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Biomass and composition of Atlantic menhaden schools in winter on the continental shelf offshore of New Jersey: Application of a novel hydroacoustic survey with midwater trawl sampling

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Abstract

Atlantic menhaden (*Brevoortia tyrannus*) is a migratory forage fish of ecological and economic importance that are difficult to sample because they are infrequently encountered in scientific surveys conducted along the U.S. East Coast. Thus, information to support assessment and management of this stock is lacking, particularly in the northern offshore portion of the range where a winter bait fishery has operated since 2014. A cooperative team of scientists and fishing industry members conducted the first targeted survey for Atlantic menhaden in continental shelf waters 25-80 km off the coast of New Jersey in winter 2022 using a novel hydroacoustic survey design with midwater trawl sampling. Acoustic data collected from 23 schools along 351 km of systematic transects was used to estimate a study area (10,990 km^2) biomass of 9,089,167 kg with a 95% confidence interval of 713,207-17,465,128 kg. Most acoustically derived school biomass estimates were comparable with trawl catch weights. All schools sampled were composed of highly homogeneous Atlantic menhaden ages 3-4 (range 2-6) with median fork length of 266 mm and weight of 0.288 kg. Most Atlantic menhaden sampled were mature and resting between batches. This survey confirmed partial migratory behavior of adult Atlantic menhaden and provided proof of concept for an alternative survey design for schooling pelagic fishes.

Keywords

Brevoortia tyrannus

Hydroacoustics

Fishery-independent survey

Cooperative science

Schooling pelagics

Partial migration

1.1 Introduction

Atlantic menhaden (*Brevoortia tyrannus*) is a migratory forage fish that occur along the U.S. East Coast from Florida to Maine (Goode 1879, Ahrenholz 1991). In the spring and early summer, adult Atlantic menhaden migrate and spatially stratify along the coast by latitude such that larger, older fish are typically encountered farther north (June and Reintjes 1959, Nicholson 1971). In the fall, the northern portion of the adult population is generally thought to migrate to offshore waters south of Cape Hatteras, North Carolina (Roithmayr 1963, Nicholson 1971), although egg surveys and tagging data indicate some overwinter residency of Atlantic menhaden in the northern part of their range (Simpson et al. 2017, Liljestrand et al. 2019, Liljestrand et al. 2025).

The Atlantic menhaden stock supports the largest commercial fishery by weight of landings on the U.S. East Coast (2023 total landings 233,800,000 kg; ASMFC 2025). The commercial fishery consists of two main components: a purse seine reduction fishery (approximately 70% of landings) located in recent years primarily in Chesapeake Bay and nearby coastal waters, and a coastwide bait fishery (approximately 30% of landings; ASMFC 2025). Most bait fishing for Atlantic menhaden occurs in estuaries and coastal waters with purse seines, gill nets, and pound nets, but midwater trawl fishers initiated a new and successful winter bait fishery in 2014 along the offshore portion of the Mid-Atlantic shelf from Maryland to Southern New England. To date, overwintering of Atlantic menhaden on the coastal shelf in the northern portion of their range has not been confirmed with fishery-independent data collection.

Despite the economic and ecological importance of the Atlantic menhaden stock (Lipton 2009, Garrison et al. 2010, Anstead et al. 2021), fishery-independent data to support management are sparse, particularly in the northern portion of their range and in winter. Most biological data used to inform stock assessments are from port samples obtained from the reduction fishery; although this fishery is well-sampled, it no longer regularly operates across most of the stock's range (SEDAR 2015). Due to the closure of all but one reduction plant on the U.S. East Coast, biological samples collected during the last two decades have been concentrated in the Chesapeake Bay region from spring through early fall (Nesslage et al. 2020). Although port samples are collected from the winter bait fishery, sampling intensity is determined by catch-based quotas rather than being selected based on biological or statistical criteria and can be limited in some areas and times of year if landings are low relative to the much larger reduction fishery. Also, this species lacks a dedicated fishery-independent monitoring survey and is rarely encountered in existing offshore trawl surveys (SEDAR 2020). During winter, the National Oceanic and Atmospheric Administration (NOAA) Marine Resources Monitoring, Assessment, and Prediction program and the Ecosystem Monitoring program ichthyoplankton surveys have provided evidence of Atlantic menhaden spawning from North Carolina to southern New England throughout most of the year (Simpson et al. 2017). However, fishery-independent trawl surveys on the East Coast of the U.S. either do not operate during the coldest portion of winter, are not far enough offshore to reliably encounter overwintering adult Atlantic menhaden, or have not used gears and vessels that are capable of reliably catching Atlantic menhaden. The NOAA Northeast Fisheries Science Center's Winter Bottom Trawl Survey (Winter BTS) operated offshore from 1992 to 2007, but this survey was designed to primarily sample flatfishes and therefore encountered very few Atlantic menhaden (SEDAR 2020). Thus, a need was identified for the development of new methods to survey overwintering Atlantic menhaden to help determine sustainability of the winter bait fishery.

Hydroacoustics are commonly used to survey schooling pelagic clupeids, including Atlantic menhaden (Lucca and Warren 2018, 2019), Atlantic herring *(Clupea harengus*; Jech and Sullivan 2014), and Atlantic mackerel (*Scombra scombrus*; Loranger et al. 2022). Hydroacoustic surveys for Atlantic menhaden have been successfully conducted by Lucca and Warren (2018, 2019) at smaller scales such as in the Peconic River and Flanders Bay of Long Island, NY and along the continental shelf approximately 6 km south of Long Island during 2014-2015. These hydroacoustic surveys for Atlantic menhaden covered regions spanning 0.04-3.01 km^2 at depths ranging from approximately 2.5-20 m; however, hydroacoustics have not been used to survey Atlantic menhaden over a large spatial area or in winter.

Conducting an offshore hydroacoustic survey for Atlantic menhaden in winter poses several challenges. In contrast to summer schooling behavior, adult Atlantic menhaden in winter form extremely large, dense schools near the bottom during the day and disperse at night to feed near the surface (June and Reintjes 1959, Smith 1991). Bait fishers have reported these schools as being highly sedentary with greatly reduced vessel avoidance behavior from January to February when water temperatures are coldest. To determine an effective approach for surveying overwintering Atlantic menhaden, Liang at al. (2020) conducted a simulation study testing the performance of a suite of hydroacoustic survey designs and found that use of a traditional hydroacoustic survey design for Atlantic menhaden in winter would produce biomass estimates with poor precision and accuracy due to patchiness of large schools across the landscape (Nesslage and Liang 2018). In contrast, a two-stage survey design tailored to Atlantic menhaden overwintering biology and behavior generated biomass estimates with a coefficient of variation of approximately 25%. This survey design included traditional estimation of biomass using a downward-facing echosounder, but allowed the search range to be expanded along each transect with the use of omnidirectional sonar.

The primary goal of this study was to implement the Liang et al. (2020) hydroacoustic survey design to quantify biomass, composition, and habitat use of the portion of the Atlantic menhaden stock thought to overwinter off the coast of New Jersey where the winter bait fishery is concentrated. The objectives of this study were to 1) estimate overwintering biomass of Atlantic menhaden with acoustic data collected using a novel, two-stage survey design, 2) evaluate performance of industry acoustic equipment used in cooperative research, 3) characterize the size, age, sex, and maturity of overwintering Atlantic menhaden schools in the study area, and 4) characterize pelagic habitat use of overwintering Atlantic menhaden on the continental shelf.

2.1 Materials and methods

The two-stage hydroacoustic survey design of Liang et al. (2020) was implemented in winter 2022 by a cooperative research team composed of academic, federal, state, and private scientists and members of the Atlantic menhaden bait fishing industry, both fishers and processers. The survey used a combination of industry hydroacoustics and midwater trawling to estimate biomass within the study region and characterize school composition. Schools were detected along a series of pre-defined transects with a wide search area using omnidirectional sonar. A downward-facing echosounder provided *in situ* acoustic-based estimates of school biomass for a subset of schools encountered within the search area. In addition, midwater trawls were set on a subset of ensonified schools to compare school catch weight measured at port with school biomass estimated via acoustic data analysis. Individual fish samples were collected from trawled schools to characterize school composition.

2.1.1 Survey design

The study area encompassed 10,990 km^2 offshore of the coast of New Jersey extending from the southern border of Hudson Canyon to the New Jersey-Delaware border (Fig. 1). The survey was conducted in winter to determine whether a portion of the Atlantic menhaden stock resides in the Mid-Atlantic and does not undergo migration to coastal waters south of Cape Hatteras. Six systematic transects oriented perpendicular to shore and spaced 29 km apart were surveyed, covering a total distance of 351 km (Table 1) and spanning depths of 14-51 m. Transects were of variable length due to the irregular shape of the study area and random start location (mean transect length = 58 km). To determine transect positions across the study area, the latitude of the northernmost transect was randomly selected between 73°44'56.4919"W 40°5'23.5729"N and 73°51'57.8296"W 39°38'15.5024"N to ensure adequate room for the subsequent five transects. Survey implementation began with the southernmost Transect 1 near shore and proceeded sequentially northward (Table 1). The direction of transects alternated such that Transect 1 proceeded inshore to offshore, Transect 2 proceeded offshore to inshore, and so on. All transects were surveyed during daylight hours to avoid disaggregation of Atlantic menhaden schools during vertical diel migrations at night. Transects 1 and 2 were surveyed February 14-15, 2022 (Table S1). The vessel returned to port to offload and weigh the catch on February 15. The survey was suspended February 16-19 due to a severe storm, and the survey resumed February 20-24 to complete Transects 3-6.

All operations were conducted using a 49-m commercial midwater trawling vessel, the *F/V Dyrsten*, that is owned and operated by H&L Axelsson, Inc. The *F/V Dyrsten* used a Cosmos Trawl net with an 18-m vertical opening, 51-m horizontal opening, and mesh size of 3.8 cm in the codend. The vessel was equipped with a recordable Simrad ES80 echosounder with a 7° split-beam, hull-mounted 38kHz ES38B transducer, and Furuno FSV25S (20 kHz) omnidirectional sonar. Unlike previous Simrad industry-grade echosounders, the ES80 echosounder does not contain a systematic “triangle-wave” error component that would preclude use of these data for scientific surveys. The ES80 was configured to collect at the fastest ping rate setting in narrowband (“continuous wave”) mode with a 0.256-ms pulse duration. The ES80 echosounder was calibrated offshore of Cape May, New Jersey during February 11-13, 2022 to map the beam pattern and measure the on-axis response using the standard sphere method (Foote et al. 1987, Demer 2015). The sphere was attached by monofilament line to a wireless calibration system developed at the NOAA Northeast Fisheries Science Center. The tungsten carbide (with 6% cobalt binder) 38.1-mm diameter sphere was lowered under the transducer to a range of approximately 8.3 to 11.9 m with weights added to the line approximately 2 m below the sphere to provide additional stability in the currents.

As the vessel proceeded along each transect at approximately 3.6 m/s, acoustic backscatter from the omnidirectional sonar was scrutinized in real time by the fishing captain, an experienced Atlantic menhaden bait fisher, and the chief scientist. Backscatter deemed characteristic of an Atlantic menhaden school detected within the search area 1,600 m to each side of the vessel was assigned a unique school identification number, and the school's Global Positioning System (GPS) coordinates, heading, and approximate distance from the vessel were recorded. The vessel location was then noted before leaving the transect to ensonify the school(s). When possible, the school was ensonified twice with two perpendicular passes to better characterize school geometry. Once acoustic data were collected, the vessel proceeded to the closest point on the original transect and resumed following the transect. All schools detected within the search area along each transect were ensonified to provide acoustic data for *in situ* estimation of school biomass unless the school exhibited vessel avoidance or was located too close to the surface.

Schools that did not avoid the vessel after initial ensonification were captured using the midwater trawl net. GPS coordinates and times (synchronized with the echosounder clock) marking the beginning and end of each tow were recorded. Fish captured from each school were pumped into separate tanks and individually weighed at port by Lund's Fisheries (bait processor located in Cape May, New Jersey) for later comparison with *in situ* acoustic estimates of individual school biomass.

Biological samples were collected from each trawled school to characterize school composition. School number, trawl set number, and GPS location of the trawl set was associated with each biological sample. Scientists subsampled the catch from the net pump using the Northeast Fisheries Observer Program's Catch Composition Technique for midwater trawl operations (NOAA 2013). Once the cod-end had been brought alongside the vessel, the chief scientist asked the captain for an estimate of pumping time for that haul, which was divided by 10 to yield the sampling interval (e.g., estimated pumping time = 20 minutes, sampling interval = 2 minutes, yield = 10 baskets of sample). From each basket, 10 individual fish received full processing, which included the following elements: fork length (FL, mm), total length (TL, mm), whole weight (kg), eviscerated weight (kg), macroscopic sex (male/female/unknown), and macroscopic maturity stage (immature/mature-resting/mature-ripe/mature-spent; Table S2). A scale patch (~50 scales) was also collected, stored in labeled vials, and frozen. The head was removed and frozen for later extraction and preparation of both sagittal otoliths for ageing. For female Atlantic menhaden, both ovaries were removed, weighed, and preserved in Normalin for later reproductive evaluation. Once 10 menhaden from each basket had been sampled in this manner, individual length (fork and total) and individual whole weight were recorded for the remaining Atlantic menhaden specimens.

Although survey protocols were prepared in advance for ensonifying and sampling schools of non-target species such as Atlantic herring and Atlantic mackerel, all schools sampled on this survey were composed almost entirely of Atlantic menhaden. All other species collected during sampling procedures were recorded and individual length and individual whole weight data were collected.

Hydrographic data were collected systematically every 10 km along each transect to characterize ocean conditions across the study area and at each trawl set location to characterize Atlantic menhaden habitat use. Each profile included depth (m), water temperature (ºC), salinity (PSU), and dissolved oxygen concentration (mg/L) recorded.

2.1.2 Post-survey fishery-dependent data collection

Because the survey was completed earlier than expected, the scientific team was able to return to the vessel February 28-March 4 to collect supplementary fishery-dependent acoustic data and at-sea biological samples (Table S1). This allowed for comparison of biomass, composition, and location of schools encountered during captain-selected fishery-dependent operations versus fishery-independent survey operations. Trawled schools were sampled using survey data collection methodology, and hydrographic data were collected at school locations. Upon the conclusion of at-sea fishery-dependent sampling, project collaborators at Lund's Fisheries collected port samples (three standard 10-fish samples per trip) for size and age analyses throughout the remainder of the fishing season March 6-March 22.

2.1.3 Acoustic data analysis

Schools were identified as Atlantic menhaden either through direct sampling, visual sighting at surface, or via observed shoaling behavior (formation of extremely large, dense schools; e.g., Fig. S1). Schools that could not be identified in this way were categorized as "other fish" (e.g., medium to large individual fish echo traces) or "small pelagic school" (e.g., small, less coherent regions of weaker volume backscattering strength (S_v, dB re m^2 m^{-3}) in the middle to upper water column) based on visual scrutiny of the location, morphology and magnitude of the S_v echogram region. ES80 data files corresponding to ensonified schools identified in real time by the captain and chief scientist from the omnidirectional sonar were processed using Echoview software (version 12.1 or 13, Hobart, Tasmania) to generate acoustic estimates of Atlantic menhaden biomass for each school ensonified. ES80 data files of the calibration sphere were used to adjust calibration results from the field (additional details in Supplemental Materials). The *F/V Dyrsten* has a draft of approximately 4.3 m (14 ft) with no fish/water cargo and 5.2 m (17 ft) under full load, and the transducer was mounted 1.8 m (6 ft) below the keel. For purposes of processing data and approximating the water depth, the transducer was assumed to be at a water depth of 6.5 m. The transducer was mounted securely in reverse direction such that the forward arrow on the transducer was pointed to the stern.

To compensate for this, a beam rotation of 180° was used during processing. Hydrolab profile measurements were used to estimate representative average hydrographic conditions during each trip. Differences in sound speed estimates were negligible; therefore, the final calibration file was updated for sound speed for each trip taken during the survey and post-survey data collection periods.

Minimum S_v threshold curves for selected fish backscatter versus water column background S_v following methods of Jech and Michaels (2006) would indicate a minimum S_v threshold could have been set between -50 dB and -60 dB. However, Rudstam et al. (2009) suggested setting the minimum S_v threshold to be equivalent to the minimum target strength (TS, dB re m^2) of interest. Assuming the minimum TS of interest and minimum single echo detection criterion to be -50 dB, then the TS uncompensated for beam pattern would be -56 dB, which converts to approximately -63 dB assuming sound speed of 1475 m/s and 55 m in range. Given the minimum TS threshold of -63 dB and -66 dB minimum S_v threshold used by Jech and Michaels (2006) for Atlantic herring, the minimum S_v threshold used in this study was a conservative nominal value of -64 dB. S_v backscatter was filtered by masking the upper water column and removing the impulse noise spikes (Figs. S1 and S7). Noise may have been due to other depth sensors or the omnidirectional sonar equipped on the vessel.

To convert to fish per m^3 or m^2, target strength was back-transformed from a dB value to a linear quantity called the backscattering cross-section ($\sigma_{bs} = 10^{(TS/10)}$, m^2). The TS representative of a single Atlantic menhaden to use for this study was uncertain given the lack of species-specific experimental data, model estimates, and *in situ* estimates. Exploratory analysis of the echograms containing Atlantic menhaden during this survey indicated that schools were too dense to obtain an *in situ* TS estimate. Instead, TS was estimated based on total length (TL; Simmonds and MacLennan 2008) as was done by Lucca and Warren (2018), who used a generalized TS-TL equation to acoustically estimate distribution and abundance of Atlantic menhaden in estuarine waters of Long Island, New York. Thus, the mean TS (-32.2 dB re 1 m^2) of Atlantic menhaden at 38 kHz used in this study was estimated following equation:

$$\mathrm{TS} = 19.1\mathrm{Log}_{10}(\mathrm{TL}) + 0.9\mathrm{Log}_{10}(\mathrm{f}) - 62, \quad (1)$$

where f = acoustic frequency (kHz) and mean the mean TL was 30.5 cm.

Volumetric fish density of each classified echogram region (number of fish per m^3) was calculated using the mean S_v exported from Ecohoview (Sv_Mean) as

$$\text{Volumetric fish density} = 10^{(\text{Sv\_mean}/10)}/(10^{(\text{meanTS}/10)}). \quad (2)$$

Volumetric biomass density of each classified echogram region (kg/m^3) was calculated as volumetric fish density multiplied by the mean weight of individual fish from this study (0.285 kg). Given the difference in shape between schools located near the ocean floor and schools located midwater, we used the equation for the volume of a dome to approximate the volume of all schools with a minimum altitude <=0 m:

$$V = \frac{1}{6}\pi h(3r^2 + h^2), \quad (3)$$

where h was the height of the school dome, and r was the radius of the dome's base. We used the equation for an ellipsoid to approximate the volume of all schools with a minimum altitude >0 m:

$$V = \frac{4}{3}\pi {r_L}^2 r_H, \quad (4)$$

where r_L was the radius (i.e., half of the observed trace length), and r_H was half the ellipsoid height (Misund et al. 1992, Misund 1993, Fréon and Misund 1999, Peña et al. 2021).

Altitude of each school was based on minimum altitude of the school region's bottom boundary referenced to the back step off bottom, which allowed minimum altitude to be <0 m. Volumetric biomass density was then multiplied by school volume to estimate the biomass of each school (kg). Only conservative estimates that excluded echoes related to side lobe or multiple scattering contributions and likely to be menhaden were included. Given logistical constraints, we were unable to re-ensonify the trawled area to estimate trawl efficiency as originally planned. Therefore, we assumed 100% trawl efficiency when estimating biomass.

Sampling was synchronized between the 51-m wide midwater trawl and the ES80 echosounder for comparison of *in situ* and trawled catch biomass estimates. Acoustically-derived biomass in kg corresponding to each school sampled by midwater trawl ($B_{sch,t}$) was estimated as:

$$B_{sch,t} = (s_a / \sigma_{bs})(A_t)(\bar{W}) \tag{5}$$

where s_a was area backscattering coefficient ($m^2\,m^{-2}$) from echo integration of the classified school, σ_{bs} was the backscattering cross-section as defined earlier, A_t served as a proxy for trawl swept area (m^2), which was the product of the observed school trace length (m) and the trawl width of 51 m, and $\bar{W}$ was the average individual weight of 0.285 kg.

Acoustic biomass estimates for each Atlantic menhaden school sampled were then compared with catch from each sampled school that was stored in separate holds and weighed individually at port. The second school sampled (School 12) was sedentary enough to allow two passes, so both were included in this comparison; however, the fifth Atlantic menhaden school sampled (School 123) was too large to identify as a unique school in the ES80 echograms and was not included in this comparison.

2.1.4 Survey area biomass estimation

To estimate total study area (Fig. 1) biomass of Atlantic menhaden during the study period ($\hat{B}$), mean biomass per transect, calculated as the total acoustic biomass of schools on each transect multiplied by the search area of each transect, was expanded using the equation:

$$\hat{B} = \frac{\sum_i^n \frac{y_i}{t_i a}}{n} \text{A}, \tag{6}$$

where *n* was the number of transects, y_i was the total biomass of schools encountered on transect i,

t_i was the length of each transect, a was the omnidirectional sonar search distance (1.6 km each side of vessel), and A was the study area (km^2).

2.1.5 Atlantic menhaden school composition

Paired otolith and scale samples collected in the field were prepared using standard Virginia Institute of Marine Science (VIMS) survey protocols and procedures (Bonzek et al. 2017). Scale-based ages reported here were estimated by a scientist experienced in reading Atlantic menhaden scales at the NOAA Southeast Fisheries Science Center (SEFSC; ASMFC 2015). Otolith-based ages were estimated by a scientist experienced in reading Atlantic menhaden otoliths (Bonzek et al. 2017, VanderKooy 2020). Size, age, sex, and maturity composition were characterized by school and data collection type (fishery-independent at-sea, fishery-dependent at-sea, and fishery-dependent port samples). Given similarity between fishery-independent and fishery-dependent size-at-age observations, all size samples collected were used to estimate weight-at-length and total length vs fork length relationships.

2.1.6 Pelagic habitat use

Average school depth derived from ES80 data and *in situ* salinity, dissolved oxygen, bottom temperature, and surface temperature at sampled school locations (n=5) were summarized to characterize confirmed pelagic habitat use by Atlantic menhaden. Also, depth derived from ES80 data of all schools ensonified during the survey period (n=23) was summarized across the survey area.

Associations between presence of a sonar-identified school (n=38) and hydrographic conditions were explored quantitatively using a spatial binomial generalized additive model (GAM) with a logit link. Bottom temperature and salinity were selected because most schools ensonified and sampled were located at 20-35m. Hydrographic conditions at the location of all spotted schools were estimated by associating school geographic coordinates with rasters of average bottom temperature and salinity generated using inverse distance weighting of all *in situ* hydrographic data collected during the survey at regular intervals along survey transects and at sampling locations. School presence vs absence (*pres*) was modeled as follows:

$$\text{pres} = \beta_0 + f_1(depth) + f_2(btemp) + f_3(bsal) + f_4(lon, lat), \tag{7}$$

where *depth* was depth to sea floor, *btemp* was bottom temperature, *bsal* was bottom salinity, *lon* was longitude and *lat* was latitude.

3.1 Results

3.1.1 School behavior and biomass

During the survey, a total of 38 schools were identified as Atlantic menhaden with the omnidirectional sonar (Fig. 1), 23 of these were ensonified with the ES80 echosounder, and three ensonified schools were sampled. Although fishers report being able to pass over sedentary Atlantic menhaden schools in winter without disturbing them, Atlantic menhaden schools encountered during our survey exhibited more complex behavior that may be due to warmer than expected February bottom water temperatures. The winter midwater trawl fishery for Atlantic menhaden typically begins operations when temperatures drop to ~4-6^{o}C (S. Axelsson, H&L Axelsson, Inc., personal communication), but water temperatures during our survey averaged 6.3 ^{o}C with a range of 4.9-7.9 ^{o}C. Some schools remained sedentary to be both ensonified and sampled with midwater trawling, but many schools fled the vessel and avoided ensonification or dispersed after ensonification, likely due to elevated water temperatures. Most Atlantic menhaden schools encountered on the first two transects were extremely large, dense, and located near the middle-bottom of the water column. The survey period was then punctuated by a severe storm that suspended operations for four days. During the latter portion of the survey, Atlantic menhaden schools encountered were highly active, smaller in size, and tended to be located closer to the surface (Table 2). As a result, only three of 15 schools identified on the omnidirectional sonar on Transects 3-6 were ensonified (and sometimes visually identified from the vessel), but most were either too close to the surface or too active or dispersed to be ensonified and sampled.

During the survey, an additional 49 schools spotted on the omnidirectional sonar did not display typical Atlantic menhaden shoaling dimensions or density; three of these additional schools were categorized as “other fish” and 46 were categorized as “small pelagic school”. Similarly, during fishery-dependent post-survey acoustic data collection, an additional 24 schools were spotted on the omnidirectional sonar of which five were categorized as “other fish” and 19 were categorized as “small pelagic school”. Across both survey and post-survey acoustic sampling, the total biomass ensonified that did not display typical Atlantic menhaden backscatter was 58,661 kg, representing only 3% of the total biomass ensonified (1,754,563 kg).

During fishery-dependent sampling conducted post-survey (Table S1), schools were large, dense, and below the surface in a manner more similar to schools encountered on survey Transects 1-2. An additional 155 schools were identified on the omnidirectional sonar and 84 schools ensonified over five days (Fig. 1, Table S1).

Schools encountered during the survey were more likely to be found in colder, more saline waters at mean depths of 25-30 m in the southern end of the study area (Fig. S8-S9); however, no covariates of the spatial GAM were found to be good predictors of school presence (i.e., no significant covariates at α level of 0.05). Atlantic menhaden schools ensonified during both the survey and post-survey periods were located primarily at a mean depth range of 20-30 m (Fig. 2). However, schools were encountered throughout the study area at depths ranging from 11-40 m.

Acoustically derived biomass estimates of sampled Atlantic menhaden schools were compared with associated trawl catch weighed dockside (Fig. 3). Two of the five school biomass estimates (Schools 10 and 49) only differed by approximately 2% and 5% (749 and 10,388 kg), respectively. Passes 1 and 2 of School 12 differed from the dockside weight of that school by approximately 68 and 54% (19,899 and 16,678 kg). However, the estimate for School 13 differed substantially from its dockside weight by approximately 115% (68,898 kg).

3.1.2 School composition

All schools identified as Atlantic menhaden by the captain with omnidirectional sonar and subsequently sampled during survey and post-survey fishing operations were confirmed to be nearly homogeneous schools of Atlantic menhaden. Out of 3,110,380 kg of Atlantic menhaden landed and >4,299 fish sampled during the 2022 survey and fishing season, only one American shad (*Alosa sapidissima*) was collected in a sampled basket during post-survey sampling operations. Throughout all survey and post-survey sampling, other species were noted when observed in the chute or bycatch grate, recorded in the cruise notes, and given sampling workups for inclusion in the biosamples database when it was safe to collect them. This additional bycatch included one Atlantic mackerel, one Atlantic herring, one spiny dogfish (*Squalus acanthias*) and 10 striped bass (*Morone saxatilis*), all of which were collected during post-survey fishing operations. An additional 10-15 striped bass were caught but released during catch processing.

During the survey, a total of 81 individual Atlantic menhaden samples were selected for full data collection, including sex, maturity, eviscerated weight, and age (both scale- and otolith-based reads; Table 3). An additional 72 individual Atlantic menhaden samples were fully processed from the post-survey fishery-dependent sampling conducted by the scientific crew at-sea. An additional 150 fish were collected at port over five additional trips composed of seven hauls; all port samples received full workups.

The six schools of Atlantic menhaden sampled during the survey and two schools sampled post-survey were also nearly homogeneous in size (Fig. S10), sex ratio (Fig. S11), and age (Fig. S13). Average weight of all Atlantic menhaden sampled was 0.291 kg (SD = 0.055 kg) and average fork length was 265.7 mm (SD = 17.9 mm). We also noted that Atlantic menhaden appeared to be schooling by size, not age, given the size measurements across schools (Fig. S10) were less variable than age composition (Fig. S13); however, the variability in ages among schools may be indicative of aging error, which has been documented to be of concern for Atlantic menhaden age-3 and older (SEDAR 2020). Relationships between total length and fork length and weight and length of Atlantic menhaden sampled at sea were similar to previously published analyses of port samples collected primarily from the reduction fishery (Figs. 4-5; Smith et al. 2008).

Among Atlantic menhaden samples that received full workups (Table 3), 56% were female (SD = 9%), and sex ratio by school varied from 40% - 73% female (Fig. S11). Average length and weight of female Atlantic menhaden samples were slightly larger (273 mm, 0.32 kg; Fig. 6) than that of males (267 mm, 0.30 kg). In previous studies of Atlantic menhaden size conducted in New York (Westman and Nigrelli 1955) and Chesapeake Bay (McHugh et al. 1959), similar results were found for length, but not weight.

Most Atlantic menhaden sampled during this project were age-3 or age-4, regardless of sex and ageing method (Fig. 7) or collection period (Fig. S12). Ages ranged from age-2 to age-6 for scale-based age estimates and age-2 to age-5 for otolith-based ages. Most schools contained a mixture of 3-4 age classes (Fig. S13), and most Atlantic menhaden sampled that received full workups were visually identified as being mature (resting) regardless of age and sex, but some were identified as spent, ripe, or immature (Fig. 8).

3.1.3 Study area biomass

Total biomass of Atlantic menhaden in the 10,999 km^2-study area at the time of the survey was estimated to be 9,089,167 kg with a 95% confidence interval of 713,207 – 17,465,128 kg. Individual school biomass estimates were variable with a mean biomass of 41,129 kg (range 2 – 462,289 kg). Variability among transects in the number of Atlantic menhaden schools encountered ranged from 0 to 13 (Table 3). Mean encounter rate during the survey was 0.02 schools/km^2 (range 0 – 0.07) in terms of area surveyed or 0.07 schools/km (range 0 – 0.22) in terms of distance surveyed. One area of high-density school concentration was encountered during the survey on Transect 2 and another was found by the captain during fishing operations post-survey just south of the study area (Figs. 1 and 3).

4.1 Discussion

This study represents the first targeted, fishery-independent survey of adult Atlantic menhaden conducted offshore and the first to be implemented in winter. Although Atlantic menhaden have high socioeconomic and ecological value (Lipton 2009, Garrison et al. 2010, Anstead et al. 2021), available fishery-independent survey data are primarily collected from inshore multispecies surveys which use gears and methodologies not designed to target schooling pelagic species (SEDAR 2020). Two hydroacoustic surveys targeting Atlantic menhaden in spring through fall were conducted by Lucca and Warren (2018, 2019) in 2014 and 2015 over a much smaller area (2.83 and 4.68 km^2) than this study (10,999 km^2) in estuarine and nearshore coastal waters of New York. The only other offshore fishery-independent survey of adult fish conducted in winter in the Mid-Atlantic was the NOAA NEFSC Winter BTS (NEFSC 2025), which operated from 1992 to 2007. However, the Winter BTS caught very few Atlantic menhaden (28 in 14 out of 2,096 tows conducted in February; Fig. S14). Although it is possible that the spatiotemporal distribution of Atlantic menhaden along the coast in winter has shifted northward since the Winter BTS ended operation, fishery-independent ichthyoplankton surveys identified Atlantic menhaden eggs in winter in the Mid-Atlantic in some years concurrent with the Winter BTS (Simpson et al. 2017). Also, fishery-dependent at-sea observer data in the Mid-Atlantic have recorded the presence of Atlantic menhaden offshore in winter during some of the same years as the Winter BTS (Liang et al. 2020). Differences in catch of Atlantic menhaden between our survey and the Winter BTS are most likely due to use of a commercial fishing vessel and net and midwater trawling (vs bottom trawling).

Our survey has confirmed the partial migratory behavior of adult Atlantic menhaden that had been reported by the fishery and inferred by previous ichthyoplankton surveys. Partial migration is said to occur when a population is composed of a mixture of resident and migratory individuals (Chapman et al. 2012). Conclusions drawn from spatiotemporal analysis of fishery-dependent data (Roithmayr 1963, Nicholson 1971, 1972) and a mark-recapture study conducted 1967-1969 (Nicholson 1978) were that most, if not all, adult Atlantic menhaden migrate south in winter to waters offshore of Cape Hatteras. Spatial seasonality in the observation of Atlantic menhaden adults most likely reflects a combination of partial migratory behavior, temperature-driven location of schools lower in the water column in winter as in this study and in June and Reintjes (1959), and winter weather conditions prohibiting the safe fishing operations in northern coastal waters. Reanalysis of historical mark-recapture data spanning 1967-1975 indicated that Atlantic menhaden are likely partial migrants such that 33-55% of adults tagged in the northern portion of their range migrated in late fall with the majority of migrants being recaptured south of Cape Hatteras (Liljestrand et al. 2019, Liljestrand et al. 2025). Also, long-term ichthyoplankton surveys (1977-1987, 2000-2013) have documented Atlantic menhaden larvae in northern regions in winter months, which suggests the presence of spawning adults in winter across the Mid-Atlantic (Simpson et al. 2016, Simpson et al. 2017). The catch of five adult Atlantic menhaden offshore north of Delaware Bay over the 16 years that the Winter BTS operated (NEFSC 2025) was insufficient to confirm the presence of significant overwintering biomass. In contrast, our targeted survey encountered numerous large schools of adult Atlantic menhaden along the Mid-Atlantic shelf from the New Jersey-Delaware border to Hudson Canyon (Fig. 1) during a time of year when migratory adult Atlantic menhaden are typically found south of Cape Hatteras. Our study provides conclusive evidence that adult Atlantic menhaden are partial migrants. Other clupeids such as Atlantic herring in the North Sea have been shown to exhibit partial migration behavior as well (Ruzzante et al. 2006).

We found that overwintering Atlantic menhaden were patchily distributed across the offshore shelf (Fig. 1). Clustering of schools was also reported by Lucca and Warren (2019) in their spring-fall surveys of Atlantic menhaden in coastal waters of New York approximately 6 km offshore. Use of the novel survey design of Liang et al. (2020) allowed us to expand the search area along each transect from that of a traditional, echosounder-only hydroacoustic survey with an approximate width of 6 m in our study area (i.e., maximum diameter of echosounder cone) to a transect width of 3.2 km. We were thus able to efficiently survey a large area without having to greatly increase the number of transects and their associated costs. Schools located on the transect that may have moved to avoid being passed over by the vessel could be observed with our omnidirectional sonar, but would likely have been missed by the downsounder in a traditional hydroacoustic survey. Conclusions drawn from the Liang et al. (2020) simulation study proved correct in that a traditional acoustic survey design employing only a downward-facing echosounder collecting data only below the vessel along the transect would have had a very low probability of encountering Atlantic menhaden schools directly on the transects. This approach could be used to develop future surveys for Atlantic menhaden or other schooling pelagics that have proven too difficult or costly to survey with traditional bottom trawling and hydroacoustic survey designs. Given we found Atlantic menhaden schooling behavior to be highly dependent on water temperature, we recommend that future surveys incorporate real-time oceanographic condition monitoring to determine the most appropriate time to conduct the survey.

By employing advanced echosounder and sonar equipment already present on an active fishing vessel with experienced captains and crew, we were able to explore the utility of industry-series acoustic technology in cooperative research. Additional post-survey calibration and processing of ES80 files was required relative to the use of scientific-series sonar. Thus, future hydroacoustic studies that use industry-series acoustic equipment should anticipate substantial additional processing time. Despite these complications, we found that most acoustically derived biomass estimates and trawl catch weights obtained dockside by individually weighing each school were similar (Fig. 3). O'Driscoll et al. (2002) found scientific-series acoustic estimates of abundance and the abundance of midwater trawl survey catches of capelin (*Mallotus villosus*) were similar in magnitude while midwater trawl catches tended to be larger than acoustic estimates; however, our study was the first to individually weigh large clupeid schools for comparison of biomass. Estimation of biomass for large, dense schools is often problematic (Simmonds and MacLennan 2008), and can be affected by a variety of factors such as density, shape, and behavior of the school as well as efficiency of the trawl set and quality of the sonar data collected. For example, the large difference we observed between trawl catch and acoustic school biomass estimates for School 13 (Fig. 3) was likely due to this school being a highly mobile relative to others encountered. It is possible that the ensonification pass or net deployment triggered avoidance behavior that resulted in trawled catch being much smaller than the acoustic biomass estimate. Avoidance is a common issue in all vessel-based fish surveys that can lead to underestimation of biomass (Brehmer et al. 2019). Future applications of this survey design should explore methods for reducing vessel noise and school disturbance during net deployment.

Estimated overwintering biomass of Atlantic menhaden in the study area (9,089,167 kg) likely represents a minimum estimate for several reasons. First, we assumed 100% trawl efficiency even though we were not able to achieve it because we were not able to pass over most trawled schools to collect the acoustic data necessary to estimate trawl efficiency due to vessel avoidance after trawling. We did not use published estimates of midwater trawl efficiency because they largely focus on groundfish and other species with schooling behavior dissimilar to Atlantic menhaden (Williams et al. 2015); however, efficiency estimates for midwater trawl surveys of forage fish such as capelin have found that acoustic abundance estimates and trawl catches were similar (O'Driscoll et al. 2002). Second, it is possible that some Atlantic menhaden do not exhibit dense schooling behavior during the daytime in winter, which would lead us to underestimate total biomass. We also observed a marked change in schooling behavior mid-survey that may have reduced our ability to detect schools and hindered our ability to ensonify and sample schools detected on the transects (Tables 2-3, Fig. 1). With a rise in water temperature and salinity between Transects 2 and 3, we found that Atlantic menhaden schools were smaller, highly dispersed, and often nearer the surface during the day (Fig. S15). This change in behavior may have been due to the diffusion of warm eddy waters onto the shelf as detected in satellite-derived images of sea surface temperature during the survey period (pers. comm. Avijit Gangopadhyay and Sarah Salois). We also noted during post-survey, fishery-dependent sampling that extremely large Atlantic menhaden schools appeared to be densely aggregated in a location just south of our study area (Figs. 1 and 3), indicating our survey results may not be representative of the entire Mid-Atlantic region and that Atlantic menhaden were associated with pelagic habitat characteristics we were unable to characterize. Other sources of uncertainty in our estimate of study area biomass include low independent sample size (i.e., ensonification of six schools), mobility and density of schools, and lack of a menhaden-specific estimate of target strength (TS). Digital computed tomography or magnetic resonance imaging of a subset of sampled fish could be used to inform Atlantic menhaden-specific TS values and could substantially reduce uncertainty in acoustic estimates of biomass.

Despite these challenges, our study provides valuable information for stock assessment and management of Atlantic menhaden. In addition to confirming the presence of large numbers of overwintering, mature, adult Atlantic menhaden in the Mid-Atlantic, we anticipate that life history data collected from this study can inform stock assessment estimates of growth. Most Atlantic menhaden sampled in this winter survey were age-3 and age-4 with a median fork length and weight of 266 mm and 0.288 kg, respectively. Thus, survey-caught Atlantic menhaden were larger and older than fish typically encountered in the port samples used to inform the stock assessment (median fork length = 219 mm; median weight = 0.184 g). Most port samples used in the stock assessment for Atlantic menhaden are collected from the reduction fishery, which operates primarily in estuarine and inshore waters in Chesapeake Bay and the southern Mid-Atlantic where smaller, younger fish typically reside (SEDAR 2020). Fishery-independent size-at-age data for older, larger Atlantic menhaden are rare; therefore, we anticipate data collected from this survey will help provide context for the estimation of population size-at-age in the stock assessment. Also, it may be possible in the future to monitor the adult overwintering portion of the stock using samples collected from the midwater trawl fleet given similarity in size, age, and sex ratio between fishery-independent and fishery-dependent samples collected in this study (Figs. S10-S13). Our survey was limited in spatial extent to shelf waters offshore of New Jersey, yet the winter midwater trawl fleet typically ranges from Rhode Island to Maryland and may, therefore, have the potential to collect valuable data from the overwintering portion of the Atlantic menhaden stock in the Mid-Atlantic and Southern New England area if sampled more thoroughly. Such monitoring could provide information on changes over time in size and age structure to help ensure sustainable development of the winter midwater bait fishery in this region.

This study also provided novel information for assessment and management by estimating Atlantic menhaden biomass across a large region independent of the stock assessment. Our results indicated that the magnitude of Atlantic menhaden biomass overwintering in the study area was a small fraction of the population. Estimated Atlantic menhaden biomass in our study area was approximately 0.78% of coastwide age 2+ biomass estimated by the most recent stock assessment (ASMFC 2025). Visual inspection of fish examined for maturity stage in our study indicated that most of the Atlantic menhaden encountered did not exhibit signs of active spawning at time of capture (Fig. 8); however, females spawn at night and most mature Atlantic menhaden caught in our survey appeared to be resting between batches, which are typically released 5-10 days apart (Latour et al. 2023). Our findings are consistent with ichthyoplankton surveys conducted in the region that have documented spawning in February (Simpson et al. 2017). Potential spatial heterogeneity in growth and fecundity resulting from partial migratory behavior observed in this study should be taken into account when assessing the stock and when considering coastwide management measures that may affect spatial distribution of fishing effort across the stock's range (Chapman et al. 2012).

In conclusion, the novel survey design applied in this study can be used to generate a biomass estimate for a schooling pelagic species that is patchily distributed because it allows the search area to be expanded without losing the scientific integrity of a line transect sampling approach. However, Atlantic menhaden biomass was likely underestimated due to several limiting factors, namely unknown trawl efficiency (assumed to be 100% efficient) and temperature-dependent Atlantic menhaden schooling and vessel/net avoidance behavior. Lack of a species-specific target strength estimate could also have affected the accuracy of school biomass estimates. The information this study provides on school size and composition, school encounter rate, and temperature-driven schooling behavior can be used to modify and improve future Atlantic menhaden surveys.

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CRediT authorship contribution statement

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Data availability

Biological sample and school biomass estimate data have been archived with Mendeley Data (Nesslage et al. 2026a, Nesslage et al. 2026b). Raw echosounder and calibration data have been archived at the National Centers for Environmental Information. All scales and otoliths collected have been archived at the NOAA Southeast Fisheries Science Center Beaufort Laboratory.

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Tables

Table 1. Length, direction, and starting and ending coordinates of survey transects.

Transect	**Length (km)**	**Direction**	**Start Latitude**	**Start Longitude**	**End Latitude**	**End Longitude**
1	56	Offshore	38°48'29.688"N	-74°38'18.819"W	38°27'6.619"N	-74°11'13.343"W
2	60	Inshore	38°40'48.059"N	-73°57'14.729"W	39°5'14.631"N	-74°24'53.822"W
3	57	Offshore	39°14'24.743"N	-74°10'38.48"W	38°52'33.051"N	-73°43'19.613"W
4	58	Inshore	39°6'23.956"N	-73°29'57.635"W	39°26'44.378"N	-74°0'30.014"W
5	57	Offshore	39°39'10.03"N	-73°51'19.167"W	39°20'2.715"N	-73°19'46.881"W
6	63	Inshore	39°35'1.342"N	-73°11'25.5"W	39°54'43.975"N	-73°47'27.592"W

Table 2. Atlantic menhaden schools ensonified, mean school depth (m), mean school biomass (kg), and total biomass (kg) of Atlantic menhaden estimated during each fishery-independent survey trip and during post-survey fishery-dependent sampling.

Data collection period	**Number of ensonified schools**	**Mean school depth (m)**	**Mean school biomass (kg)**	**Total biomass (kg)**
Survey Transects 1-2	20	25.7	47,291	945,811
Survey Transects 3-6	3	20.1	54	162
Post-Survey	84	26.1	23,662	1,987,620

Table 3. Schools or trips/hauls sampled and samples collected pre- and post-survey.

Transect	**Sampling period**	**Schools ensonified**	**Schools/trips sampled**	**Number of fork length, total length, whole weight samples**	**Number of sex, maturity, eviscerated weight, age (scale & otolith) samples**
1	Survey	7			
2	Survey	13	3 schools	2,132	80
3	Survey	2			
4	Survey	1			
5	Survey	0			
6	Survey	0			
N/A	Post-survey (at-sea)	84	2 schools	2,005	72
N/A	Post-survey (port)	N/A	5 trips (7 hauls)	150	150
Total		107		4,287	302

Figures

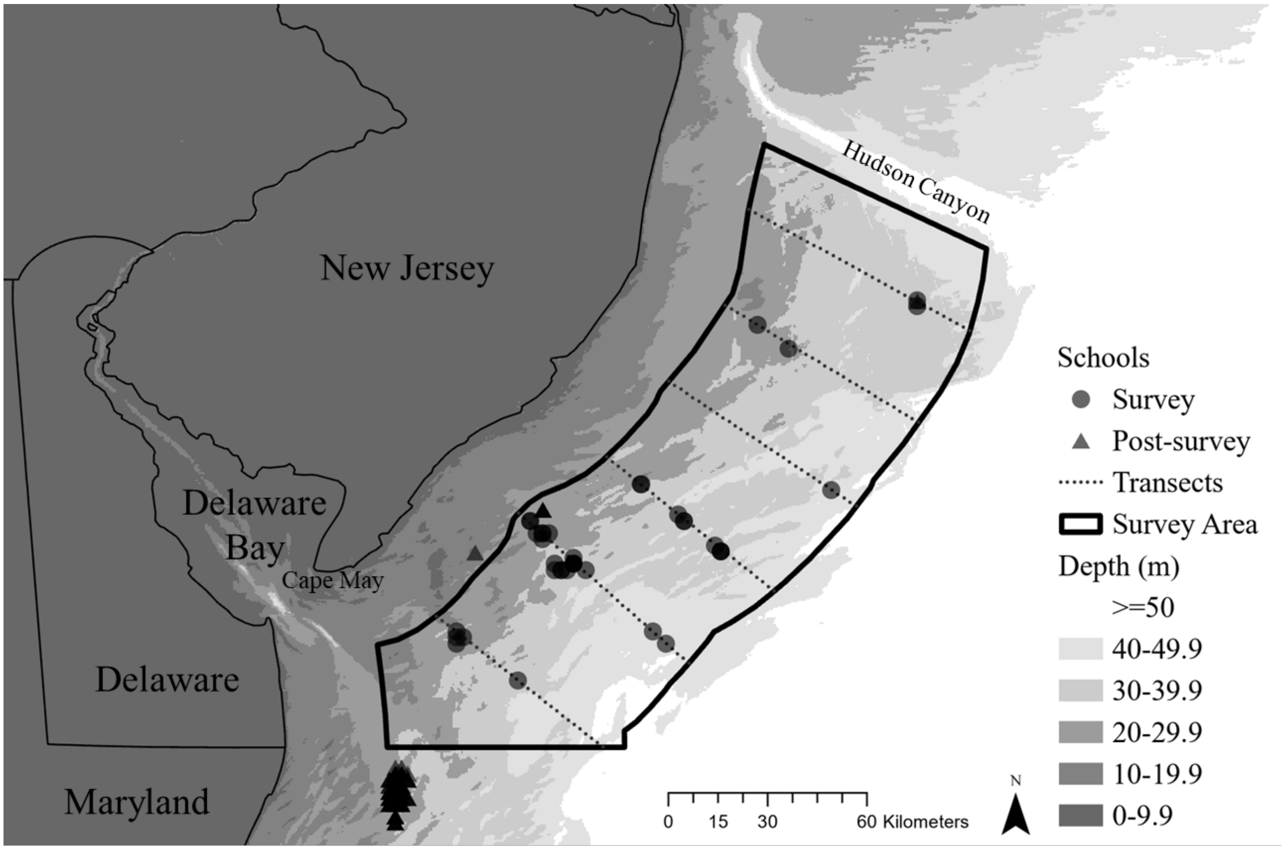


Figure 1. Cooperative Atlantic Menhaden Winter Survey study area extent, survey transects, regional bathymetry, and locations of schools encountered during the fishery-independent survey period (circles) and post-survey fishery-dependent sampling (triangles). School location symbols are semi-transparent to highlight the presence of multiple schools in high-density areas.

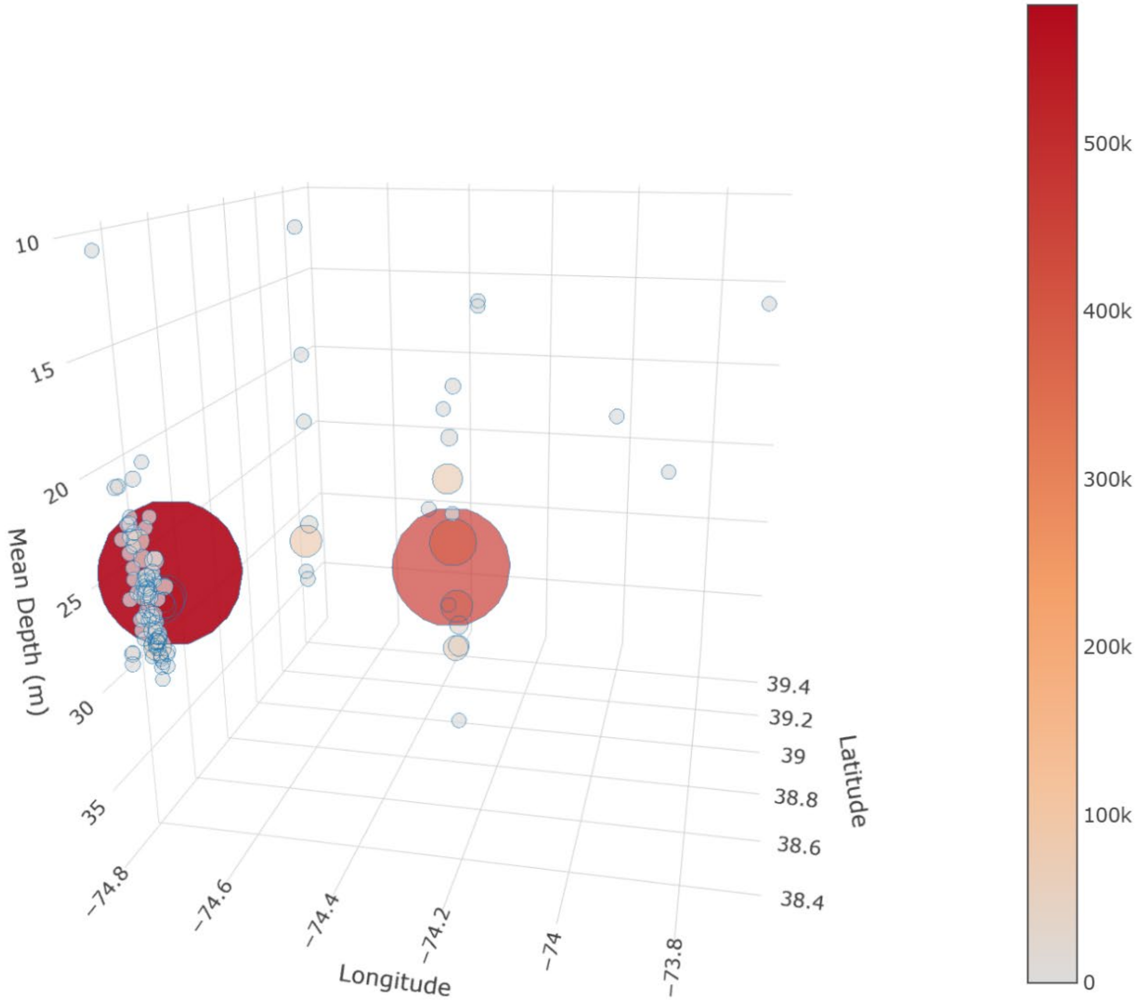


Figure 2. Geographic location and mean depth (m) of all schools identified as Atlantic menhaden during survey and post-survey acoustic sampling. Size and color indicate acoustically estimated weight (kg) of each school. The color bar represents 1,000s of kg.

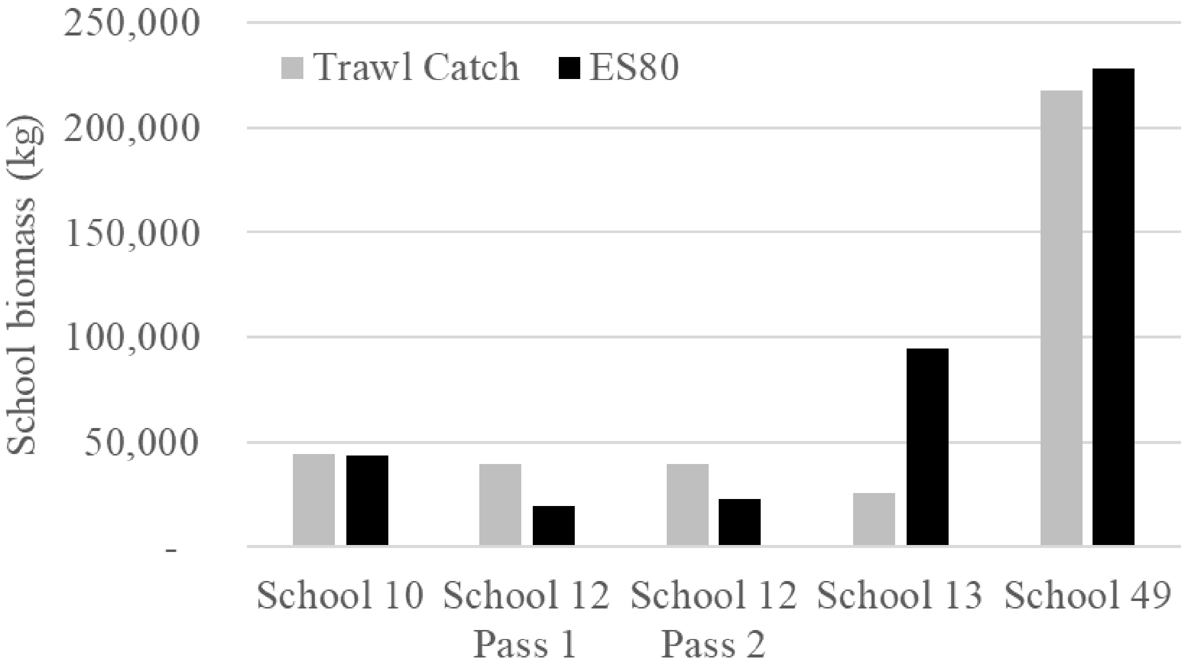


Figure 3. Atlantic menhaden school biomass (kg) estimated from synchronized sampling by 51-m midwater trawl (Trawl Catch) and a 38-kHz Simrad ES80 split-beam echosounder (ES80). Note that Schools 10, 12, and 13 were sampled during the survey period in the survey area; however, School 49 was sampled during the post-survey period south of the survey area (Fig. 1).

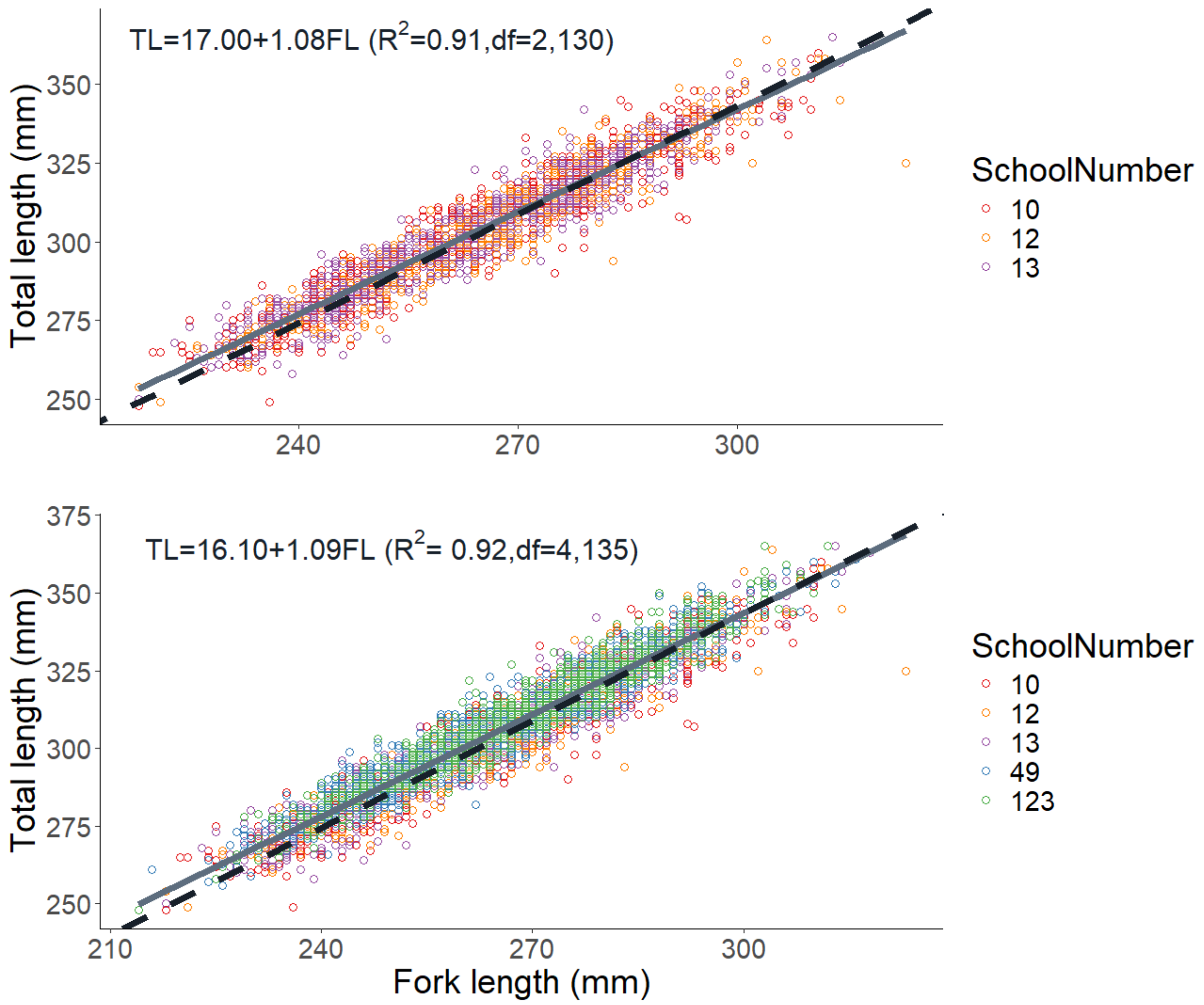


Figure 4. Relationship between total length (mm) and fork length (mm) for Atlantic menhaden sampled at-sea during the survey (TOP) and both survey and post-survey at-sea sampling (BOTTOM). Dashed black line represents relationships estimated from data collected during this study, and solid gray lines represents reduction fishery port sampling-based relationship published by Smith (2008).

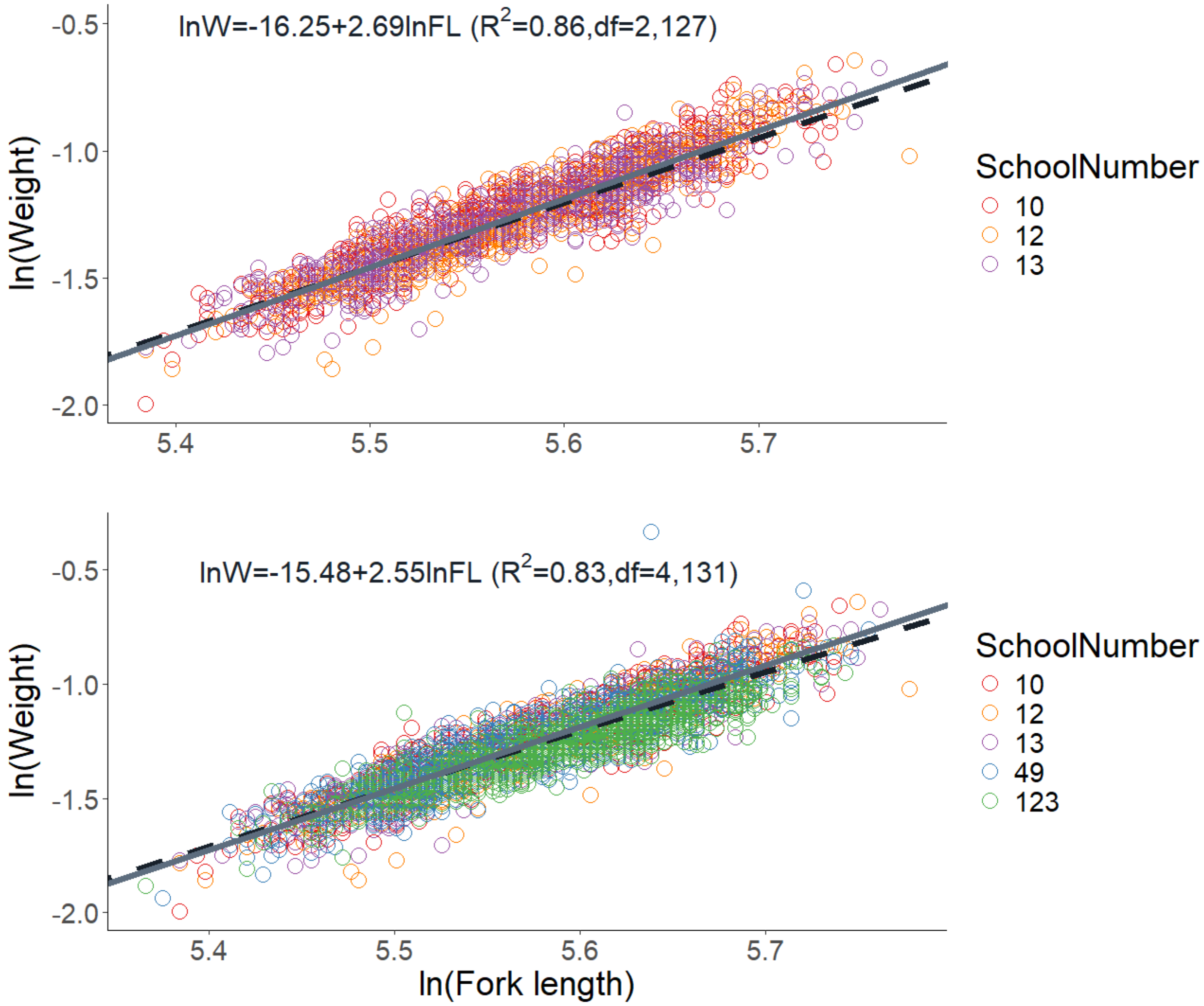


Figure 5. Relationship between the natural log of weight (kg) and the natural log of fork length (mm) for Atlantic menhaden sampled at-sea during the survey (TOP) and both survey and post-survey at-sea sampling (BOTTOM). Dashed black line represents relationships estimated from data collected during this study and solid gray lines represents reduction fishery port sampling-based relationship published by Smith (2008).

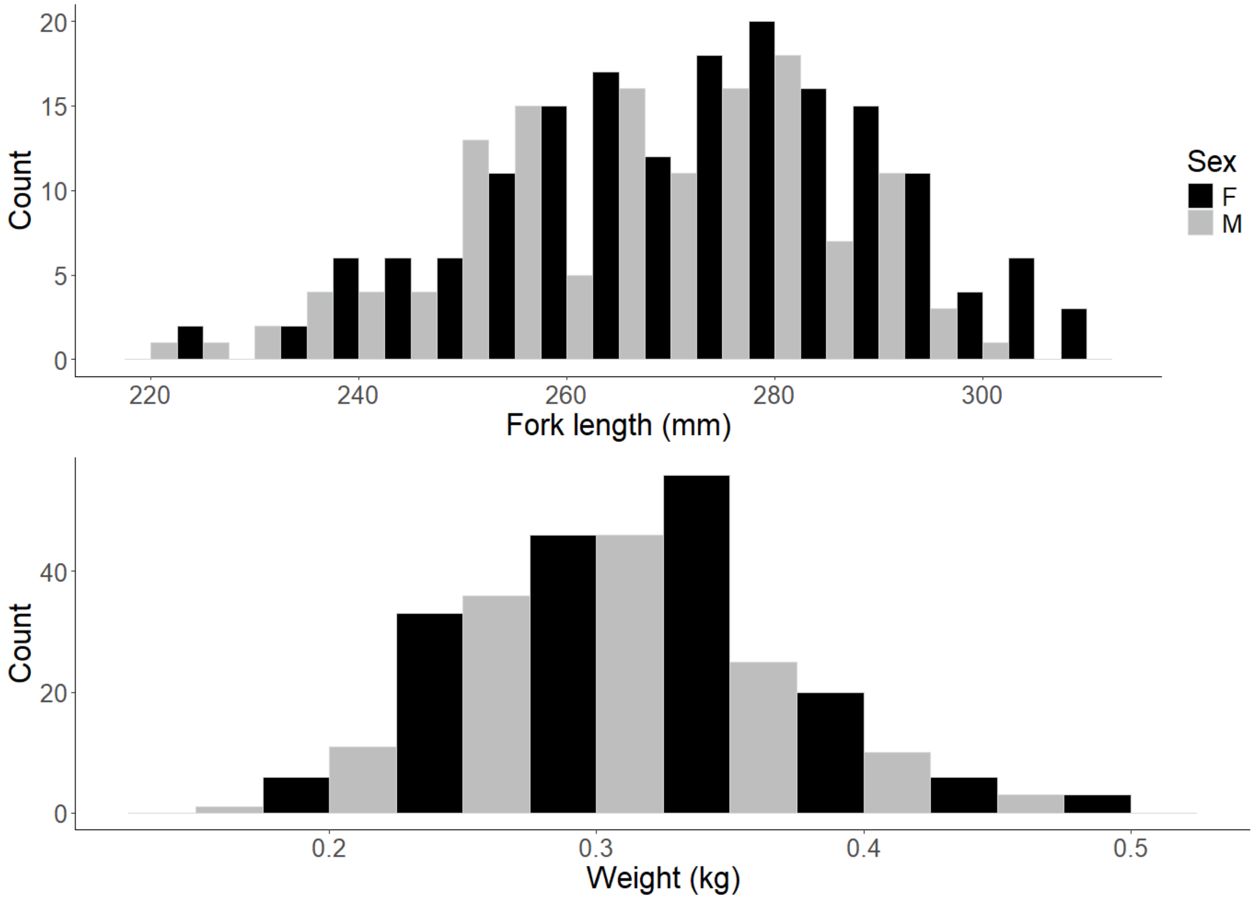


Figure 6. Fork length (mm) and weight (kg) distribution of Atlantic menhaden across all samples collected and proportion of all Atlantic menhaden samples categorized by sex. “F” denotes female and “M” denotes male.

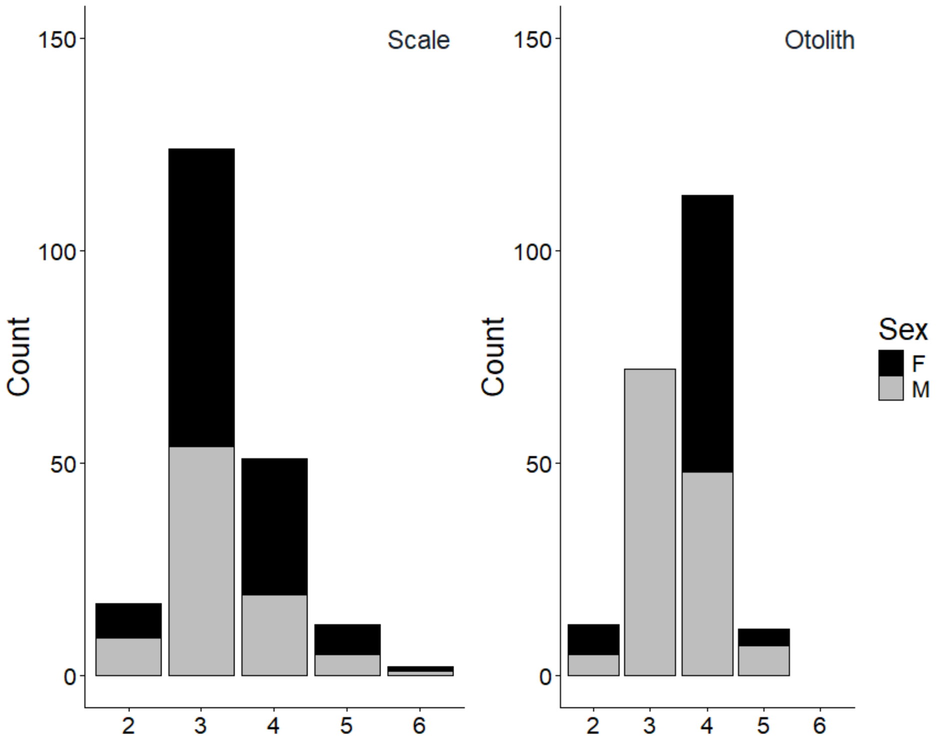


Figure 7. Proportion of all Atlantic menhaden samples at age by sex determined by NOAA Beaufort Laboratory readings of scales (left) versus VIMS readings of otoliths (right). “F” denotes female and “M” denotes male.

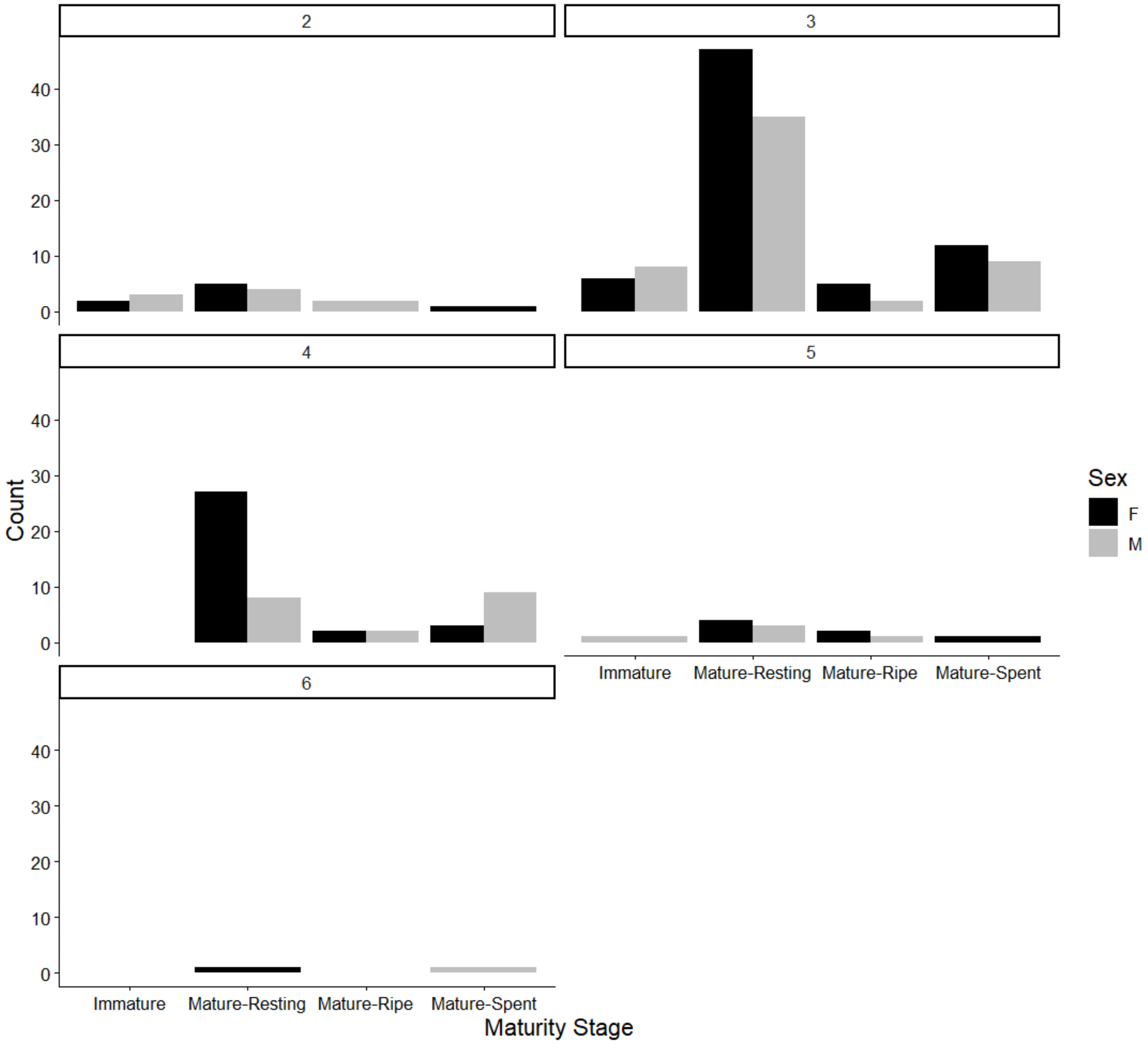


Figure 8. Maturity stage (visual identification) by age (scale-based) and sex of all Atlantic menhaden sampled.

Supplemental materials

Table S1. 2022 Cooperative Atlantic Menhaden Winter Survey timeline.

Date	Survey event
Feb 11-Feb 13, 2022	At-sea sonar calibration
Feb 14-Feb 15, 2022	Transects 1-2
Feb 16-Feb 19, 2022	Survey suspended due to severe storm
Feb 20-Feb 24, 2022	Transects 3-6
Feb 28-Mar 4, 2022	Additional at-sea samples collected by VIMS during fishing
Mar 6-Mar 22, 2022	Additional port samples collected by Lund's Fisheries

Table S2. Macroscopic maturity classification criteria for Atlantic menhaden by sex.

Maturity Stage	**Male Description**	**Female Description**
Immature	Testes small, flat; translucent or opaque	Ovaries small, cylindrical; translucent
Mature – resting	Testes triangular, firm; white; milt absent	Ovaries cylindrical; yellow–orange; oocytes not visible
Mature – ripe	Milt expressible or freely flowing	Ovaries cylindrical; orange; oocytes visible
Mature – spent	Testes triangular, flaccid; gray/mottled; often bloody	Ovaries cylindrical, flaccid; red–purple; often bloody

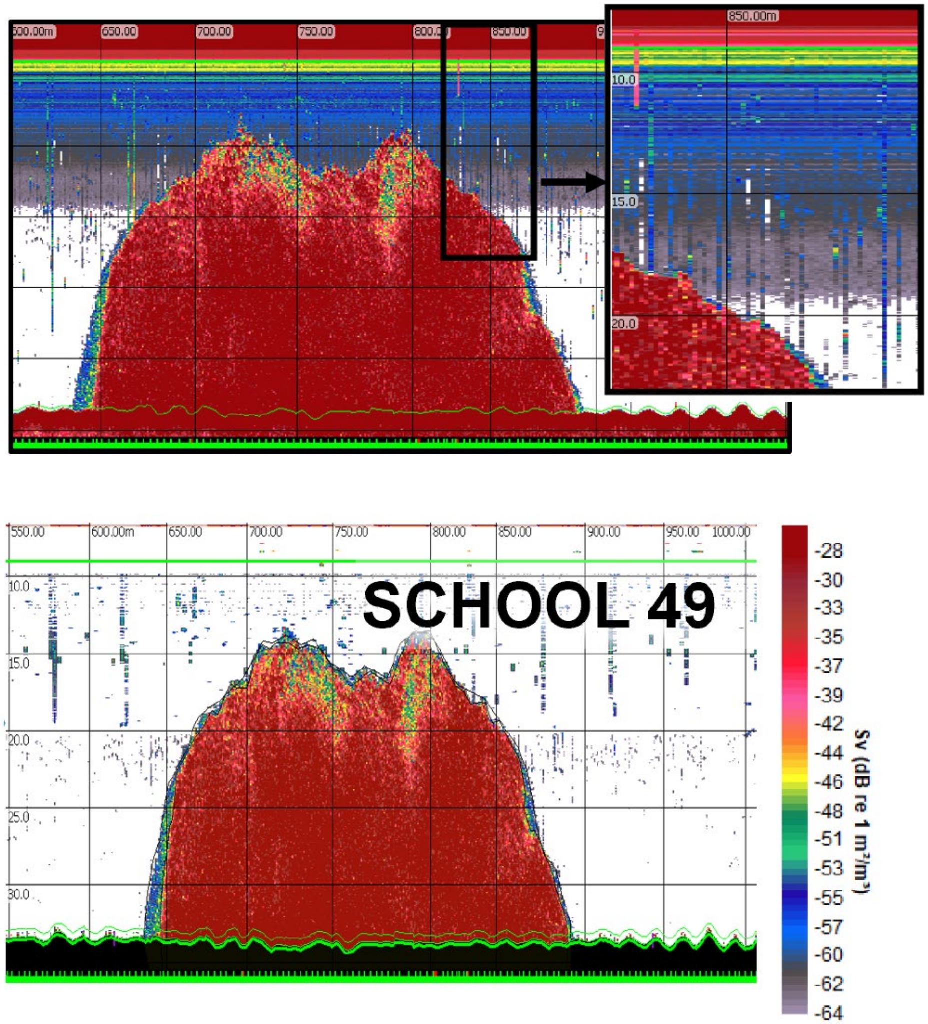


Fig. S1. Example of Sv backscatter of School 49 in ES80 raw data. (TOP) shows apparent noise ringing down to approximately 20 m and random impulse noise. (BOTTOM) Filtered Sv backscatter after masking the upper water column and remove the impulse noise spikes.

Supplement to Section 2.1.2 Hydroacoustic data analysis

ES80 data files of the calibration sphere were used to adjust calibration results from the field. Sound speed was updated in Echoview based on water surface temperature from the ship's National Marine Electronics Association network recorded in the data file source and user-entered salinity estimate. Target strength of the sphere was determined from single echo detections within the region in the echogram corresponding to the echo traces of the sphere (Figs. S2 – S3).

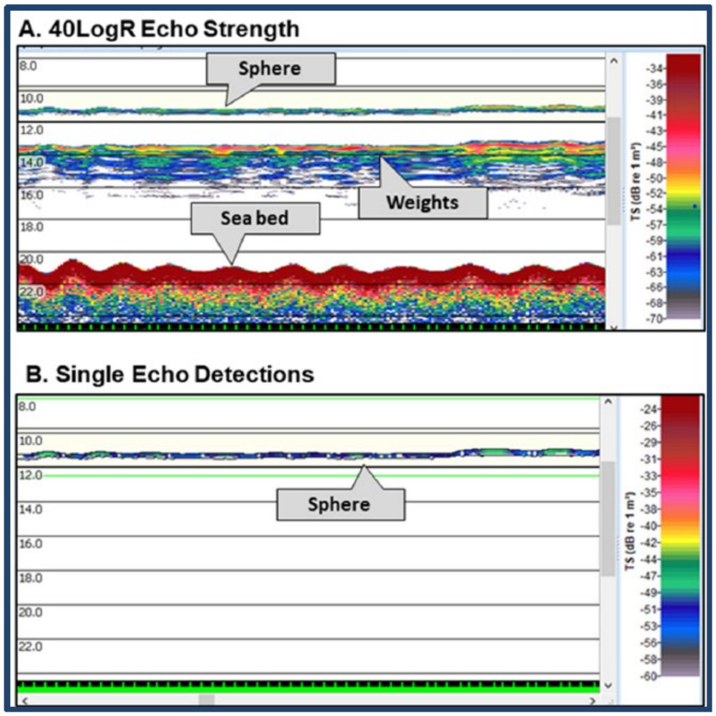


Figure S2. (A) Raw echo strength (40Log R) ES80 amplitudes during calibration on 11 February 2022, (B) single echo detections sphere near 11 m.

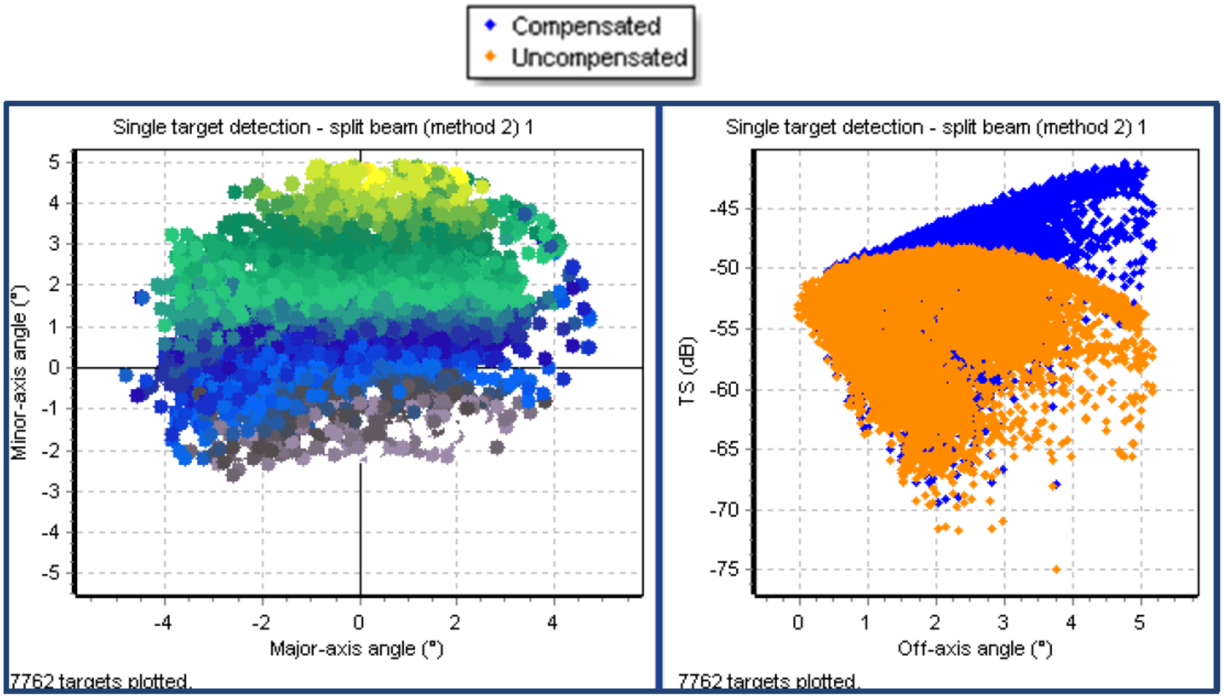
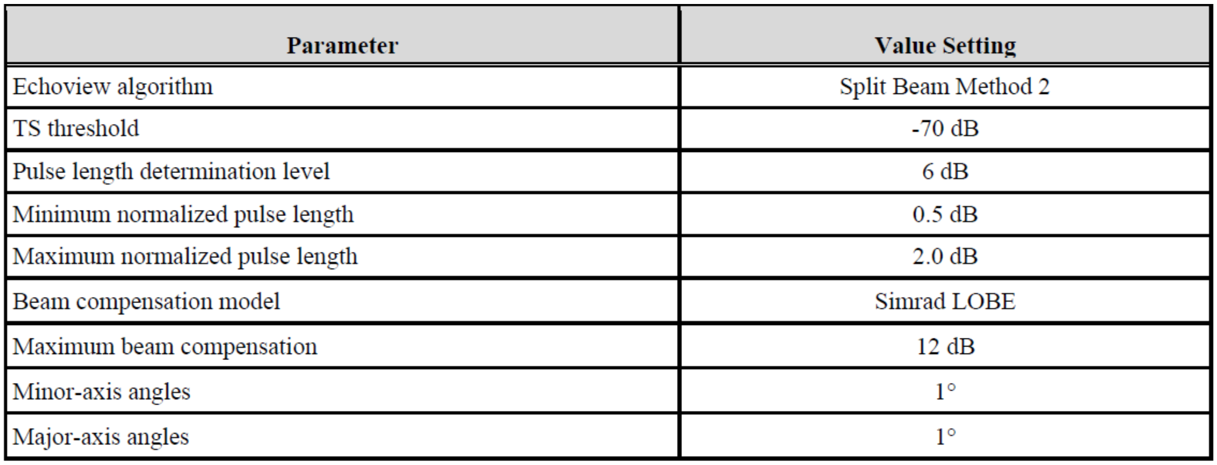


Figure S3. Angular TS compensation plots of 38.1 mm tungsten carbide sphere with default Transducer Gain at 23 dB.

Single echo detection criteria selected in Echoview are given in Table S2 below. Single echo detections were also analyzed after filtering out single echoes greater than 0.5° off the acoustic axis.

Table S2. Single echo detection criteria used in Echoview software settings.



Parameter	Value Setting
Echoview algorithm	Split Beam Method 2
TS threshold	-70 dB
Pulse length determination level	6 dB
Minimum normalized pulse length	0.5 dB
Maximum normalized pulse length	2.0 dB
Beam compensation model	Simrad LOBE
Maximum beam compensation	12 dB
Minor-axis angles	1°
Major-axis angles	1°

The target strength of the sphere under field conditions prior to field calibration adjustments to angles (Fig. S4) and after angular offsets were applied (Fig. S5) indicated further improvement was possible. Based on all single echo detections in Echoview, the echo strength peaked at a major axis angle offset of -0.43° and minor axis angle offset at 2.02° (Fig. S6). The transducer gain was adjusted to 19.67 dB such that the mean target strength of on-axis single echo detections matched the reference target strength of -42.31 dB re m^2. After the transducer gain was adjusted, a new S_a correction factor of 1.2652 dB was determined based on the on-axis sphere targets and equation 4.9 from Demer (2015). The adjusted transducer gain and S_a correction factor from the post-hoc analysis of the calibration data in Echoview was updated in the Echoview calibration supplement file.

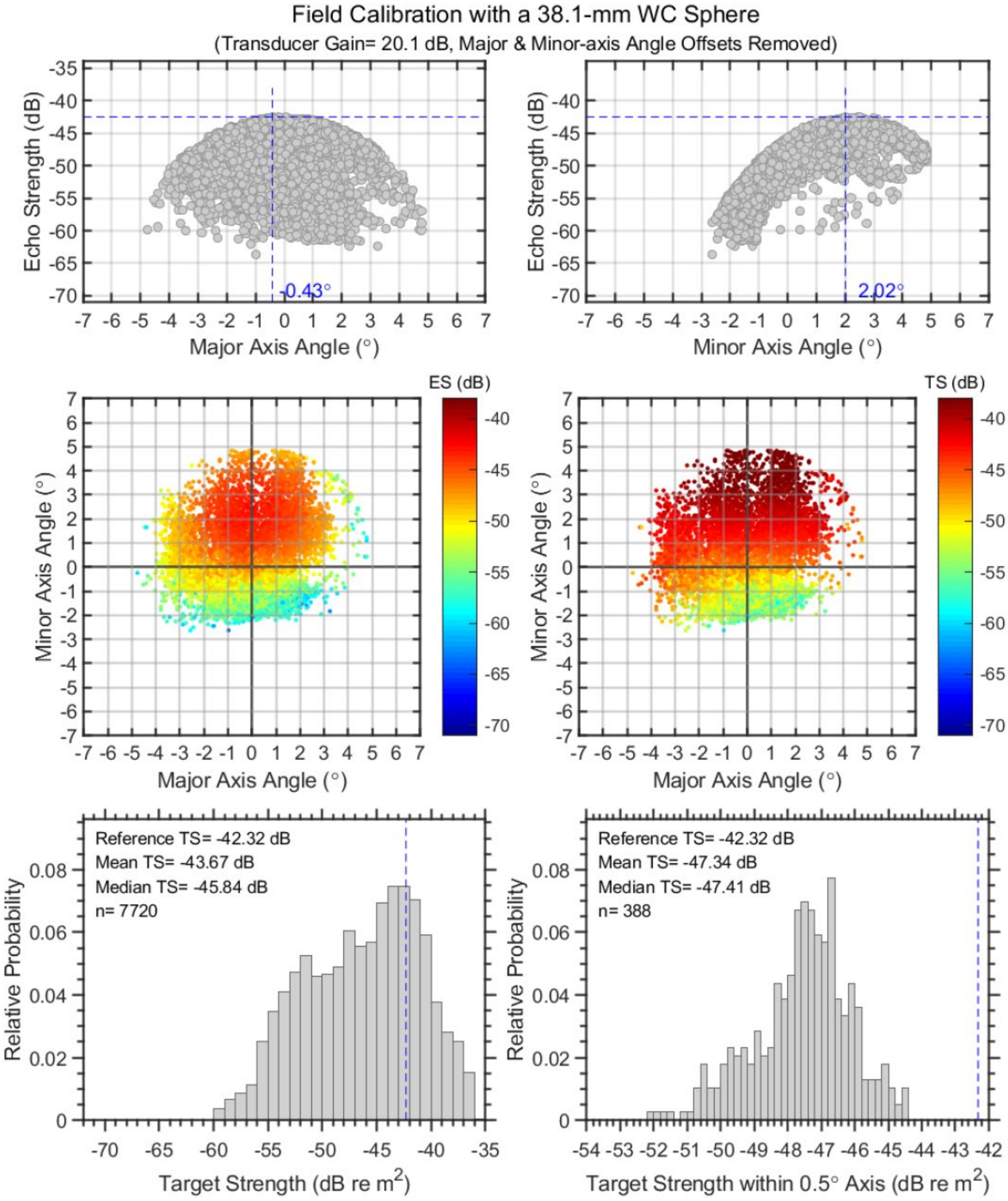


Fig. S4. TOP and MIDDLE: Angular target strength plots of a 38.1-mm Tungsten Carbide sphere with field-calibrated transducer gain of 20.1 dB and major and minor axis angle offsets from field calibrations removed; BOTTOM: target strength histograms of all (left) and on-axis (right) single echo detections.

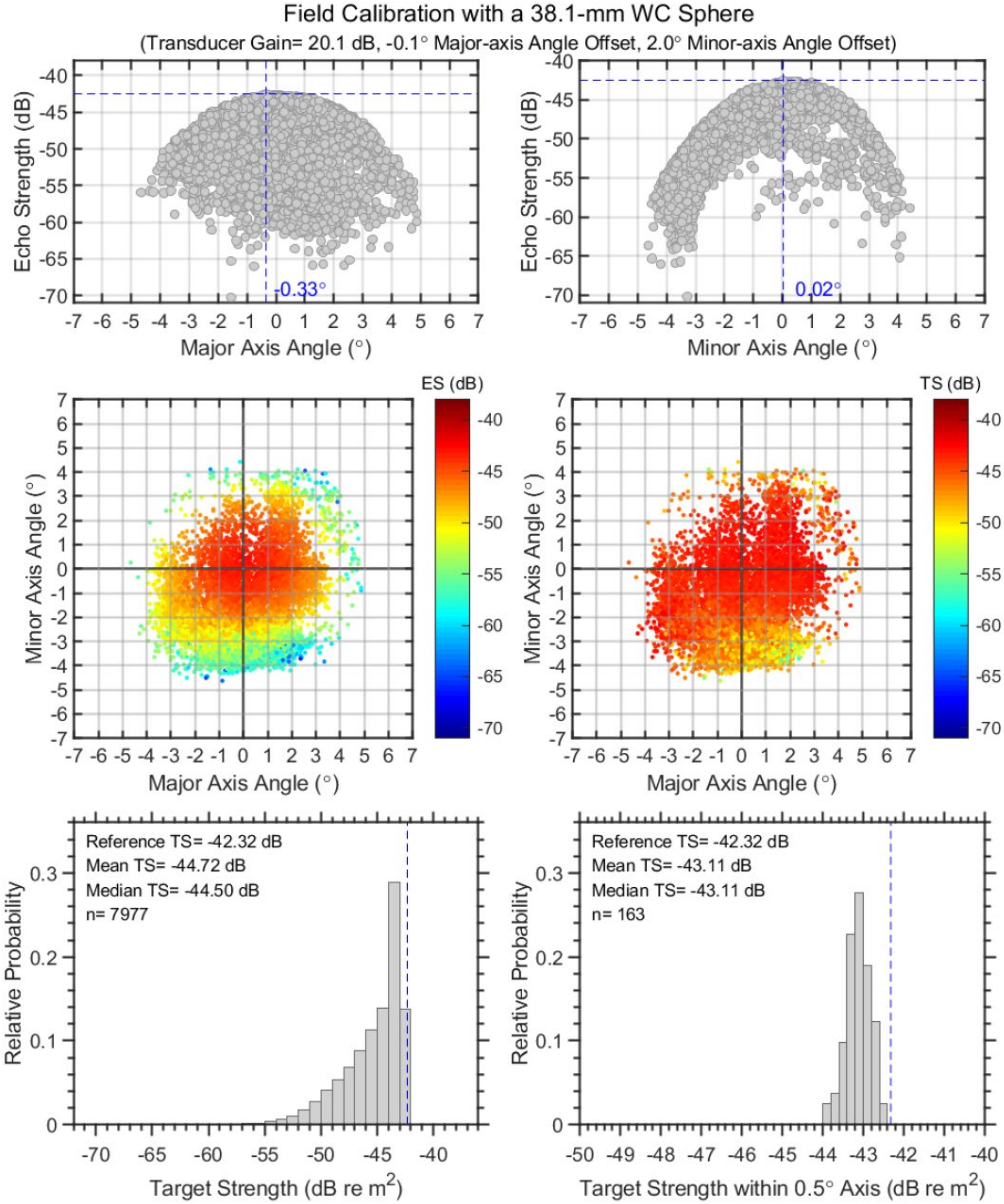


Fig. S5. TOP and MIDDLE: Angular target strength plots of a 38.1-mm Tungsten Carbide sphere with field-calibrated transducer gain of 20.1dB and major and minor axis angle offsets applied; BOTTOM: target strength histograms of all (left) and on-axis (right) single echo detections.

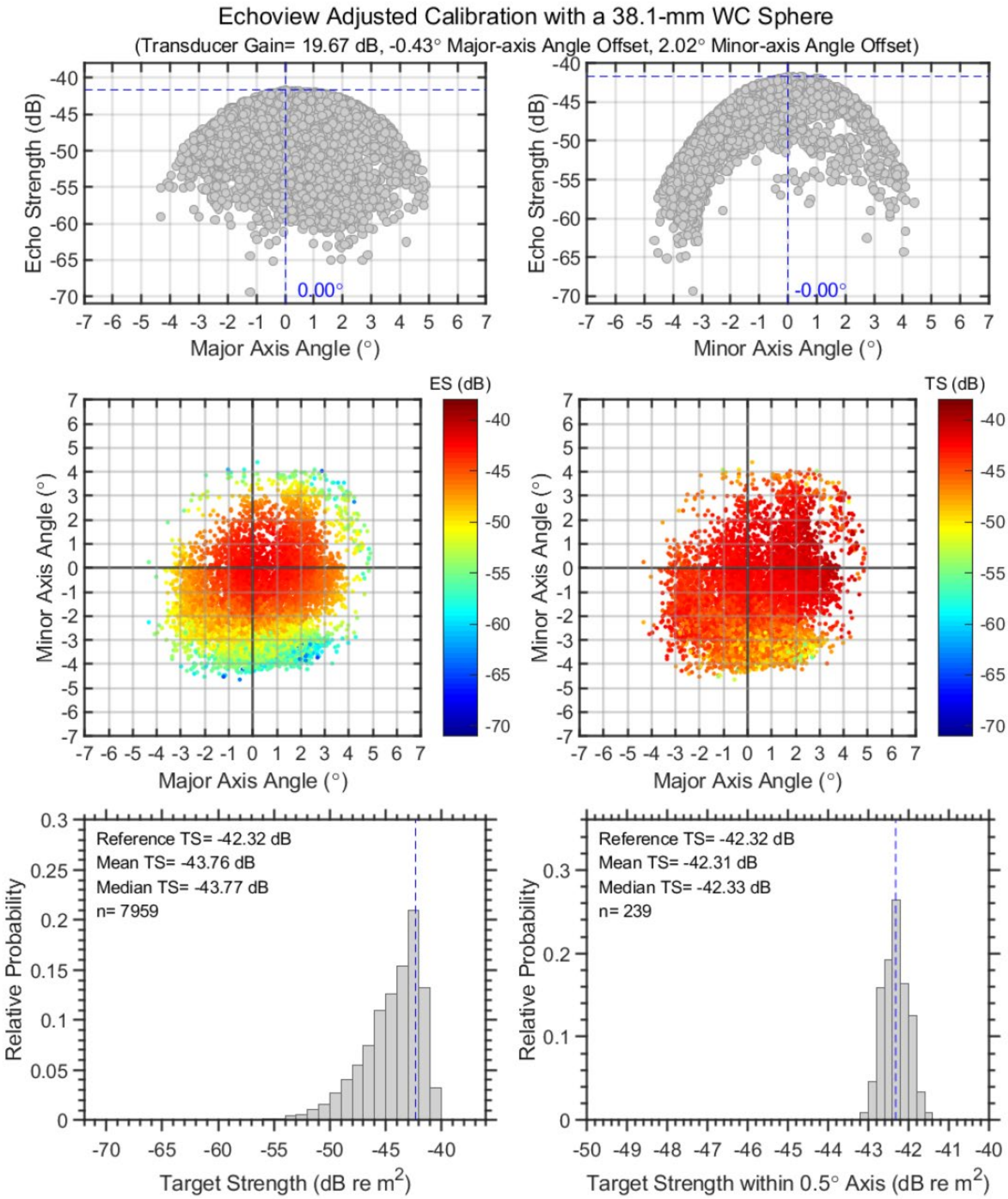


Fig. S6. TOP and MIDDLE: Angular target strength plots of 38.1 mm Tungsten Carbide sphere with on-axis adjustments of transducer gain to 19.67 dB and major and minor axis angle offsets of -0.43° and 2.02°; BOTTOM: target strength histograms of all (left) and on-axis (right) single echo detections.

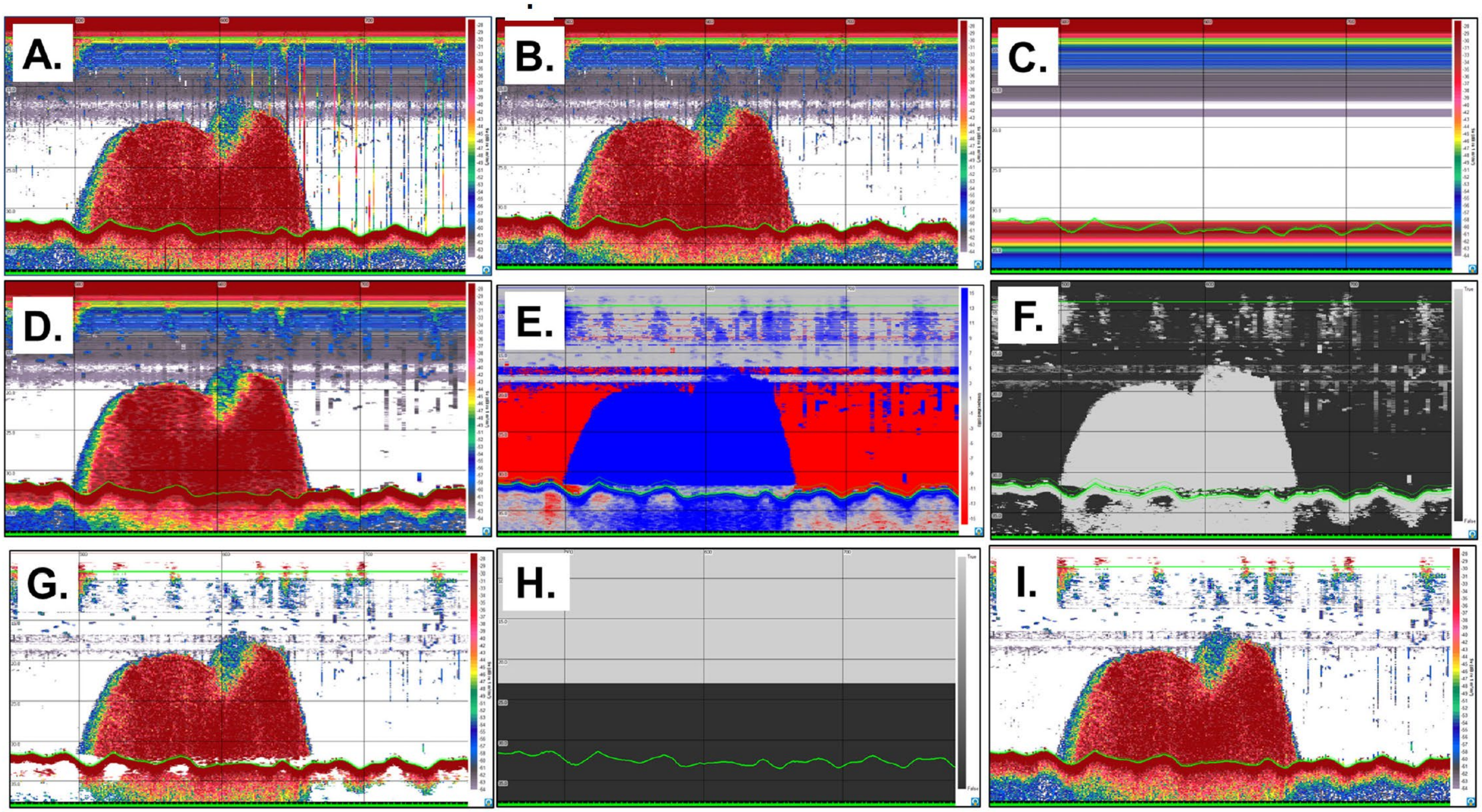


Fig. S7. Step by step echogram processing: A. Raw Sv. B. Impulse noise removed (Ryan et al. 2015). C. Resampled (median of 2000 ping × 3 sample window and matched Sv pings. D. Smoothed 3×3 Sv. E. Signal-to-Noise Ratio (SNR). F. Mask |SNR| > 3 dB. G. Filtered Sv Mask to water column. H. Upper (23 m) water column mask. I. Filtered Sv.

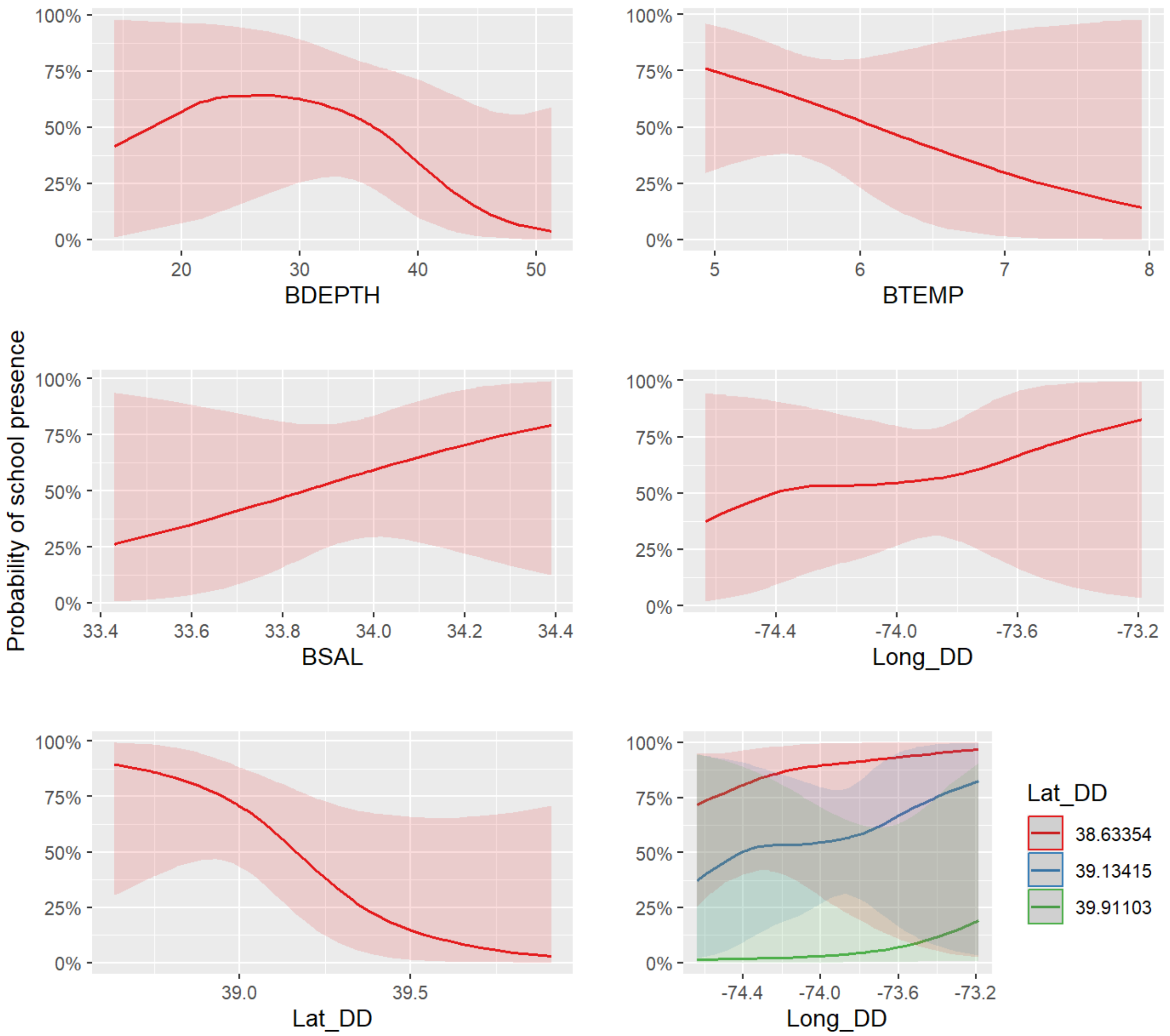


Figure S8. Predicted values (marginal effects) for probability of school presence given depth of sea floor (BDEPTH), bottom temperature (BTEMP), bottom salinity (BSAL), longitude (Long_DD), and latitude (Lat_DD) across all surveys ensonified during the survey period.

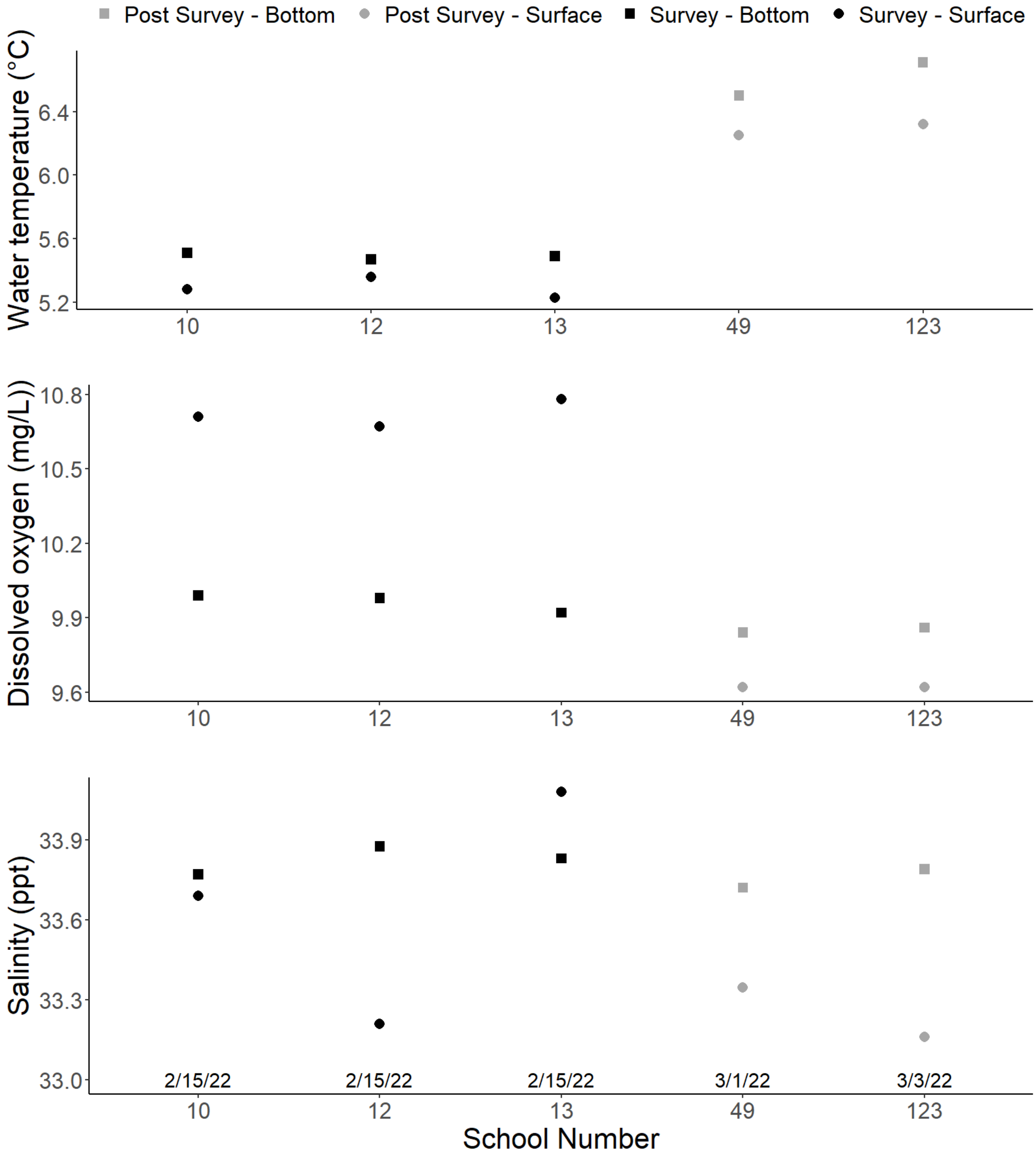


Figure S9. Surface and bottom water temperature (°C), dissolved oxygen (mg/L), and salinity (ppt) at the location of Atlantic menhaden schools sampled during the survey and post-survey periods.

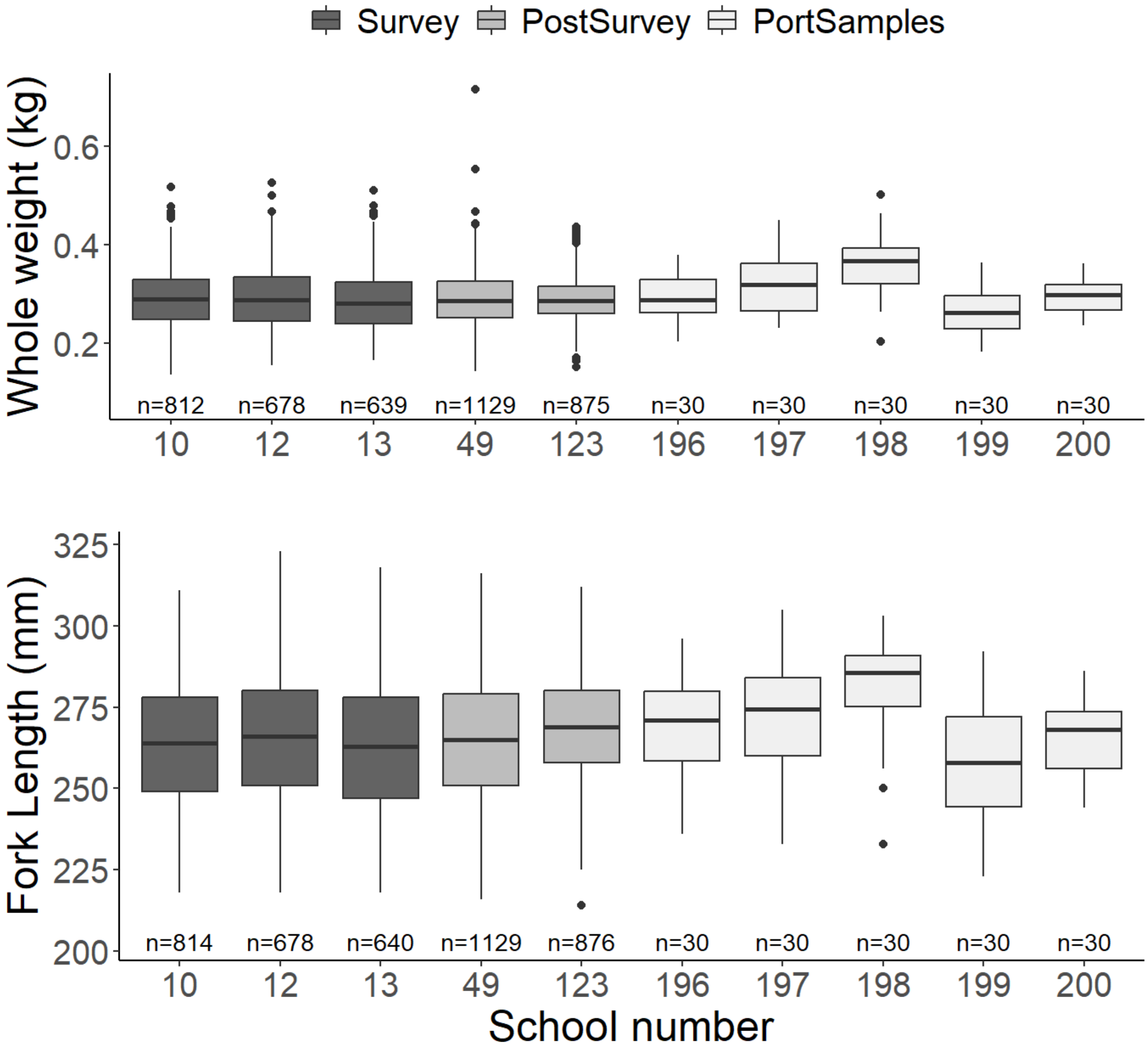


Figure S10. Distribution of weight (kg) and fork length (mm) from samples collected during the survey at sea, post-survey at-sea sampling, and port sampling. Survey and post-survey samples and port sample trips sampled are denoted with an "n".

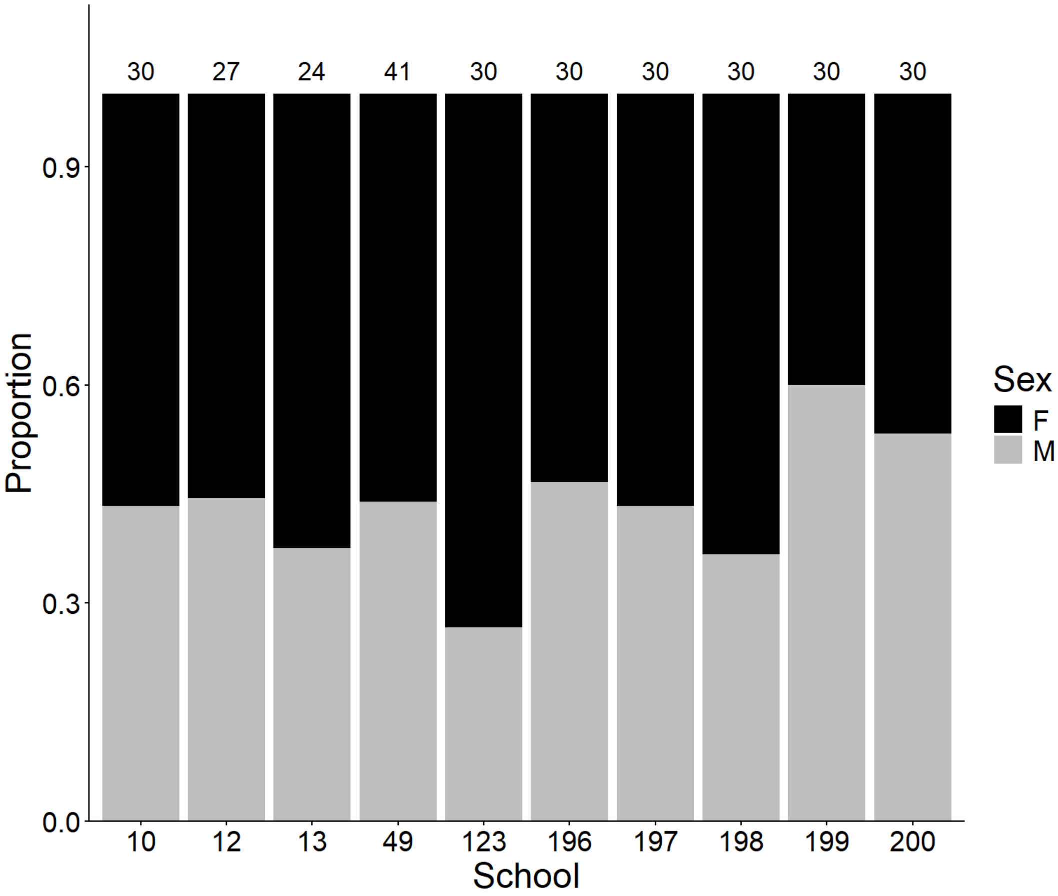


Figure S11. Sex ratio of Atlantic menhaden in each school sampled. F indicates female, M indicates male, and number above bars indicates sample size.

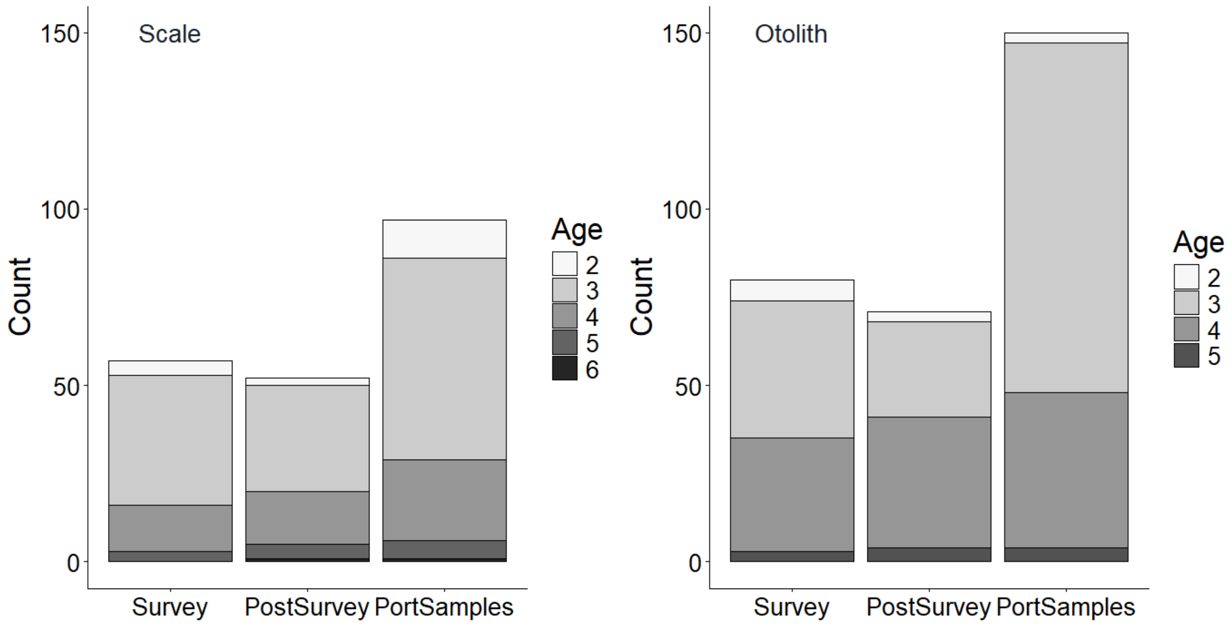


Figure S12. Sample composition of Atlantic menhaden by age using scales (left) and otoliths (right) during each collection period. Note that more scales were deemed unreadable by agers than otoliths due to damage to scales during trawling operations.

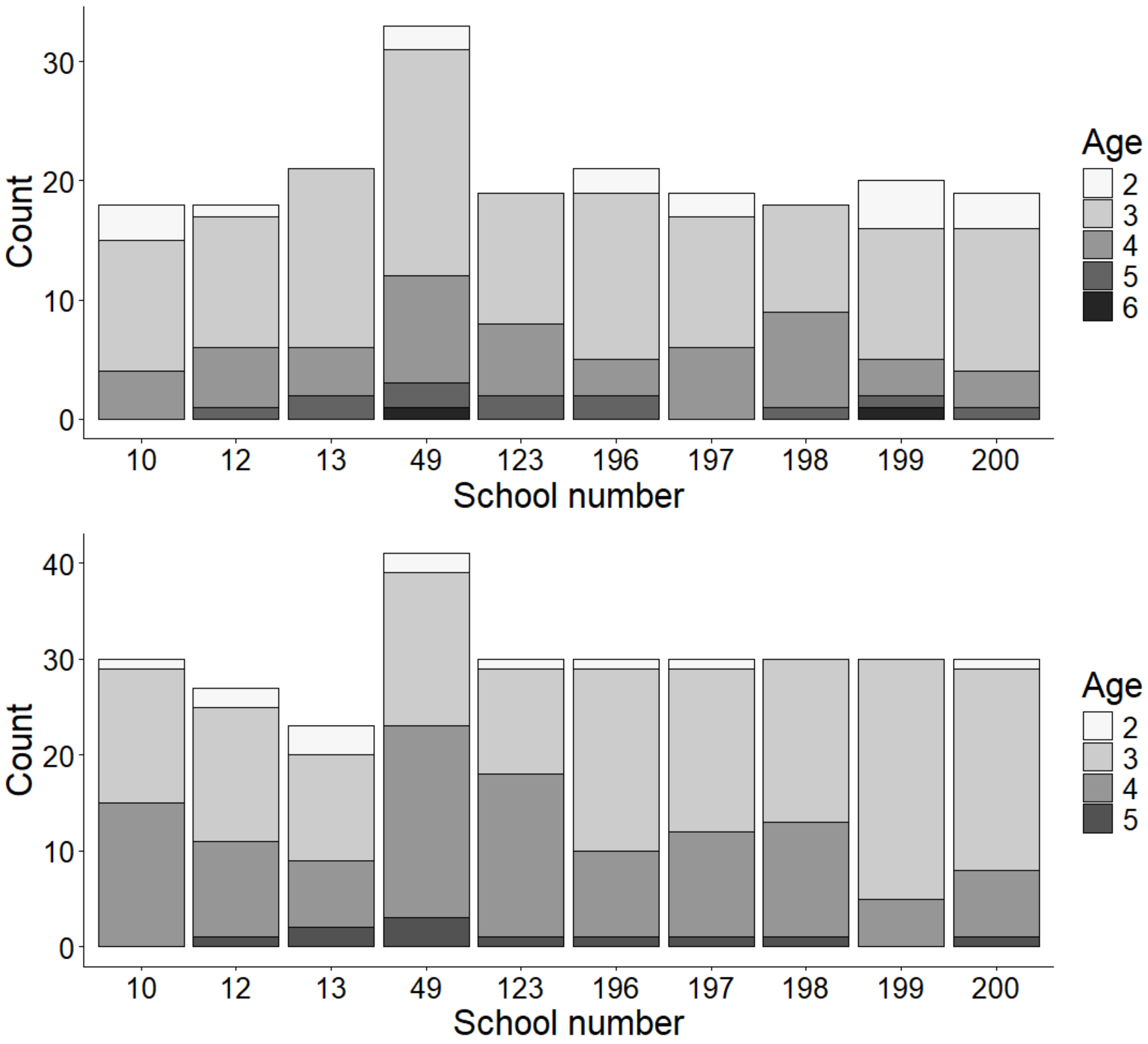


Figure S13. Variability in otolith-based age composition among Atlantic menhaden schools sampled either during the survey period (10, 12, 13), post-survey at-sea (49, 123), or at port (196-200) using scales (top) and otoliths (bottom).

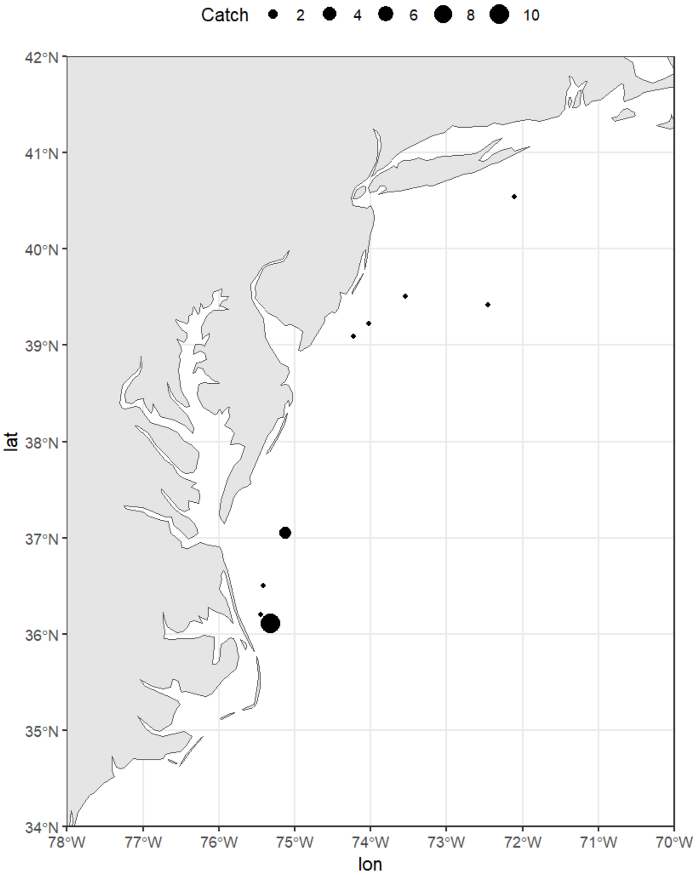


Figure S14. Location of NEFSC Winter Bottom Trawl Survey tows that caught Atlantic menhaden. Size of point indicates number of Atlantic menhaden caught in each tow.

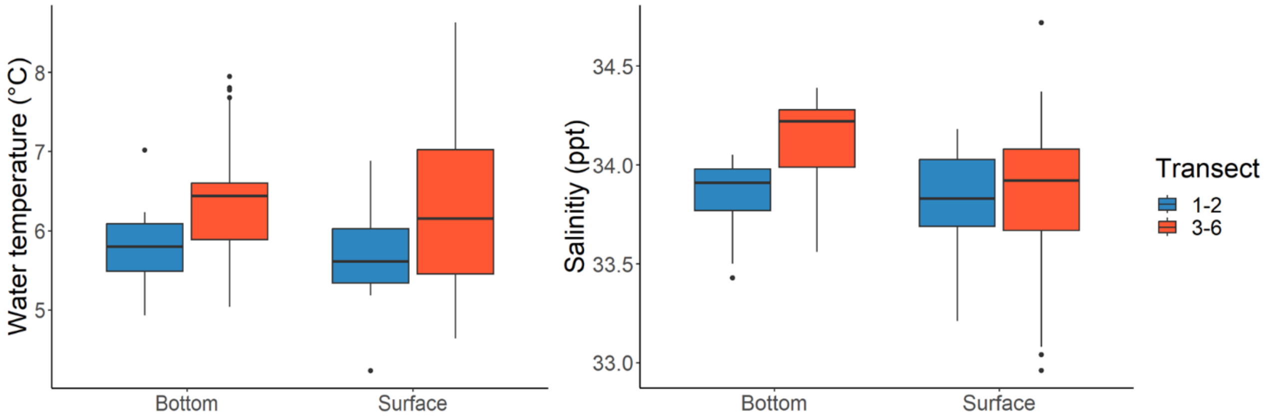


Figure S15. Average water temperature (°C; left) and salinity (ppt; right) at bottom and surface of water column during the first survey trip (Transects 1-2) and second survey trip (Transects 3-6).

Literature Cited

Demer, D. 2015. Calibration of acoustic instruments. ICES Cooperative Research Report No. 326. 133 pp.