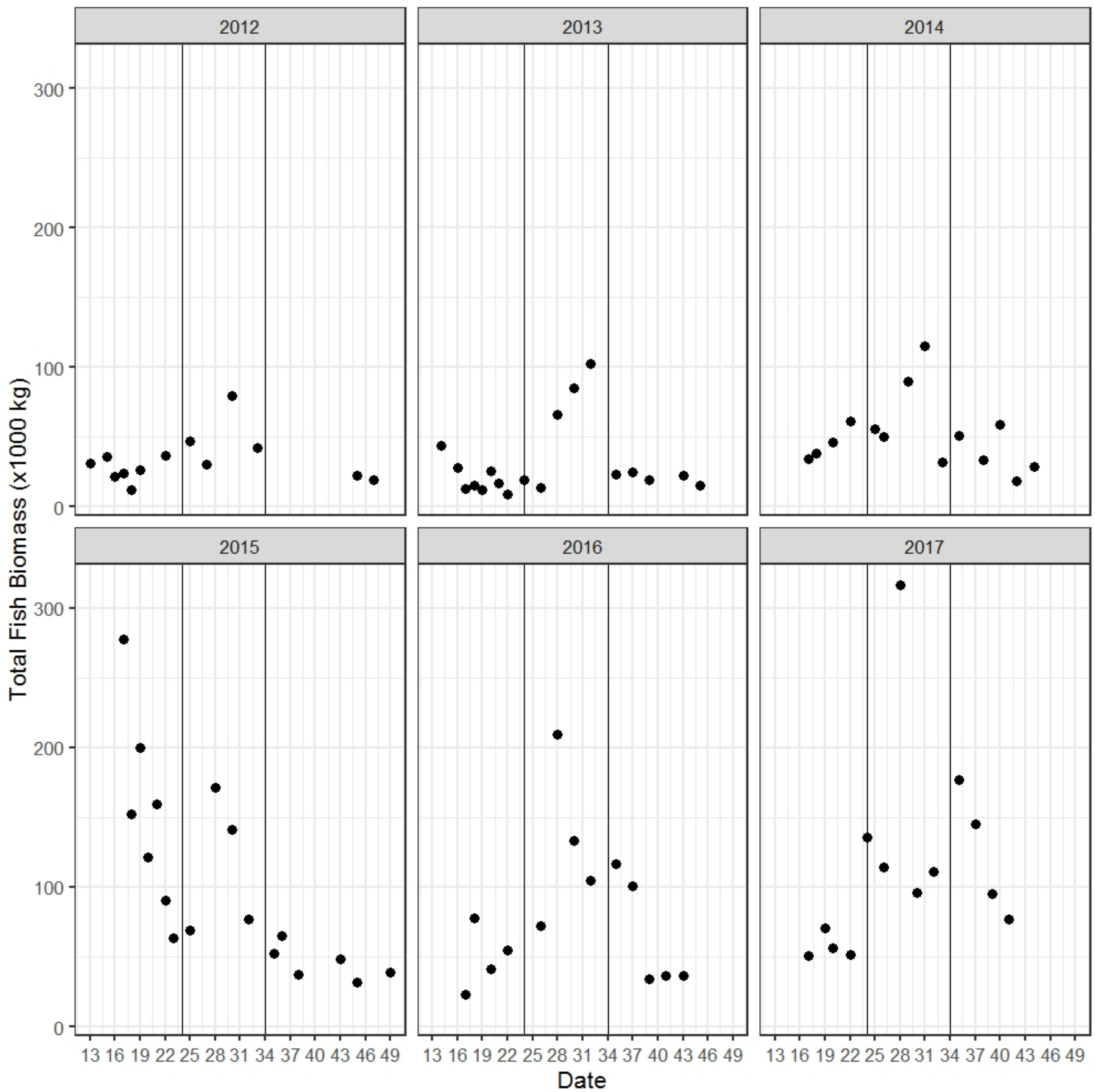


Figure 2.2 Acoustically derived fish biomass. Acoustically derived fish biomass (kg) of fish calculated from seasonal survey data 2012 to 2017 in the Penobscot River Estuary.

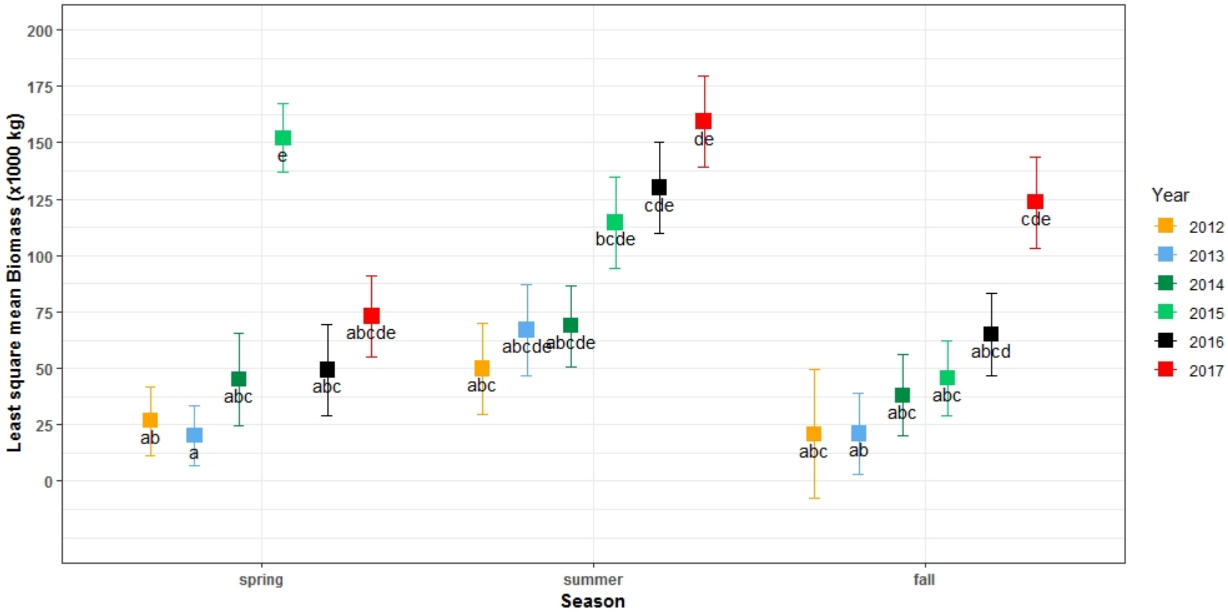


Figure 2.3 Seasonal mean biomass. Least square means with computed standard error bars and Tukey HSD test significance (letters) for temporal groups for acoustic biomass derived from survey data 2012 to 2017 in the Penobscot River Estuary. Tukey HSD letters indicate the degree of overlap of confidence intervals between measurements where groups sharing letters are not significantly different at the 0.05 level.

### 2.4.2 <u>Fish Density</u>

Fish density, inferred from NASC, generally followed a seasonal trend with higher median and higher variability (greater range) for surveys as spring progressed and peak density observed in summer with decreasing values in fall. The exception was in 2015 when the greatest survey median was observed in week 19 (Figure 2.4). Generally, median NASC was less than 750 $m^2$ $nmi^{-2}$ during pre-restoration years 2012 through 2014, however in post-restoration years 2015 through 2017 NASC was greater than 1000 $m^2$ $nmi^{-2}$ (Figure 2.4). Variability as indicated by the interquartile range, was generally greater in summer of all years except in spring 2015. In periods of higher overall density, fish density was higher in more areas of the study area. The median NASC was consistently lower than the mean indicating a left-hand skewed distribution with a majority of EDSU having low values (Figure 2.4).

An ANOVA for acoustic density revealed that year and season predict a significant amount of variance mean sA, $R^2$= 0.58, F (17, 70) = 5.73, p= <.001. Further, year and season were both significant effects (*p*= <.001) with the interaction only slightly so (p=0.0498; Table 2.2). The Tukey test identified several significant different groups with the largest LS mean was observed in spring 2015, and 2012-13 significantly different than (lower) than other years. LS mean in summer was significantly different for two groups, 2012-14 and 2015-2017. LS mean in fall was greatest in 2017 with 2012-2013, 2014, 2015, 2016 and 2017 differing significantly (Figure 2.5; Table S2.3).

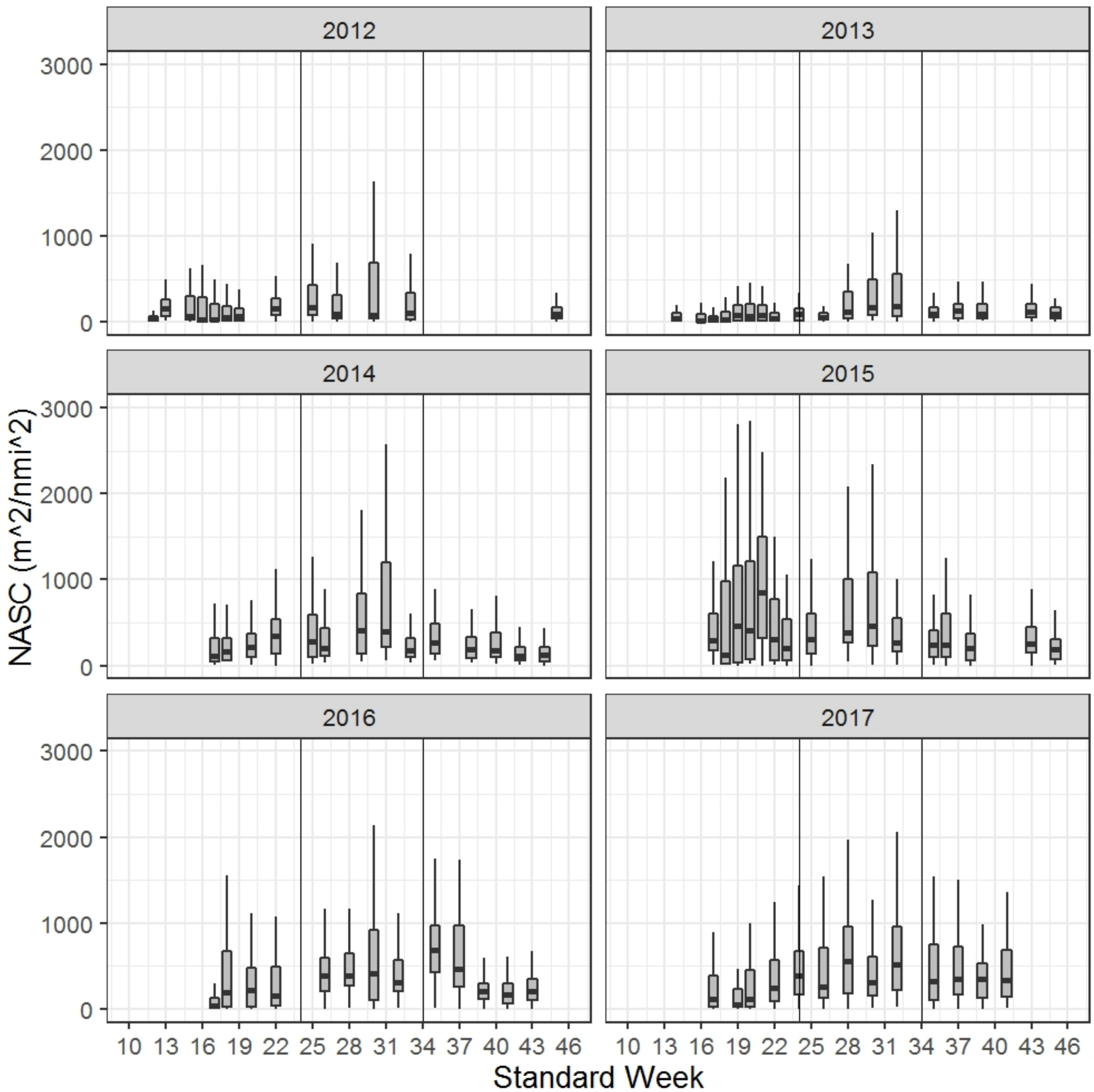


Figure 2.4 Fish density plots. Boxplot (box = 25-75%, line = median, whiskers = 1.5 times IQR) of values of sA (38 kHz - 120 kHz) for 500 m sections by standard week for surveys conducted from 2012 to 2017 in the Penobscot River Estuary. Vertical lines at week 24 and 34 represent seasonal breaks of spring, summer, and fall referenced in analysis. Note: outlier values have been removed from display for clarity.

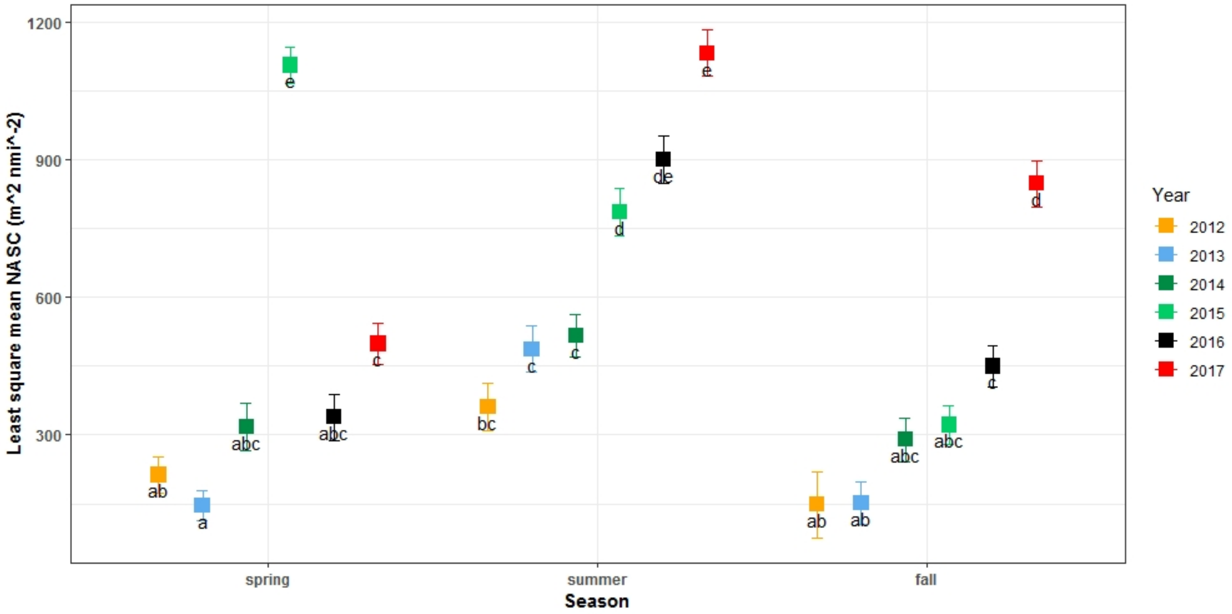


Figure 2.5 Seasonal mean acoustic density. Least square means with computed standard error bars and Tukey HSD test significance (letters) for temporal groups for acoustic density measured by NASC ($m^2$ $nmi^{-2}$) derived from survey data 2012 to 2017 in the Penobscot River Estuary. Tukey HSD letters indicate the degree of overlap of confidence intervals between measurements where groups sharing letters are not significantly different at the 0.05 level.

Trawl catch-per-unit (km) generally followed the density patterns observed with acoustics with some exceptions. As with NASC, the highest median survey CPUE was generally in late spring to early summer and annual lows observed early and late in the year. However, the highest median survey CPUE for the time series was observed in spring 2016 as opposed to spring 2015 for acoustics (Figure 2.6). Similar to the acoustic densities, the median trawl CPUE was lower than mean CPUE for all sample days indicating relatively few high value data points in the study area for a given survey.

An ANOVA of Trawl CPUE was significant, $R^2$= 0.07, F (17, 402) = 1.89, p= 0.017, but factors of year and season did not explain most of the variability in CPUE with season being the only significant parameter (*p*= <.001) (Table 2.2; Figure 2.7). The Tukey test did not reveal any significantly different groups.

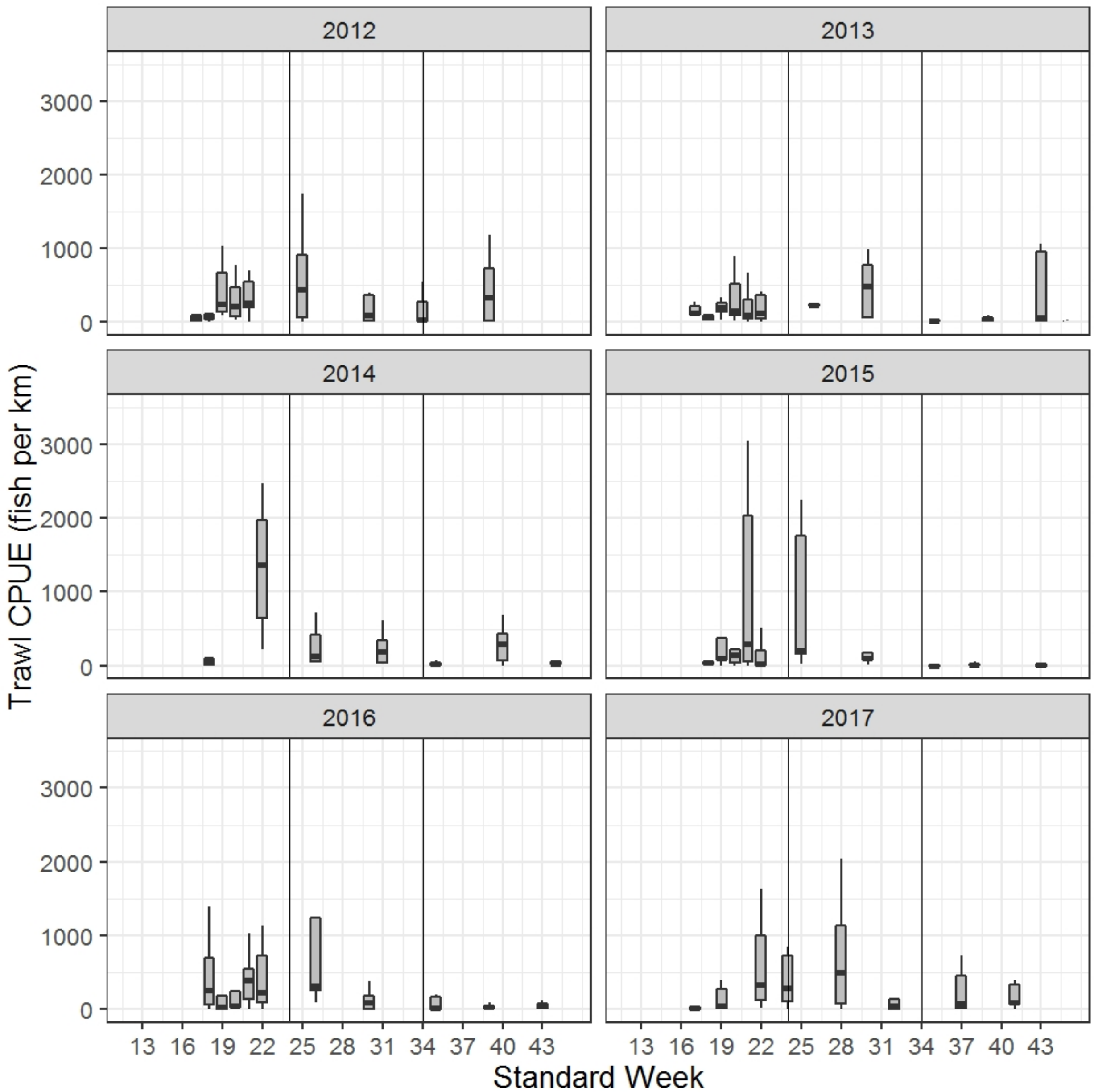


Figure 2.6 Trawl CPUE plots. Boxplot (box = 25-75%, line = median, whiskers = 1.5 times IQR) of trawl catch-per-unit-effort (CPUE) standardized by kilometers towed in the Penobscot River Estuary by standard week from 2012 to 2017. Vertical lines at week 24 and 34 represent seasonal breaks of spring, summer, and fall referenced in analysis. Note: outlier values have been removed from display for clarity.

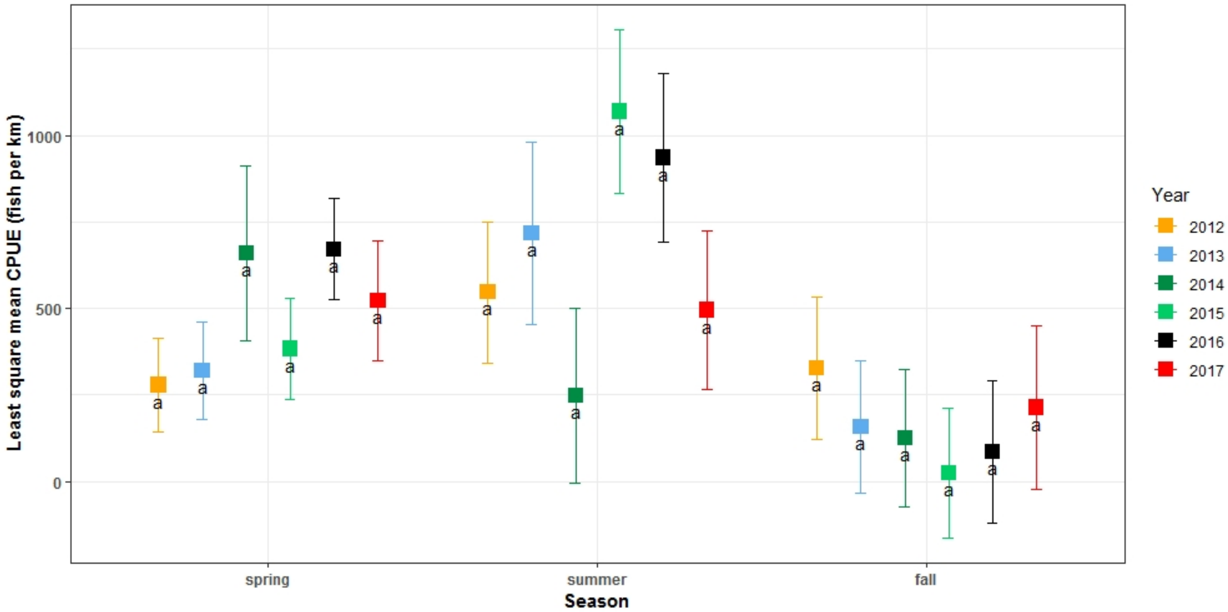


Figure 2.7 Seasonal mean density from trawling. Least square means with computed standard error bars and Tukey HSD test significance (letters) for temporal groups for acoustic density (top) measured by $s_A$ (NASC, $m^2$ $nmi^2$) and trawl CPUE (bottom) measured by fish per km derived from survey data 2012 to 2017 in the Penobscot River Estuary. Tukey HSD letters indicate the degree of overlap of confidence intervals between measurements where groups sharing letters are not significantly different at the 0.05 level.

### 2.4.3 Fish Length

Fish length inferred from acoustic measurements (TS) were generally greater in spring compared to summer and fall in each year (Figure 2.8). Highest mean TS in spring was generally near - 45 dB, corresponding with fish ~11 cm, compared to summer when mean TS was -55 dB (~4 cm). The variation in TS was large for most surveys regardless of season or year with the interquartile range covering over 10 dB, which is over an order of magnitude and equates to ~8 cm range in fish length. In fall, there was an increase in mean TS compared to summer in all years except 2012.

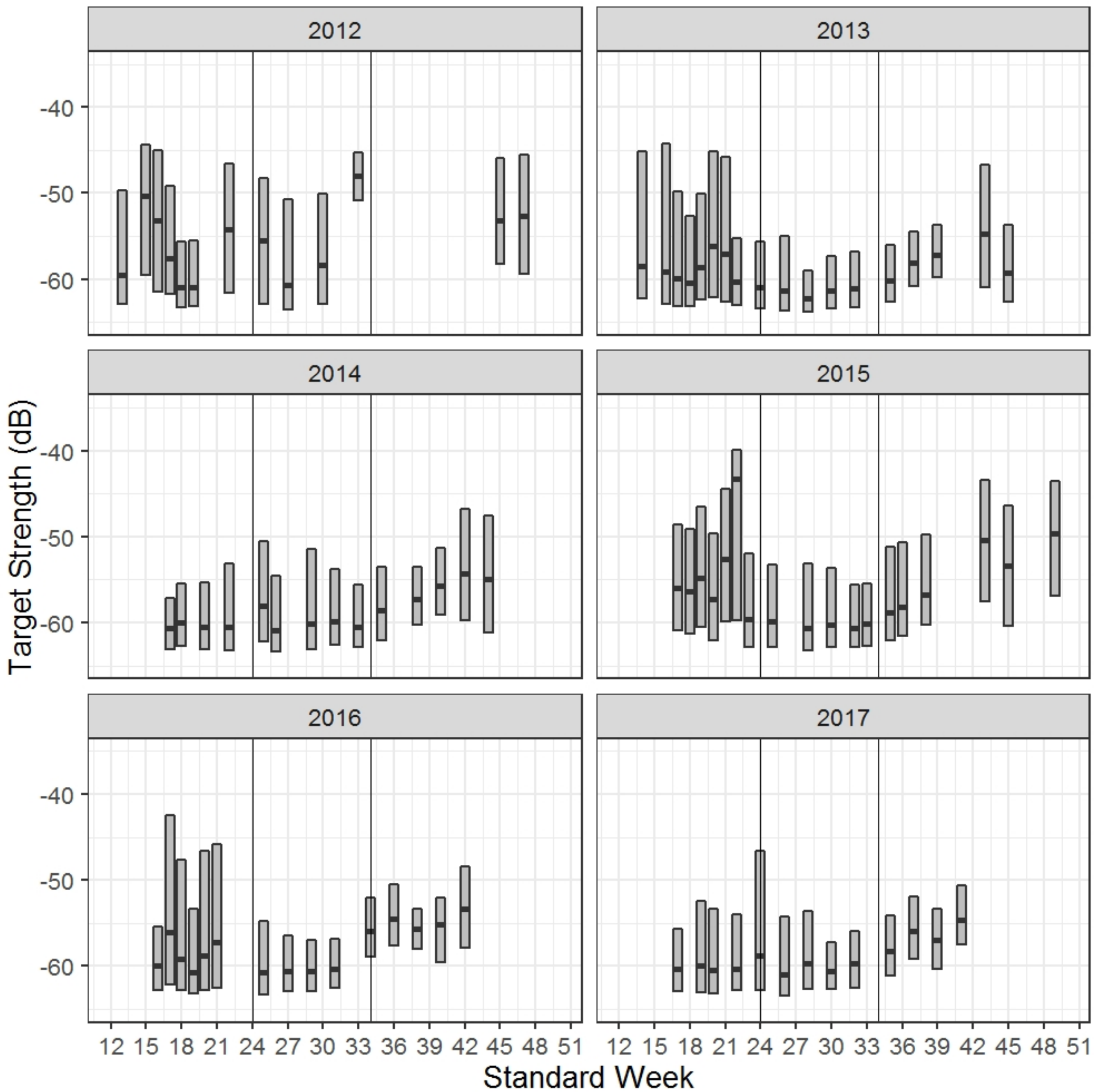


Figure 2.8 Target strength plots. Boxplot of acoustic target strength (TS) measurements from surveys during 2012 to 2017 in the Penobscot River Estuary with box representing 25-75 percentile and the horizontal bar the median value. Vertical lines at week 24 and 34 represent seasonal breaks of spring, summer, and fall referenced in analysis. Note: outlier values and whiskers have been removed from display for clarity.

Four species were consistently caught in the trawl: Alewife, Blueback Herring, Rainbow Smelt *Osmerus mordax*, and Atlantic Herring *Clupea harengus*. Length frequency analysis indicated that multiple age classes of each species were present in the estuary. In most seasons and years the smallest mode of the length distribution was near 5 cm and was from Atlantic Herring followed by a mode near 10 cm from juvenile Alewife and/or Blueback Herring, and then multiple modes from 12 to 25 cm from Smelt and adult Blueback and Alewife (Figure 2.9). The largest fish captured in the trawl were 30 cm and these larger fish were rare (< 1 % of the catch by abundance) in all years and seasons. Juvenile Atlantic Herring comprised a large component of fish caught in all seasons of 2012 and 2013 and spring of each year but were less frequent in summer and fall in 2014-2017. Conversely, adult herring were a very small component of the trawl catches throughout the time series when compared to juvenile Cludeids. Adult River herring were relatively more common in 2014-2017 but mostly in summer surveys (Figure 2.9).

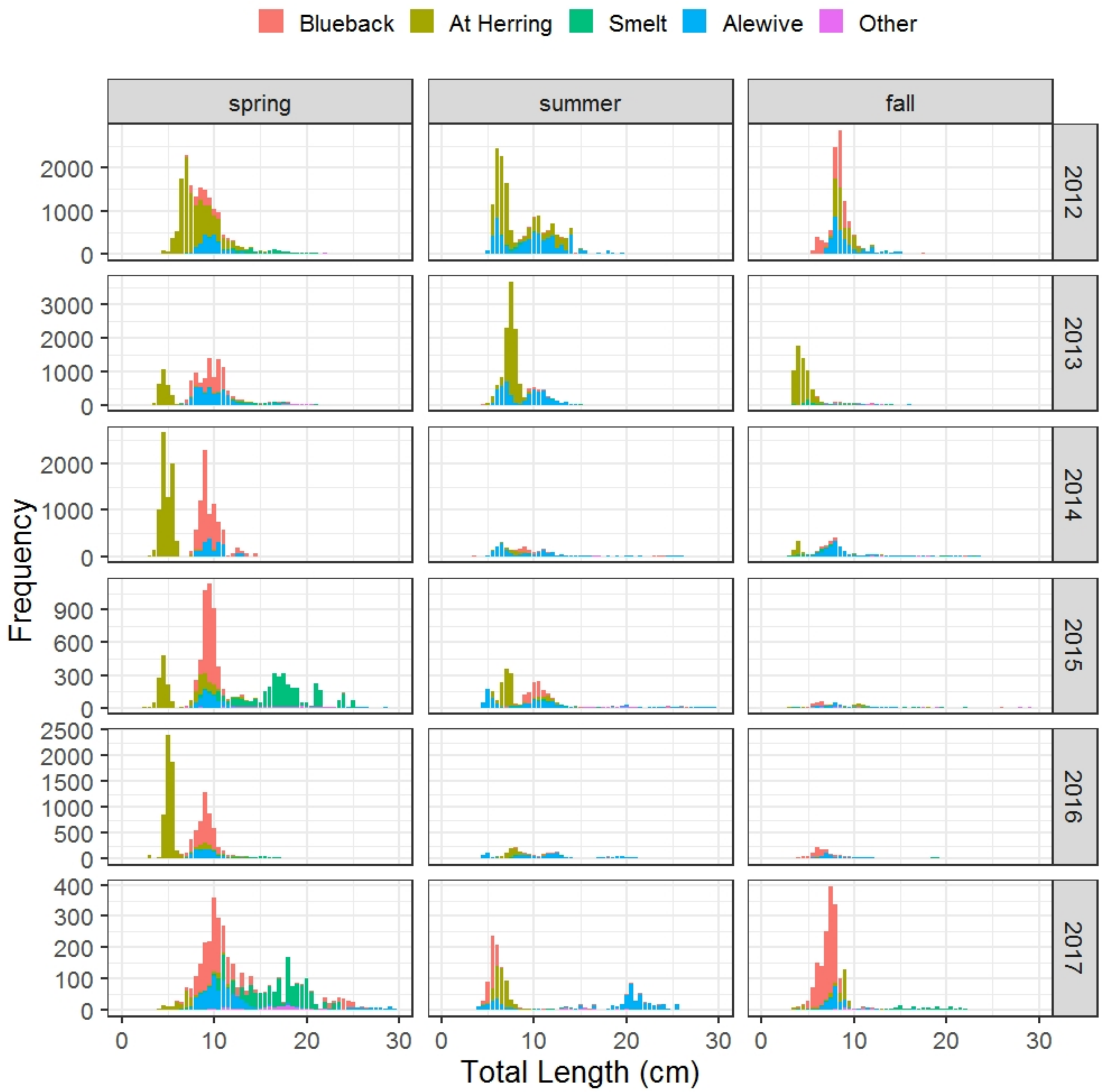


Figure 2.9 Trawl length frequency. Length frequency distributions for predominant species captured in Penobscot Estuary trawls by season and year. Note y-axis scale differs between years.

A cluster analysis of TS distributions, using two-sided KS test as measure of similarity, had 6 groups with KS statistic D > 0.3 indicating that the distributions come from different populations (Simmonds and MacLennan 2005). These clusters revealed temporal patterns of TS distribution through the time series. The first, grouping generally included surveys from spring and summer (groups A, B, C) and fall (groups D, E, F) (Figure 2.10). Group ‘A’ and ‘B’ indicate similarity of size distributions for spring surveys from pre-restoration (A) as compared to post-restoration (B) surveys.

The ANOVA of trawl length was significant, $R^2$= 0.03, F (17, 25555) = 46.28, p= <.001, but season and year poorly explained variability in fish length (Table 2.2). The Tukey analysis revealed most groups (season and year) were significantly different (Figure 2.11; Table S2.3). The largest LS mean length in spring was in 2017 whereas the largest LS mean in fall was in 2012. Overall, the results do not suggest any inter-seasonal trend (increase or decrease) for fish length in spring but a general increase in summer and decrease in fall.

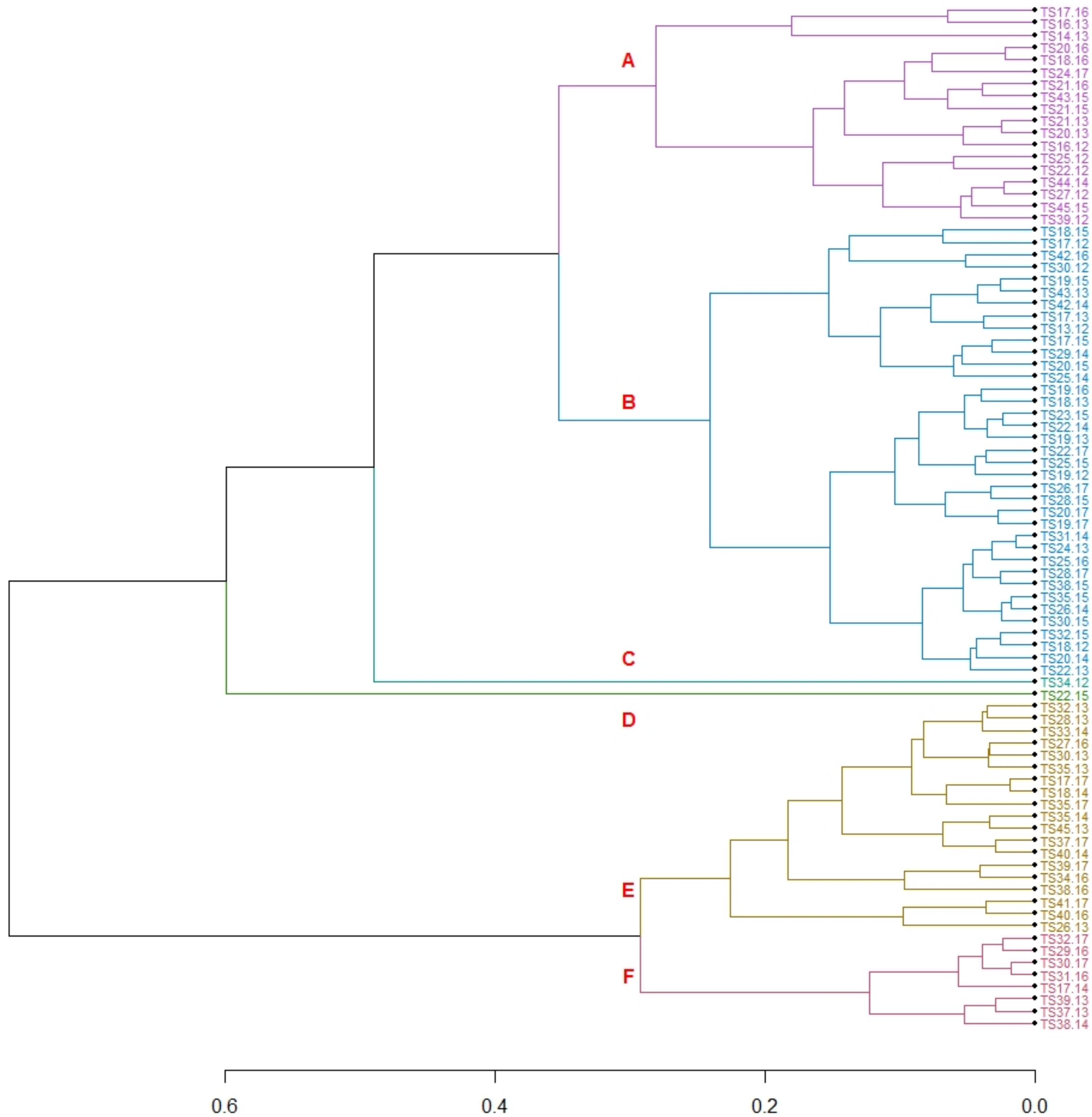


Figure 2.10 Target strength cluster analysis. Dendrogram of two-sided Kolmogorov–Smirnov test result statistic (D; y-axis) of acoustic target strength (TS) distributions for surveys conducted 2012 to 2017 in the Penobscot River Estuary with example length frequencies from each of 6 major clusters (inset; A:F).

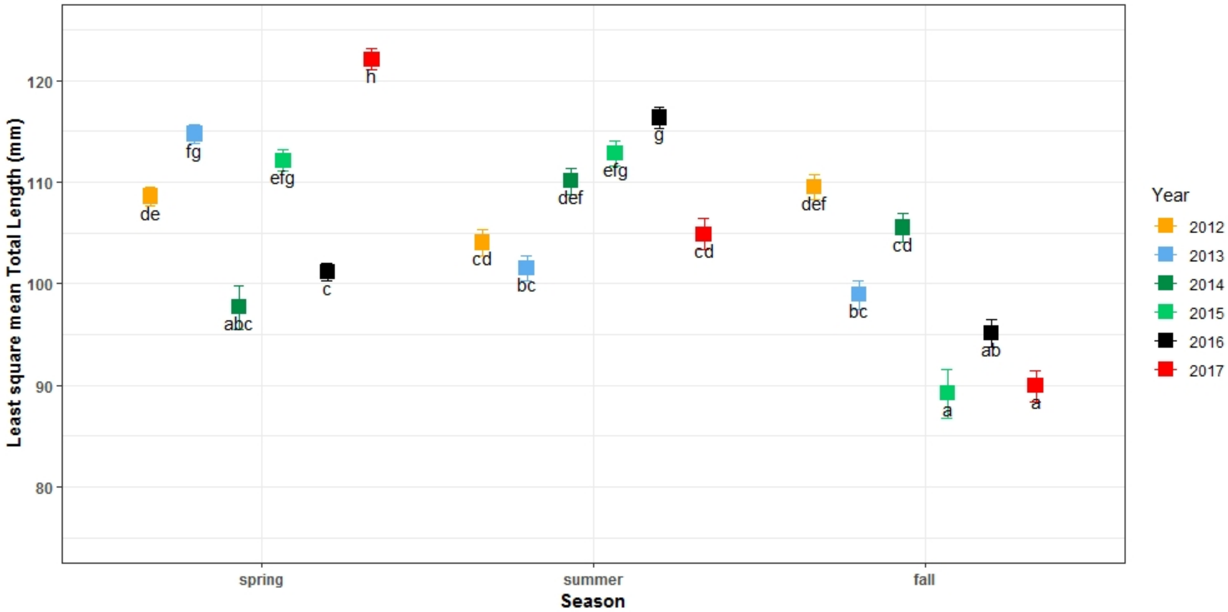


Figure 2.11 Seasonal mean fish length from trawling. Least square means with computed standard error bars and Tukey HSD test significance (letters) for temporal groups for fish size measured and trawl length (mm) and derived from survey data 2012 to 2017 in the Penobscot River Estuary. Tukey HSD letters indicate the degree of overlap of confidence intervals between measurements where groups sharing letters are not significantly different at the 0.05 level.

Table 2.2 ANOVA results. Results of ANOVA modelling response metrics of biomass, acoustic density, trawl CPUE, trawl length, acoustic size with Year and Season effect terms for differences from the Penobscot River Estuary surveys 2012-2017.

| Response variable | Model $R^2$, F, p | Predictor variables | Sum Squares | Df | F value | Pr (>F) |
|---|---|---|---|---|---|---|
| Acoustic Biomass | 0.61, 6.44, <0.001 | (Intercept) | 397096979719 | 1 | 242.0116 | 0.0000 |
| | | Year | 88495789826 | 5 | 10.7868 | 0.0000 |
| | | Season | 29777890704 | 2 | 9.0741 | 0.0003 |
| | | Year:Season | 47513413961 | 10 | 2.8957 | 0.0044 |
| | | Residuals | 114857267467 | 70 | NA | NA |
| Acoustic Density | 0.09, 49.85, <.001 | (Intercept) | 2026819196 | 1 | 1909.705 | 0 |
| | | Year | 420967438 | 5 | 79.329 | 0 |
| | | Season | 153264774 | 2 | 72.204 | 0 |
| | | Year:Season | 258323203 | 10 | 24.340 | 0 |
| | | Residuals | 9424574893 | 8880 | NA | NA |
| Trawl Length | 0.03, 46.28, <.001 | (Intercept) | 213113121.30 | 1 | 104136.028 | 0.000 |
| | | Year | 28918.09 | 5 | 2.826 | 0.015 |
| | | Season | 432249.30 | 2 | 105.608 | 0.000 |
| | | Year:Season | 1083581.33 | 10 | 52.948 | 0.000 |
| | | Residuals | 52297998.30 | 25555 | NA | NA |
| Trawl CPUE | 0.07, 1.89, 0.017 | (Intercept) | 65679007 | 1 | 78.605 | 0.000 |
| | | Year | 1909816 | 5 | 0.457 | 0.808 |
| | | Season | 14296009 | 2 | 8.555 | 0.000 |
| | | Year:Season | 9795909 | 10 | 1.172 | 0.308 |
| | | Residuals | 335895239 | 402 | NA | NA |

## 2.5 Discussion

Based on our analyses, fish distributions in the Penobscot River Estuary vary seasonally and inter-annually. The highest fish density (NASC values) was observed in late spring and early summer surveys compared with early spring and fall. The lowest overall densities were observed in the earliest spring and latest fall surveys. O'Malley et al. (2017) reported these patterns for the early portion of the time series and they appear to remain true throughout. Trawl CPUE was generally consistent with acoustic densities patterns where the trawl captured highest abundances in late spring and summer. The variability, as evident in size of the boxplots, of NASC and CPUE was also greater in the surveys with higher density suggesting that more fish were more distributed throughout the study area. Together, these density patterns suggest changes from pre-restoration to post-restoration with higher densities of fish in more areas of the estuary, but that some areas still remain low in fish density.

Combined, these results are consistent with investigations from other temperate estuaries that demonstrate seasonal distribution shifts of fish densities with colder seasons exhibiting lower densities (Recksiek and McCleave 1973; Potter et al. 1986; Hagan and Able 2003). Species composition was consistent among seasons and years with Clupeid species comprising a majority of fish captured with only Rainbow Smelt comprising any other major contribution to abundance. Estuary fish distributions fluctuate due to several ecological processes including emigration or immigration of facultative and obligatory estuary residents (Able 2005). For example, in systems with diadromous fish, estuaries experience large seasonal changes in biomass coinciding with adult migrations (Hall et al. 2011; Hall et al. 2012). Understanding these patterns are critical to establish a baseline to evaluate changes from sources such as restoration activities.

Restoration activities in this system have shown order of magnitude increases in Alewife and Blueback Herring as evident of counts at upriver fishways of nearly 2 million fish in 2017 (MDMR 2018). Despite the relatively large increase in river herring, diadromous populations throughout this survey time series were a fraction of their historic levels of 10's of millions (Saunders et al. 2006). We found estuary biomass in spring was higher in 2015-2017 than the 2012-2014 period coincident with these population increases. Our estimates of nearly 50,000 kg in spring during the latter time period is more than twice the less than 20,000 kg seen early in the period. Unexpectedly, the greatest difference in biomass pre and post-restoration was evident in summer surveys. During 2012-14 summer biomass was 50-60,000 kg compared to 110-160,000 kg during 2015-2017. Also, adult river herring were more frequent in summer trawl surveys than spring.

This study reveals a more complex system than simply the increased magnitude of short biomass pulses from spring migrants. Instead, we demonstrate that biomass changes occur over several weeks to months. For all years except 2015, the peak biomass were observed during summer. This was when juvenile and adult River Herring species were present as well as Atlantic Herring in varying abundances. Indeed, this estuary system demonstrates patterns consistent with the hypothesis of Pess et al. (2014) that rate of populations are likely influenced by interactions of life-history and ecological interactions. Adding dam removal and population enhancement (stocking) activities adds further complexity to the system. The changes documented here during the period before and after restoration are confounded by the stocking of upriver habitat for 'seeding' purposes. By stocking Alewife, Blueback Herring, and Atlantic salmon smolts, it is difficult to parse the effects of seeding from the effects of habitat expansion achieved through dam removal (Pess et al. 2014). Therefore, we note the results of our analysis may not entirely reflect the effects of the removal of dams or improvement of passage facilities. In addition, the relatively short period of this assessment (6 years) may not be sufficient to detect changes occurring at longer time scales. For example, Alewife, Blueback Herring and American Shad have lifecycles of 3-9 years, thus the current assessment would be covering less than one full generation. Also, species such as Atlantic Herring undergo various population fluctuations such as the 2011 cohort (potentially part of 2012 and 2013 estuary population) being the second largest in the 30 year time series (Deroba 2015). Also during this study, several unusual environmental conditions were present including the unusually warm year of 2012 (Mills et al. 2013), increased extreme precipitation events (Huang et al. 2017), and historically high and low flow events (USGS 2018). The study design in place from O'Malley et al. (2017) provides for the ability to investigate long-term patterns such as population flux and environmental variability and their impact on rates of diadromous fish recovery in the Penobscot River.

Deciphering the complex patterns of fish distribution are necessary to draw inferences as to change resulting from restoration activities rather than natural stochasticity in species populations. Detecting temporal distribution patterns can be difficult due to the high degree of spatial variation (Rotherham et al. 2011). As such, sample design should consider the frequency and extent of sampling to characterize desired variability (Livingston 1987). This survey considered these factors in design (O'Malley et al. 2017; Lipsky et al. 2019) but prior to this analysis, a description of variation in fish distributions had not been conducted in this system. We found that indeed variability in fish density was high in the estuary with some EDSUs having nearly any fish even during period of high overall biomass. The sampling frequency allowed for detection of change at seasonal and annual scales especially in spring when surveys were more frequent (i.e., once a week). The combination of data from the two survey techniques in this study allowed for more detailed trends as it relates to species composition in density and biomass trends. Atlantic herring were present in the estuary in most springs but were small and therefore contributed to the general patterns in length distribution but less to biomass. In contrast, Rainbow smelt were abundant in some seasons and years and their longer length likely had variable impact in fish length, density, and biomass depending on the season and year. Finally, juvenile River Herring were a dominant component of the estuary and they were likely key driver to size, density, and biomass in all seasons and years. This variability exemplifies the need for complementary techniques to evaluate fish populations where one method (i.e. acoustics) can describe spatial and temporal aspects of the community (i.e. density) but not other components such as species.

Various validation techniques such as trawling, video, gillnets, all have relevant assumptions that must be accepted or quantified as they relate to capture and selectivity bias in length or abundance (Simmonds and MacLennan 2005). In this system, it appears that the trawl is a biased sampler for a narrow range of sizes than observed in acoustic surveys (Chapter 1) and these should be considered in the metrics derived for this analysis. Biomass would be biased to lower values if the system has larger fish with larger TS-TL regression parameters than used for this study. An example would be various species of gadoids that have a lower TS for length than herring species (Foote 1987). As restoration may also shift the assemblage and increase larger piscivores (Ames 2004), validation techniques should be pursued to determine mechanisms for any changes in acoustic data.

The stated goal of the Penobscot River restoration was to restore diadromous fish and their ecological functions (Day 2006). Our hypothesis is that the ecological functions provided by diadromous fish in this estuary are related to biomass and their components, size and density because they drive biomass computations. Biomass is the universal currency in measuring ecological services involving nutrient exchange from freshwater to marine habitats as well as any ecological interactions between species. For example, estuarine biomass from juvenile river herring in fall is a measure of the magnitude of basin-wide production for a given year. We measured nearly 200,000 kg of biomass in 2017 and assuming most were juvenile river herring (as indicated by trawls) and their size was ~5g/fish this would equate to nearly 40 million juveniles. Maine had a pre-dammed potential of 1.4 billion juveniles as estimated by Hall et al. (2012) suggesting this system is less than 3% of those targets. Even with biomass far from restoration goals, these type of estimates provide indices to measure progress.

Biomass estimates also provide measures for the evaluation of ecological processes hypothesized from increasing diadromous populations. We found that spring biomass has increased at least 3 times (50 to 150k kg) from pre to post restoration suggesting at least the mechanism for the ecological interaction is quantifiable. For example, these estimates could measure prey subsidies available for groundfish or other piscivores in the system (Ames 2004; Ames and Lichter 2013, McDermott et al. 2015). The magnitude and timing of biomass in the spring may also be a metric for the degree of predator swamping Atlantic Salmon smolts encounter during their seaward migration as proposed by Saunders et al (2006). Further, fish length as determined by acoustics (TS) allows inference of broad description of fish community at least to functional guild level as reviewed in Elliott et al. (2007). Their categorical scheme “feeding mode functional group” allows for evaluation of trophic interactions given the predictable size groups of zooplanktivores (Clupeid and Smelt) seen in this system compared to larger piscivores.

The rate of dam removal in the US has increased as structures age and economic and ecological costs preclude redevelopment (O'Connor et al. 2015). The cost of implementing habitat restoration projects often precludes post-project assessment and as a result data on restoration impacts are lacking (Hart et al. 2002; Palmer et al. 2005, Foley et al. 2017). Assessment is also rarely done at the timescale needed for detecting ecological response for species with long and complicated life-cycles (Bellmore et al. 2017). Our analysis provides for analytical techniques which provide measures for changes in the estuary fish community during the period of upriver restoration. This is unique as these metrics are collected without bias of upstream dams (for upstream) migrants and these can be repeated in the future if the underlying surveys continue to collect consistent data. Our results indicate that changes have occurred and are likely still changing several years after the last dam was breached in this system. The ecological complexity of the fish community dynamics and degree of temporal variability suggest this system requires systematic assessment on a long-term scale. The high degree of inter-annual variability seen in this system should be consider in determining future sample designs.

### 2.5.1 Conclusion

Diadromous fish restoration typically focuses on adult returns to base success, however this study demonstrates the more complex ecological processes that may occur when these species are allowed reestablish to the estuary ecosystem again (sensu Pess et al. 2014). The presence of juvenile and adult lifestages suggest that diadromous fish provide more than short-timed surges of biomass during migration, rather they utilize the resources of the estuary and themselves become a resource for higher trophic levels. We characterized the complex pattern of seasonal change in species assemblage, biological and abundance metrics while being able to detect overall changes during the time series. We detected significant changes in most fish metrics in the Penobscot River Estuary concurrent with upriver restoration activities per our hypotheses. Biomass was generally greater during the post-restoration surveys. Fish length (from trawl) was larger in spring and summer and smaller in fall. Acoustic density was generally higher during post-restoration and trawl CPUE was not different among years or seasons. Alewife, Blueback Herring, and Rainbow Smelt abundance proportions varied annually but were consistent constituents of the estuary biomass. Whereas Atlantic Herring made seasonally large contributions but not for the entire time series. All of these patterns were the result of the temporal extent of the trawl and acoustic datasets providing a robust volume of data in which to evaluate ecologically meaningful metrics. River restoration and the subsequent ecological changes are difficult to characterize but our approach offers a template for this system over time and for other systems with similar goals. Most importantly, these results provide the baseline conditions for the system as restoration proceeds and optimistically fish populations continue to increase.

## 2.6 Supplemental Material: Tukey Results

Table S2.3 Tukey results. Results of Tukey adjusted pairwise comparisons of least-squares (LS) means, standard error (SE), degrees of freedom (df), lower and upper confidence limit (CL), and group letter of acoustic density, acoustic size, trawl CPUE, trawl length, and biomass with Year and Season effect terms. Tukey HSD letters indicate the degree of overlap of confidence intervals between measurements where groups sharing letters are not significantly different at the 0.05 level.

| Model | Year | Season | LS mean | SE | df | Lower CL | Upper CL | group |
|---|---|---|---|---|---|---|---|---|
| Acoustic Density (sA,m$^{2}$ nmi$^{-2}$) | 2012 | spring | 212.935 | 40.439 | 8880 | 92.233 | 333.637 | ab |
| | 2013 | spring | 145.790 | 33.302 | 8880 | 46.391 | 245.189 | a |
| | 2014 | spring | 317.338 | 51.003 | 8880 | 165.106 | 469.570 | abc |
| | 2015 | spring | 1105.213 | 39.362 | 8880 | 987.725 | 1222.700 | e |
| | 2016 | spring | 338.463 | 50.693 | 8880 | 187.155 | 489.770 | abc |
| | 2017 | spring | 498.824 | 45.221 | 8880 | 363.849 | 633.799 | c |
| | 2012 | summer | 360.875 | 51.003 | 8880 | 208.643 | 513.107 | bc |
| | 2013 | summer | 487.041 | 50.940 | 8880 | 334.995 | 639.087 | c |
| | 2014 | summer | 516.655 | 46.876 | 8880 | 376.741 | 656.570 | c |
| | 2015 | summer | 785.299 | 50.693 | 8880 | 633.991 | 936.607 | d |
| | 2016 | summer | 899.611 | 50.693 | 8880 | 748.304 | 1050.919 | de |
| | 2017 | summer | 1131.848 | 50.510 | 8880 | 981.087 | 1282.610 | e |
| | 2012 | fall | 148.464 | 72.129 | 8880 | -66.825 | 363.752 | ab |
| | 2013 | fall | 151.792 | 45.618 | 8880 | 15.632 | 287.953 | ab |
| | 2014 | fall | 289.683 | 47.520 | 8880 | 147.847 | 431.520 | abc |
| | 2015 | fall | 321.999 | 41.746 | 8880 | 197.396 | 446.601 | abc |
| | 2016 | fall | 449.813 | 45.134 | 8880 | 315.097 | 584.528 | c |
| | 2017 | fall | 847.173 | 50.816 | 8880 | 695.497 | 998.849 | d |
| Trawl CPUE (fish per km) | 2012 | spring | 277.840 | 134.775 | 402 | -126.813 | 682.493 | a |
| | 2013 | spring | 318.821 | 141.047 | 402 | -104.663 | 742.305 | a |
| | 2014 | spring | 659.312 | 253.523 | 402 | -101.872 | 1420.497 | a |
| | 2015 | spring | 382.567 | 146.372 | 402 | -56.904 | 822.037 | a |
| | 2016 | spring | 670.438 | 146.372 | 402 | 230.967 | 1109.908 | a |
| | 2017 | spring | 521.982 | 172.747 | 402 | 3.322 | 1040.642 | a |
| | 2012 | summer | 546.232 | 204.397 | 402 | -67.455 | 1159.919 | a |
| | 2013 | summer | 717.850 | 263.875 | 402 | -74.416 | 1510.116 | a |
| | 2014 | summer | 247.450 | 253.523 | 402 | -513.735 | 1008.635 | a |
| | 2015 | summer | 1068.904 | 236.017 | 402 | 360.280 | 1777.528 | a |
| | 2016 | summer | 935.123 | 244.301 | 402 | 201.627 | 1668.619 | a |
| | 2017 | summer | 494.738 | 228.522 | 402 | -191.385 | 1180.860 | a |
| | 2012 | fall | 327.288 | 204.397 | 402 | -286.399 | 940.975 | a |
| | 2013 | fall | 157.050 | 190.601 | 402 | -415.216 | 729.316 | a |
| | 2014 | fall | 124.439 | 199.471 | 402 | -474.458 | 723.336 | a |
| | 2015 | fall | 23.937 | 186.588 | 402 | -536.280 | 584.154 | a |
| | 2016 | fall | 85.020 | 204.397 | 402 | -528.667 | 698.706 | a |
| | 2017 | fall | 213.288 | 236.017 | 402 | -495.336 | 921.913 | a |

Table S2.3 Tukey results. *Continued*

| Model | Year | Season | LS mean | SE | df | Lower CL | Upper CL | group |
|---|---|---|---|---|---|---|---|---|
| Trawl Length (TL, mm) | 2012 | spring | 108.594 | 0.872 | 25555 | 105.991 | 111.197 | de |
| | 2013 | spring | 114.735 | 0.891 | 25555 | 112.076 | 117.394 | fg |
| | 2014 | spring | 97.670 | 2.144 | 25555 | 91.270 | 104.069 | abc |
| | 2015 | spring | 112.139 | 1.075 | 25555 | 108.932 | 115.346 | efg |
| | 2016 | spring | 101.191 | 0.872 | 25555 | 98.587 | 103.794 | c |
| | 2017 | spring | 122.105 | 1.084 | 25555 | 118.871 | 125.340 | h |
| | 2012 | summer | 104.045 | 1.275 | 25555 | 100.241 | 107.850 | cd |
| | 2013 | summer | 101.495 | 1.229 | 25555 | 97.826 | 105.164 | bc |
| | 2014 | summer | 110.111 | 1.311 | 25555 | 106.199 | 114.023 | def |
| | 2015 | summer | 112.810 | 1.223 | 25555 | 109.161 | 116.459 | efg |
| | 2016 | summer | 116.350 | 1.034 | 25555 | 113.264 | 119.435 | g |
| | 2017 | summer | 104.867 | 1.536 | 25555 | 100.282 | 109.452 | cd |
| | 2012 | fall | 109.502 | 1.250 | 25555 | 105.772 | 113.232 | def |
| | 2013 | fall | 98.912 | 1.410 | 25555 | 94.703 | 103.120 | bc |
| | 2014 | fall | 105.509 | 1.427 | 25555 | 101.251 | 109.768 | cd |
| | 2015 | fall | 89.194 | 2.384 | 25555 | 82.079 | 96.310 | a |
| | 2016 | fall | 95.167 | 1.347 | 25555 | 91.147 | 99.186 | ab |
| | 2017 | fall | 89.939 | 1.533 | 25555 | 85.365 | 94.513 | a |
| Biomass (kg) | 2012 | spring | 26711.49 | 15310.21 | 70 | -20643.236 | 74066.21 | ab |
| | 2013 | spring | 20222.34 | 13502.34 | 70 | -21540.599 | 61985.28 | a |
| | 2014 | spring | 45056.03 | 20253.51 | 70 | -17588.380 | 107700.44 | abc |
| | 2015 | spring | 152051.03 | 15310.21 | 70 | 104696.309 | 199405.76 | e |
| | 2016 | spring | 49290.60 | 20253.51 | 70 | -13353.811 | 111935.01 | abc |
| | 2017 | spring | 73099.98 | 18115.29 | 70 | 17069.112 | 129130.84 | abcde |
| | 2012 | summer | 49811.51 | 20253.51 | 70 | -12832.906 | 112455.92 | abc |
| | 2013 | summer | 66989.16 | 20253.51 | 70 | 4344.748 | 129633.57 | abcde |
| | 2014 | summer | 68712.26 | 18115.29 | 70 | 12681.395 | 124743.12 | abcde |
| | 2015 | summer | 114571.51 | 20253.51 | 70 | 51927.094 | 177215.92 | bcde |
| | 2016 | summer | 130037.00 | 20253.51 | 70 | 67392.590 | 192681.41 | cde |
| | 2017 | summer | 159347.72 | 20253.51 | 70 | 96703.309 | 221992.13 | de |
| | 2012 | fall | 20920.54 | 28642.78 | 70 | -67672.035 | 109513.12 | abc |
| | 2013 | fall | 21055.59 | 18115.29 | 70 | -34975.273 | 77086.46 | ab |
| | 2014 | fall | 38076.30 | 18115.29 | 70 | -17954.562 | 94107.17 | abc |
| | 2015 | fall | 45745.15 | 16536.92 | 70 | -5403.802 | 96894.09 | abc |
| | 2016 | fall | 65014.52 | 18115.29 | 70 | 8983.655 | 121045.38 | abcd |
| | 2017 | fall | 123563.00 | 20253.51 | 70 | 60918.588 | 186207.41 | cde |

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