Final Report: Changes in availability of Mid-Atlantic fish stocks to fisheries-independent surveys

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Executive Summary

This project addressed Research Need #1 to "Investigate NEFSC trawl survey efficiency, catchability, and availability" for three of the species identified in this priority; summer flounder, black sea bass and spiny dogfish. Like many Mid-Atlantic species, our three focal species (summer flounder, black sea bass and spiny dogfish) all undertake seasonal migrations where during winter they move generally south and offshore to the edge of the continental shelf where water temperature is warmer than in the coastal ocean. This offshore movement can potentially shift a proportion of their population out of the NEFSC trawl survey area. The NEFSC bottom trawl survey extends from Cape Hatteras to the Gulf of Maine and occurs over a two-month interval in both the spring and the fall when the temperature on the shelf is rapidly changing. Thus, the timing of the survey combined with variability in the timing and rate of spring warming and fall cooling in each season may impact availability of species to the survey, particularly those with temperature-induced migration patterns. Because environmental conditions strongly drives their movement offshore and south in the winter, there is high interannual variability in their distribution on the shelf, consequently changing the availability of each of these species to the survey. Here we quantified the degree to which multiple habitat variables affect availability and catchability in the NEFSC trawl survey for spiny dogfish, summer flounder and black sea bass. Specifically; our objectives were to:

1. Identify habitat variable(s) for which each species and if necessary each sex, age or size class selects for habitat.
2. Develop a habitat model for each species using Generalized Additive Models (GAMs) that will allow incorporation of multiple habitat parameters if necessary.
3. Create hindcasts of availability to the survey by combining habitat models with hindcasts of dynamic oceanographic variables to create a time series of catchability during the spring and fall NEFSC surveys.

The methods are similar throughout; however, we report on the results of this work in separate sections for each species for clarity.

The main findings include

- In all three species it was critical to consider life stage and/or size to evaluate the importance of environmental variables on catchability
- Mature female spiny dogfish may be less abundant when accounting for environmental factors than based on swept-area estimates from the trawl survey which do not consider environmental influences.
- Occurrence of spiny dogfish was predominantly driven by bottom temperature
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Introduction

This project addressed Research Need #1 to "Investigate NEFSC trawl survey efficiency, catchability, and availability" for three of the species identified in this priority; summer flounder, black sea bass and spiny dogfish. It is often assumed that abundance indices from fisheries-independent trawl surveys are not prone to the pitfalls of fisheries-dependent catch rates and specifically that catchability does not change with fish density or interannual environmental variability. This assumption is dangerous in light of the fact that many stocks in the Northeast US have shifted their distributions and/or have experienced range contractions and expansions that are related to both population size and rapid warming (Nye et al. 2009). The implications for these shifts in distribution have not been fully addressed despite there being important ramifications for stock assessments (Link et al. 2011). In particular, shifts in distribution can alter availability and subsequently catchability of a stock to fisheries-independent surveys upon which many stock assessments are dependent, especially for seasonally migrating stocks whose distributions may fall outside of the survey area (Walters 2003, Wilberg et al. 2009).

Like many Mid-Atlantic species, our three focal species (summer flounder, black sea bass and spiny dogfish) all undertake seasonal migrations where during winter they move generally south and offshore to the edge of the continental shelf where water temperature is warmer than in the coastal ocean. This offshore movement can potentially shift a proportion of their population out of the NEFSC trawl survey area. The NEFSC bottom trawl survey extends from Cape Hatteras to the Gulf of Maine and occurs over a two-month interval in both the spring and the fall when the temperature on the shelf is rapidly changing. Thus, the timing of the survey combined with variability in the timing and rate of spring warming and fall cooling in each season may impact availability of species to the survey, particularly those with temperature-induced migration patterns. Because environmental conditions strongly drives their movement offshore and south in the winter, there is high interannual variability in their distribution on the shelf, consequently changing the availability of each of these species to the survey.

Stock assessment of spiny dogfish, black sea bass, and summer flounder draw heavily on relative abundance indices derived from the NEFSC bottom trawl survey. Environmental conditions have the potential to change the local distribution and abundance of a species and/or introduce variability in catch patterns (O'Brien and Rago 1996, Bigelow et al. 1999). If survey catchability fluctuates with the environment, skewed estimates can misrepresent actual trends (Murawski and Finn 1988, Perry and Smith 1994, Swain and Sinclair 1994, Smith and Page 1996, Tomkiewicz et al. 1998, Shepherd et al. 2002).

Habitat models were previously developed for different sexes and life stages of spiny dogfish to evaluate the mechanisms driving occurrence and abundance and included both biotic (e.g., prey abundance) and environmental variables (Sagarese et al. 2014). Results suggested that the availability of spiny dogfish to the NEFSC survey varied with environmental conditions, particularly bottom temperature. Even a small change in temperature and/or the timing of the survey changes the availability of the stock to the survey. Relatively warmer spring temperatures cue earlier migration from wintering grounds off of Cape Hatteras to feeding grounds in northern US and Canada. Thus, earlier migration may initiate movement into Canadian waters that are outside the area of the survey.

Recent trends in relative abundance from the Northeast Fisheries Science Center trawl survey suggest that the spiny dogfish population recovered earlier than expected. Large-scale trans-boundary seasonal movements are undertaken by spiny dogfish, with a majority of the population spending colder months in the Mid-Atlantic and traveling north to the Gulf of Maine/Georges Bank during summer (Burgess 2002). As such, surveys tend to capture a high degree of (biologically unrealistic) variability (NEFSC 2006) in seasonal and decadal distributional trends of spiny dogfish (Overholtz and Tyler 1985, Rago et al. 1998, Rago and Sosebee 2009). One of the objectives of this study was to develop an index of relative abundance for the various life stages of spiny dogfish for the spring survey in order to predict availability to the NEFSC trawl survey that can be considered in the next stock assessment.

Here we quantified the degree to which multiple habitat variables affect availability and catchability in the NEFSC trawl survey for spiny dogfish, summer flounder and black sea bass. Specifically; our objectives were to:

1. Identify habitat variable(s) for each species and if necessary each sex, age or size class.
2. Develop a habitat model for each species using Generalized Additive Models (GAMs) that will allow incorporation of multiple habitat parameters.
3. Create hindcasts of availability to the survey by combining habitat models with hindcasts of dynamic oceanographic variables to create a time series of catchability during the spring and fall NEFSC surveys.

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Methods

Data

Indices of relative abundance were developed using the NEFSC trawl survey data. For spiny dogfish, six stages were modeled: aggregated male and female neonates (total length, TL ≤ 26 cm), aggregated male and female older neonates (total length, TL ≤ 35 cm), immature males (26 cm < TL < 60 cm), immature females (26 cm < TL < 80 cm), mature males (TL ≥ 60 cm), and mature females (TL ≥ 80 cm). Two neonate groups were modeled to include all male and female neonates equal to or below 26 cm and 35 cm in total length, the latter of which matches the convention used in the most recent stock assessment (Rago and Sosebee 2015). Survey estimates of relative abundance were converted to Albatross-equivalent estimates using the methods described in (Miller et al. 2010).

Models of summer flounder were developed for all length classes combined (hereafter referred to as "all fish") and for each of three different length classes separately and for different seasons. Summer Flounder life stages were split up into juveniles from 0-30 cm (ages 0-1.5), new adults from 30-40 cm (ages 1.5-2.5), and spawning adults from 40-70 cm (ages 2.5-6) based on the age-length key used in the stock assessment. Black sea bass juveniles (0-14 cm; to assess 0-1 year old age class), new adults (14-20 cm; to assess 1-2 year old age class), and older spawning adults (20-45 cm; to assess 2-6 year old age class) were defined from previous work done by Younes

(2015) and the effect of size on distributional models was assessed using these categories. Both sexes were calculated together because comprehensive sex data were not available for these species. Analyses of spring and fall combined were compared to separate models of spring, fall, and winter data. Winter was only used in CDFs, because the data for winter is too temporally limited to use in the GAMs and relative indices of abundance. Both seasons were assessed together to evaluate whether the exclusion of season would show different results.

Variable selection

Exploratory data analyses were conducted to identify candidate explanatory variables for inclusion in modeling exercises (Table 1). Although ecological factors (i.e., prey abundance) were considered in the original analysis for spiny dogfish (Sagarese et al. 2014), it was not feasible to include prey abundance as predictors for forecast purposes, since prey distributions will also be influenced by changing environmental conditions, particularly temperature. Therefore, candidate explanatory variables for describing occurrence and abundance of each dogfish stage included six abiotic variables and were based on perceived importance and data availability. Julian day was selected to capture the seasonal track of the survey which consistently runs from southerly latitudes to northerly latitudes. The potential for multicollinearity was assessed by examining correlations between variables (i.e., $r > 0.6$), and variance inflation factors (> 10) (Table 2).

For summer flounder and black sea bass, we used cumulative density functions (CDFs) to explore variables to inform the development of our habitat models. Both the CDFs and GAMs evaluated sea surface temperature (^{o}C), bottom temperature (^{o}C), surface salinity (PSU), bottom salinity (PSU), average bottom depth (m), and rugosity (terrain ruggedness index (TRI; sensu (Riley et al. 1999)). The CDF analysis also used closest bay (km), and net primary productivity (C/m^2/day; (Behrenfeld and Falkowski 1997) http://www.science.oregonstate.edu/ocean.productivity/index.php) parameters. These variables were found to be uninformative in the CDF analysis and were excluded in the HSMs.

Following Perry and Smith (1994) and Sagarese et al. (2014b), tow duration was standardized and catch per unit effort of each species was summarized by year, season and stratum for available (all of the tows in the survey) and occupied areas of the survey (only using tows where the fish of interest was found). If values are consistently related to particular habitat conditions, then it suggests a strong association between the species and that habitat condition (Perry and Smith 1994). If the species is randomly distributed with respect to the habitat covariate, the available habitat and the occupied habitat would produce identical results.

The significance of these differences was calculated using a Kolmogorov-Smirnov type test statistic with randomization methods to incorporate survey design (Perry and Smith 1994, Sagarese et al. 2014b). The random sampling design complicates the distributional assumptions for the test statistic, so standard Kolmogorov-Smirnov and goodness of fit tests cannot be used. The absolute maximum vertical difference, D, between the two CFDs ($f(t)$ (Eq. 3) and $g(t)$ (Eq. 5)) is assessed to see if the differences in habitat distribution were due to chance alone (H$_0$) or not (H$_A$). D was compared to a pseudo-population of 1,000 randomized test statistics (rD) obtained by randomizing pairings of $g(t)$ and $x_{h,i}$ for all h stratum across the entire survey

(Perry and Smith 1994). Significance p was calculated by the count of rD that were greater than D, divided over the total number of iterations (1,000) used in the permutation test (p-value < 0.05) (Sagarese et al. 2014b). The test was done between the entire survey and by subsetting the species data in two ways; 1), all individuals of the species of interest and 2) all individuals of each length class of the species of interest. The 2.5, 50, and 97.5[th] quantiles were also calculated using the probabilities obtained from the CDFs.

Statistical analysis

Model fitting

The distributions of spiny dogfish, black sea bass, and summer flounder were modeled separately for each stage or length class using generalized additive models (GAMs; Hastie and Tibshirani 1990, Wood 2006, Feyrer et al. 2007, Murase et al. 2009, Damalas et al. 2010). GAMs are semi-parametric extensions of the generalized linear model (GLM) commonly applied to the spatial distributions of fishes that utilize a smoothing function (Wintle et al. 2005) that can easily handle non-linear relationships and uncover hidden structure between variables missed by traditional linear methods (Hastie and Tibshirani 1990, Guisan et al. 2002). Two stage (i.e., hurdle or delta method) models were constructed to account for zero-inflation and overdispersion (Potts and Elith 2006, Heinänen et al. 2008, Zuur et al. 2009). The first stage predicted the probability of occurrence using a logit link function and a binomial error distribution. The second stage predicted the conditional presence using a log link function and a negative binomial error distribution (Gotway and Stroup 1997, Fewster et al. 2000, Martin et al. 2005). All GAMs were built in R (R Core Development Team 2016) with the package 'mgcv' (Wood 2016) using cubic regression splines and a maximum of 5 degrees of freedom (number of knots (k) = 5). The number of knots determines the smoothness or 'wiggliness' of the curve; the more knots used, the less smooth the curve becomes (Zuur et al. 2009). Here, each predictor variable was divided a maximum of five times (defined by k) with each break spread evenly through its range (Wood 2006, 2016). A k = 5 was chosen based on expectations within explanatory variables and recommendations in the literature (Keele 2008, Zuur et al. 2009). In addition, each model formula included a 'gamma = 1.4' to place a heavier penalty on each degree of freedom to counteract overfitting (Zuur et al. 2009, Wood 2016). The estimated smoothing parameters (i.e., estimated degrees of freedom) of the optimal model were chosen based on the lowest Unbiased Risk Estimator (UBRE) score, an AIC-type statistic (Wood 2006, 2016). Each dataset was randomly divided into a training set (66% of observations) for model fitting with the remainder used as an independent test set (remaining 33% of observations) for model validation (Miller and Franklin 2002, Brotons et al. 2004).

Model selection

Candidate GAMs for each spiny dogfish life stage, summer flounder length class, and black sea bass length class were evaluated by testing all possible combinations of main effects. The best model given the data and method used was selected on the basis of Akaike information criteria (AIC; Akaike 1974), estimated model weights (wAIC) (Wagenmakers and Farrell 2004), and performance diagnostics. Generally, lower AIC values and higher model weights (wAIC) are desired (Wagenmakers and Farrell 2004, Heinänen et al. 2008, Loots et al. 2010). Preferred

predictive performance criteria included higher values for the (1) adjusted coefficient of determination (adjusted R^2), which measures the proportion of variance of the probability of occurrence explained by the GAM, and is judged acceptable when above 0.1 (Legendre and Legendre 1998); (2) receiver operator characteristic (ROC) curve, which expresses the true positive rate as a function of the false positive rate for each probability of occurrence (Hanley and McNeil 1982); (3) Pearson's correlation coefficient (r), which indicates relative agreement between observations and predictions; and (4) Spearman's correlation coefficient (r_{sp}), which measures correspondence between two variable rankings. A lower value for the root of the mean of the squared differences between each prediction and each observation (RMSE) was also preferred (Potts and Elith 2006, Loots et al. 2010).

Model evaluation

We assessed the relative importance of predictors in determining the probability of occurrence (i.e., presence absence) and increasing abundance (i.e., presence only) of spiny dogfish life stages, summer flounder length classes, and black sea bass length classes using the approach developed by Thuiller et al. (2012) for the niche distribution model BIOMOD. The predictions of each GAM fitted are compared with the predictions of each GAM after random permutation of the values of a given predictor within the dataset. One minus the Pearson's correlation coefficient between the predictions of the full GAM and the predictions of a random GAM provides an indication of the relative importance of a given predictor in explaining the probability of occurrence or increasing abundance of a spiny dogfish life stage. Note that the Pearson's correlation coefficient between the predictions of the full GAM and the predictions of a random GAM can be negative; these cases represent an even bigger importance of the permutated predictor in explaining the probability of occurrence than with a correlation of 0 (Thuiller et al. 2012).

Test datasets for all stages and length classes were used to evaluate the predictive performance of each optimal model in terms of discrimination and calibration (Fielding and Bell 1997, Pearce and Ferrier 2000). Unbiased estimates of each optimal model's predictive performance were obtained by evaluating a test dataset (Fielding and Bell 1997, Pearce and Ferrier 2000). Occurrence models were tested for discrimination and accuracy in R (R Core Development 2016) using the packages 'pROC' (Robin et al. 2011) and 'PresenceAbsence' (Freeman 2007), respectively, and for model behavior via bias using Bland-Altman plots (Bland and Altman 1986). The ability of the model to discriminate between presence and absence sites was described using AUC (Brotons et al. 2004, Leathwick et al. 2006) with values between 0.7 and 0.9 considered reasonable and values > 0.9 good as the true positive rate was high relative to the false positive rate (Swets 1988, Pearce and Ferrier 2000). The ability to correctly predict the proportion of sites with a species given an occupied environmental profile was determined by calibration plots with perfect calibration indicated by a line with a slope = 1 and an intercept = 0 (Wintle et al. 2005, Heinänen et al. 2008). A contingency table was created to specify the rate of false positive predictions and the rate of false negative predictions, with low false negative rates preferable (Fielding and Bell 1997, Farmer and Karnauskas 2013). Model behavior was further assessed using a Bland-Altman plot, which compares the binary responses across a gradient of bins and identifies bias by examining the relationship between the difference and mean (Bland and Altman 1986).

Validation of PRES models was assessed using typical model performance estimators including calibration, correlations and mean error (Potts and Elith 2006, Heinänen et al. 2008), and Bland-Altman plots (Bland and Altman 1986). Calibration was measured with a simple linear regression between observed and predicted values with the intercept term indicative of bias and the slope reflective of the consistency in the predictions (Potts and Elith 2006). The strength of the relationship between observed and predicted values was assessed using Pearson's correlation coefficient (r), although a perfect correlation ($r = 1.0$) may still display bias in a consistent direction (Potts and Elith 2006, Heinänen et al. 2008). The similarity between ranks of observed and predicted values was assessed using Spearman's rank correlation (r_{sp}) with a high value indicating a correct order of predictions (Potts and Elith 2006). As misleading results are often obtained when relying solely on correlation coefficients (Bland and Altman 1986), model behavior was assessed using a Bland-Altman plot by binning the values and identifying bias as described above. Lastly, both root mean square error of prediction ($RMSE$) and average error (AVE) were calculated as in Potts and Elith (2006). Additional details are provided in Sagarese al. 2014.

Combined models were validated using data sets internal to their development by comparing observed and predicted values of the probability of daytime catch using 1,000 bootstrapped data sets resampled with replacement (Grüss et al. 2014). Spearman's correlation coefficients (r_{sp}) between the probability of daytime catch predicted by the GAM and the observed probability of daytime catch in the bottom trawl survey data set were estimated and tested for significance (i.e., $\neq 0$) (Vaz et al. 2006; Loots et al. 2010; Grüss et al. 2014). Model performance was also assessed by examining residual plots for strong trends and by visually inspecting response curves for ecological realism (Wintle et al. 2005; Heinänen et al. 2008).

Comparison of trends in relative abundance

The mean stratified abundance using the delta model predictions was compared to the unadjusted mean stratified abundance using the survey counts to determine whether trends differed after accounting for environmental factors.

Results

Spiny dogfish

The most common stage encountered during the spring NEFSC trawl was immature females (37%) followed by mature males (33%) (Table 3). Overall, the deviance explained by the occurrence models were relatively low (17 – 30%), whereas the deviance explained in the abundance model ranged from 27% for mature male spiny dogfish to 43% for immature male spiny dogfish (Table 4). All variables tested were retained during model selection based on AIC, with the exception of neonates (≤26 cm TL) where Julian day was excluded from the abundance only model.

Validation results for the occurrence models for each spiny dogfish life stage were generally in the preferred ranges, although immature dogfish and mature female spiny dogfish occurrence

8

exhibited relatively large false negative rates (>25%). The validation results for the abundance model revealed relatively large RMSEs for immature dogfish and mature males. For each spiny dogfish life stage, the delta-model (combined occurrence and abundance) resulted in moderate correlations (0.34 – 0.49) between predicted abundance and observed abundance in the trawl survey (Table 5).

The occurrence of the majority of life stages was predominantly driven by bottom temperature, although region was most important for both neonate groups considered (Table 3). Bottom temperature was the primary driver of abundance for mature spiny dogfish, whereas year explained the most variance for neonates and immature spiny dogfish.

Neonate spiny dogfish (≤ 26 cm TL) were predominantly captured on the shelf's edge from the Mid-Atlantic Bight to Georges Bank, with the highest predicted abundances in Southern New England during spring (Figures 1-2). The mean stratified abundance adjusted using the predicted abundance from the delta-model was highly variable (Figure 3). When compared to the unadjusted mean stratified abundance from the trawl survey of neonates (≤35 cm TL), the trend in adjusted mean stratified abundance was relatively similar for some years in terms of trend. For example, of the three highest swept-area estimates (2013, 1994, 1985), the delta index resulted in peak relative abundance during 1994 but much lower estimates for the other two years (Figure 3). In contrast, some years exhibited a dampened trend in relative abundance when using the delta predictions, such as the early- to mid-1970s and late 1980s (Figure 3).

Immature male spiny dogfish were also predominantly captured on the shelf's edge from the Mid-Atlantic Bight to the northern edge of Georges Bank, with the highest abundances on the shelf's edge of Georges Bank and Southern New England during spring (Figure 4). The mean stratified abundance adjusted using the predicted abundance from the delta-model was highly variable but generally similar in trend to the unadjusted mean stratified abundance index. Both indices revealed peak relative abundance during 2013. However, differences were evident in the 1980s and early 1990s where the adjusted mean stratified abundance index was consistently lower than the unadjusted mean stratified abundance (Figure 5).

Immature female spiny dogfish were captured both throughout the continental shelf and on the shelf's edge from the Mid-Atlantic Bight to Georges Bank, with the highest abundances along the shelf's edge during spring (Figure 6). As observed for immature males, overall trends in abundance were similar between the unadjusted and adjusted mean stratified abundance, with peak abundance observed in 2013 (Figure 7). However, differences were also evident in the 1980s and late 2000s where the adjusted mean stratified abundance index was consistently lower than the unadjusted mean stratified abundance (Figure 7).

Mature male spiny dogfish were primarily captured throughout the Mid-Atlantic Bight to Georges Bank, with the highest abundances along the shelf's edge in the Mid-Atlantic Bight during spring (Figure 8). The relative abundance of mature males was similar between the unadjusted and adjusted mean stratified abundance for many years, although some large differences were evident. Peak abundance based on the unadjusted mean stratified abundance occurred in 1985 and 2012, whereas the adjusted index peaked in 1997 (Figure 9). In addition,

relative abundance estimated from the delta index showed much lower values between 1986 and 1992 (Figure 9).

Mature female spiny dogfish were primarily captured throughout the Mid-Atlantic Bight, with the highest abundances located mid-shelf during spring (Figure 10). The mean stratified abundance adjusted using the predicted abundance from the delta-model was relatively dissimilar to the trends exhibited by the unadjusted mean stratified abundance index (Figure 11). The abundance of mature females peaked in 1992 according to the adjusted mean stratified abundance, whereas peak unadjusted mean stratified abundance occurred in 2012 and the mid-1980s (Figure 11). With the exception of 2016, the trend in relative abundance has been consistently lower since 2006 based on the adjusted mean stratified abundance (Figure 11).

Summer flounder

In the spring and the fall, all summer flounder selected for significantly habitat than was being covered by the survey; however, all conspecifics selected for similar habitat in the fall and selected for very different habitats in the spring. Small, 0-30 cm fish, inhabited cooler and narrower ranges of surface and bottom temperature than their 30-40 cm and 40-70 cm adult conspecifics (Figure 12). However, when seasons were combined there were no significant differences between the survey and the small fish.

Cumulative distribution functions of surface and bottom salinity also had similar curves (see Markowitz 2018 for full details). Summer flounder select for more saline bottom (and surface) waters in the spring and less saline waters in the fall than the survey. Average depth was significantly different for nearly all tested analyses. The length classes were consistently associated with shallow areas compared to what the survey captured. Small, 0-30 cm fish were consistently situated in more shallow areas than their adult conspecifics. Curves for the spring, winter, and for both seasons combined are very similar. Likewise, rugosity distributions and patterns appeared to be very similar to those found for average depth; however, they were much weaker (Figure 13). Only one instance between the survey and small, 0-30 cm, fish was significant in the spring. In the fall, the differences between the survey and the fish was very significant. However, small, 0-30 cm, fish were in much less rugose areas than their adult conspecifics. Almost all analyses of comparing summer flounder distribution to distance to the closest bay had significant differences from the survey and between conspecifics. In the spring and fall, juvenile summer slounder are closer to shore than adults. Net primary productivity was only significantly different between the survey and fish and deemed not an important variable to determine availability to the survey.

Generalized additive models for summer flounder and black sea bass were parameterized in two basic ways; one model that included size and season as a covariate or several separate models for each size class and sseason (Table 6,7). The best models accounted for both season and length in addition to environmental variables used season and length as covariates. For summer flounder the best models included all possible environmental factors except in the fall, where average depth and rugosity were excluded. Most of the best candidate occurrence models included bottom temperature (all did), but did not include sea surface temperature, except in fall with a length covariate and for small (0-30 cm) summer flounder with a season covariate.

In occurrence models, the calibration y-intercept was consistently near 0 and the slope was usually near 1, which is ideal. Slope was closest to 1 in model subset by season (environmental and length covariate models) and was least ideal in models subset by length class (environmental and season covariate models). Though all AUC values were within a good range (>0.7), the AUC values were highest in the in models with length covariates. The false positive rates (FPR) and false negative rates (FNR) were low and, overall, appeared to be much lower than in models with only environmental models. FPR and FNR were highest for models that were subset by length class. In the abundance/occurrence models, the calibration y-intercept and slope were close to ideal values. Pearsons (R_p) and Spearsons (R_{sp}) correlation coefficients appeared to be similar to models that used only environmental covariates, if not overall a little higher. RMSE was often around 1 and less for models with length covariates and AVE were consistently within 0.6± of 0.

The mean delta-index within each spatial cell shows that more summer flounder are predicted in the model with additional season and length covariates, but also experienced the greatest amount of standard error (Figure 14,15) . The model where spring data was subset with an additional length covariate also had a fair amount of standard error.

Overall, the observed mean stratified abundance was moderately high in the 1980s and peaks again in the mid-2000s. The predicted models, however, were similar to the mean stratified abundance, but do not exactly match the trends being observed indicating that summer flounder availability to the survey changes through time, influencing the relative abundance estimates (Figure 16). The model using all data, but using length and season as a covariate is more similar to the mean stratified abundance and the model where only data from the fall survey were examined, but the spring modeled vs. observed estimates are very different.

Black sea bass

In most instances, black sea bass length classes occupied significantly different surface and bottom thermal habitat than the survey (Figure 17). These differences in selection for different temperatures between different length classes were visually apparent in the spring but were generally not significant. In the fall, black sea bass juveniles (0-14 cm) occupied colder temperatures than other length classes, new adults (14-20 cm) occupied warmer temperatures. However, when spring and fall were combined, larger fish appeared to significantly occupy significantly colder temperatures than other length classes and the survey.

Differences in CDFs of surface and bottom salinity were only significant between length classes and the survey, but not between length classes except for small individuals (0-14 cm) when spring and fall survey data were combined. Distributions of groups over average depth were almost always significant between length classes and the survey, despite large distances between CDF curves values between length class length classes. CDFs of rugosity were only significantly between length classes and the survey when spring and fall data were combined and in the fall. Curves for distance to closest bay was only significantly different between length classes and the survey owing to the fact that the survey is randomly stratified across the survey area. In all instances, selection of small fish (0-14 cm) was significantly different from medium (14 – 20

cm) and large (20-45 cm) black sea bass indicating different habitat use by size class for black sea bass. Further details for this analysis can be found in Markowitz (2018).

In the best black sea bass Generalized Additive Models, nearly all best candidate models accounted for season and length either by being included as a covariate or if data were subset by season and length before parameterizing the model (Table 7). The only model to exclude length was the spring subset model with additional length covariate that did not include the length covariate. All best candidate occurrence models used bottom temperature. The fall subset model with length covariate excluded sea surface temperature and rugosity. The model with both length and season subsets excluded sea surface temperature, average depth, and rugosity. Deviance explained and adjusted R^2 were similar between models (Table 7). Occurrence models that included length covariates had the highest deviance explained. Of those, the fall model with a length covariate had the highest, and the model with length and season covariates (e.g. where length class and season data were combined) appeared to be "down weighted" by the poor performance of the spring models.

In occurrence models, the calibration y-intercept was consistently near 0 and the slope was usually near 1, which is ideal. Slope was closest to 1 in models subset by season (environmental and length covariate models) and was least ideal in models subset by length class (environmental and season covariate models). Though all AUC values were within a good range (>0.7), the AUC values were highest in the in models with length covariates. The false positive rates (FPR) and false negative rates (FNR) were low and, overall, appeared to be much lower than in models with only environmental models. FPR and FNR were highest for models that were subset by length class.

In the abundance/occurrence models, the calibration y-intercept and slope were nearly as poor as those models where only environmental covariates had been used. Pearson and Spearman correlation coefficients appeared to be similar to models that used only environmental covariates, if not overall a little higher. RMSE was highly variable and spanned from 2.5 to 17 (which is slightly less than for the models that only used environmental variables, Table 4) but smallest for fall and when spring and fall data was combined with an additional length covariate. AVE was near 0 for the model of the spring, fall, medium (14-20 cm), and large (20-40 cm) fish subset models but was very large for the model for small (0-14 cm) and when spring and fall survey data were combined.

The mean delta-index within each spatial cell shows that more Black Sea Bass are predicted in the fall model with an additional length covariate, but of which also experienced the greatest amount of standard error (Figure 19, 20). The model where spring data was subset with an additional length covariate also had a fair amount of predicted Black Sea Bass.

The observed coastwide mean stratified abundance of black sea bass has increased progressively over time in the fall, but seemed to vary over time without trend in the spring (Figure 21). The predicted models, however, did not appear to closely match the trends being observed and do no indicate a trend.

Discussion

In all three species, it was critical to consider length or stage to model habitat as there were significant differences in habitat preference for different size classes. The GAMs indicate that the models that combine and generalize size and season miss important distributional patterns that affect our understanding of the availability of these fish stocks to field surveys and thus survey-based estimates of abundance used in stock assessments. Bottom temperature was the most important variable for all species even though other environmental covariates were included in the best GAMs. Overall, the adjusted indices of abundance for spiny dogfish followed the trend of the unadjusted abundance time series. However, there were important deviations between the indices suggesting that environmental variables do impact the availability of the species to the survey. Spiny dogfish results suggest that mature female spiny dogfish maybe less abundant when accounting for environmental factors than based on swept-area estimates from the trawl survey. This occurred during two critical time periods. First, during the 1980's when the unadjusted index showed a large increase in mature abundance. Second, the adjusted time series was much lower after ~2006 when the population was thought to be rebuilding.

For summer flounder and black sea bass modeling by season was also critical, concurring with the practice by the stock assessments for both of these species to only use one seasonal survey as an index of relative abundance. For summer flounder and black sea bass, fall models may perform the best because more fish were found in the fall than in spring and models that combined data from the spring and fall seasons without a covariate appeared to be down-weighted in deviance explained. False negative rates were lowest the fall and highest for the spring.

There were very few instances when bottom temperature and average depth were excluded in models, and thus appeared to be a very important factor for summer flounder and black sea bass. Rugosity and sea surface temperature were more often excluded. Black Sea Bass appeared to select for rugosity habitat than Summer Flounder the survey. The relative importance of rugosity to Black Sea Bass confirms that this species prefers habitat with high rugosity, which was most obvious in the spring survey. In the fall survey black sea bass seem to be found on low rugosity habitat, but the survey only samples relatively shallow, less rugose areas. It is uncertain whether our estimates of black sea bass abundance are different from the mean stratified estimates from the survey because they effectively correct for the mismatch between the high rugosity habitat that black sea bass prefers.

Since the intention of these habitat suitability models are to correct for availability to the survey in tuning indices for the stock assessment and the stock assessments use tuning indices by length and season, it is advised that if such an approach were used to correct for availability of the fish to the survey, that survey, length, and season be included in any application. Overall, the adjusted indices of abundance for summer flounder followed the trend of the unadjusted abundance time series in models that included fall data. However, there were important deviations between the indices suggesting that environmental variables do impact the availability of the species to the survey. Black sea bass adjusted indices of abundance did not appear to

follow unadjusted abundance time series in the survey. This may be attributed to the relatively 'poor' resolution of the black sea bass distribution in the NEFSC bottom trawl survey data.

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Table 1. Variables identified as potential explanatory variables for each generalized additive model describing the occurrence and abundance of spiny dogfish life-history stages after preliminary exploratory data analyses on the spring NEFSC bottom trawl survey datasets.

Variable (units)	Type	Explanation
Depth (m)	Environmental	Measurement of depth where trawl was conducted
BT (°C)	Environmental	Measurement of bottom temperature where trawl was conducted
Zenith (°)	Environmental	Estimated solar zenith angle at trawl location
Year	Temporal	Year trawl was conducted
Julian (d)	Temporal	Julian day trawl was conducted
Region	Spatial	Georges Bank (GB), Gulf of Maine (GM), Southern New England (SNE), or Mid-Atlantic Bight (MA)

Table 2. Summary of NEFSC trawl data used to map spiny dogfish distributions in the northeast US continental shelf large marine ecosystem. Variable summaries shown include mean (range). r = Pearson's correlation.

	1968-2016	1980-2016
Training dataset		
Variable		
Year	-	-
Depth (m)	114 (12−470)	114 (12−456)
BT (°C)	7 (1−18)	7 (1−18)
Julian (d)	97 (57−176)	97 (57−156)
Zenith (°)	86 (20−151)	85 (21−151)
Region	-	-
Max *r*	0.34 (Depth, BT)	0.32 (Depth, BT)
Min *r*	-0.43 (Region, Julian)	-0.46 (Region, Julian)
Variance inflation factor	1.0 (Zenith)−4.9 (Julian)	1.0 (Zenith)−8.5 (Julian)
Testing dataset		
Variable		
Year	-	-
Depth (m)	113 (17−465)	113 (18−393)
BT (°C)	7 (1−18)	7 (2−18)
Julian (d)	96 (58−155)	96 (58−156)
Zenith (°)	85 (21−150)	86 (21−150)
Region	-	-
Max *r*	0.34 (Depth, BT)	0.32 (Depth, BT)
Min *r*	-0.42 (Region, Julian)	-0.45 (Region, Julian)
Variance inflation factor	1.0 (Zenith)−4.6 (Julian)	1.0 (Zenith)−9.0 (Julian)

Table 3. Summary of NEFSC trawl data used to map spiny dogfish distributions in the northeast US continental shelf large marine ecosystem. Proportion positive (PP) is based on the datasets selected for modeling (i.e., total = full dataset, train = training dataset, and test = testing dataset). N = number of observations where each stage was present in each dataset. Stages include neonates (Neo; TL ≤ 26 cm), older neonates (Neo35; TL ≤ 35 cm), immature males (ImmM; 26 cm < TL < 60 cm), immature females (ImmF; 26 cm < TL < 80 cm), mature males (MatM; TL ≥ 60 cm), and mature females (MatF; TL ≥ 80 cm).

Data	Neo	Neo35	ImmM	ImmF	MatM	MatF
Years	1968-2016			1980-2016		
Catch	11,513	68,458	90,843	166,875	287,755	69,029
N_{total}	10724	10724	10724	10724	10724	10724
PP_{total}	9.0	15.7	19.5	36.5	33.4	29.8
N_{train}	7077	7077	7077	7077	7077	7077
PP_{train}	9.2	15.8	19.6	36.7	33.4	30.0
N_{test}	3647	3647	3647	3647	3647	3647
PP_{test}	8.7	15.7	19.3	36.2	33.5	29.4

Table 4. Validation measures for the optimal occurrence (PA) and abundance (PRES) models for spiny dogfish life-history stages in the Northeast (US) shelf large marine ecosystem based on independent test datasets for autumn and spring. Stages as defined in Table 1. AUC = area under the receiver operating characteristic curve ± standard error, m = slope and b = y-intercept of the fitted calibration line: observed = m(predicted) + b, r = Pearson's correlation coefficient, r_{sp} = Spearman's rank correlation coefficient, $RSME$ = root mean square error of prediction and AVE = average error. See text for equations and further details. Stages are as defined in Table 3.

	Neo	Neo35	ImmM	ImmF	MatM	MatF	Neo	Neo35	ImmM	ImmF	MatM	MatF
Model Performance												
Deviance Explained (%)	28.8	29.5	19.2	19.1	20.0	17.7	40.1	38.0	43.4	28.0	27.4	41.3
Adjusted R^2	0.20	0.27	0.19	0.23	0.24	0.21	0.03	-0.04	-0.03	0.01	0.04	0.08
wAIC (%)	99.8	73.0	99.6	90.2	89.4	95.5	58.7	100.0	100.0	100.0	99.9	92.7
Variable importance (% deviance explained)												
Year	24.7	16.6	22.7	19.5	19.8	24.2	82.6	73.4	69.2	49.6	31.9	23.3
Depth	17.5	17.2	19.8	2.9	6.5	3.0	4.9	4.6	25.9	18.9	17.3	6.4
BT	18.7	20.4	45.7	50.4	44.0	42.8	28.2	42.7	21.2	28.7	38.1	40.4
Julian	16.6	3.0	3.7	12.8	28.1	3.9	-	11.8	16.0	11.9	8.0	26.7
Zenith	1.6	0.3	1.3	0.5	0.5	1.9	5.0	4.8	1.8	3.0	14.6	3.5
Region	40.5	53.6	11.3	7.4	6.1	19.6	33.6	35.3	37.4	21.4	27.1	6.6
Model Evaluation												
AUC	0.88	0.87	0.80	0.78	0.79	0.77	-	-	-	-	-	-
Thresh	0.08	0.12	0.27	0.48	0.41	0.37	-	-	-	-	-	-
False Negative Rate	14.11	14.43	27.70	28.42	24.64	29.81	-	-	-	-	-	-
Calibration												
Intercept (b)	0.00	0.00	0.00	-0.01	0.00	-0.01	6.10	17.68	17.04	13.23	35.77	3.68
Slope (m)	0.99	0.98	0.98	1.01	1.01	1.01	0.14	0.18	0.69	0.70	0.42	0.89
r	-	-	-	-	-	-	0.12	0.20	0.30	0.22	0.27	0.27
r_{sp}	-	-	-	-	-	-	0.24	0.28	0.38	0.26	0.39	0.36
$RMSE$	-	-	-	-	-	-	30	139	207	192	174	72
AVE	-	-	-	-	-	-	5	26	-2	1	19	-1

Table 5. Spearman's correlation coefficients (r_{sp}) between the abundance predicted by generalized additive models and the observed abundance in the survey data for Spiny Dogfish in the northeast US continental shelf large marine ecosystem during spring between 1968 and 2016 for neonates and between 1980 and 2016 for the remaining stages. CI reflects the 95% confidence intervals. Significance of P values is based on an *a priori* $\alpha = 0.05$.

Stage	r_{sp}	CI_{lower}	CI_{upper}	P
Neonate (≤ 26)	0.344	0.330	0.357	0.000*
Neonate (≤ 35)	0.422	0.408	0.437	0.000*
Immature Male	0.420	0.403	0.437	0.000*
Immature Female	0.457	0.441	0.475	0.000*
Mature Male	0.486	0.469	0.504	0.000*
Mature Female	0.411	0.392	0.431	0.000*

Table 6. Validation measures for the optimal occurrence and abundance models for Summer Flounder in both seasons and spring at three different length classes (0 – 30 cm age 1 fish, 30 – 45 cm age 2 fish, 45 – 70 cm age 2-6 adult fish) in the Northeast US large marine ecosystem (NEUS LME).

Covariates	ENV., SEASON, LENGTH	ENV., SEASON	ENV., SEASON	ENV., SEASON	ENV., LENGTH	ENV., LENGTH
Length Class (cm) Subset	*All SF*	*0 – 30*	*30 – 45*	*45 – 70*	*All SF*	*All SF*
Season Subset	*Spring and Fall Combined*				*Spring*	*Fall*
Occurrence						
R^2 **Adj.**	0.10	0.02	0.01	0.01	0.09	0.12
Deviance Explained	42.70	15.05	17.15	14.99	38.64	46.82
Calibration y-Intercept	0.00	0.00	0.00	0.00	0.00	0.00
Calibration Slope	0.90	0.85	0.86	0.87	0.95	0.95
AUC	0.98	0.84	0.89	0.86	0.97	0.98
False Positive Rate	0.08	0.34	0.10	0.15	0.08	0.07
False Negative Rate	0.07	0.11	0.44	0.35	0.13	0.04
Abundance						
R^2 **Adj.**	0.09	0.02	0.01	0.05	0.08	0.11
Deviance Explained	12.83	4.06	2.82	7.58	10.99	16.41
Calibration y-Intercept	0.08	-0.26	-0.34	-0.27	-0.22	-0.19
Calibration Slope	0.93	1.16	1.20	1.19	1.15	1.11
R_p	0.27	0.16	0.12	0.22	0.29	0.33
R_{sp}	0.29	0.23	0.11	0.25	0.28	0.38
RMSE	0.83	1.22	1.44	1.29	0.92	0.86
AVE	0.02	0.00	0.00	-0.06	-0.01	0.01

Table 7. Validation measures for the optimal occurrence and abundance models for Black Sea Bass in both seasons and spring at three different length classes (0 – 14 cm age 1 fish, 14 – 20 cm age 2 fish, 20 – 45 cm age 2-6 adult fish) in the Northeast US large marine ecosystem.

Covariate	ENV., SEASON, LENGTH	ENV., SEASON	ENV., SEASON	ENV., SEASON	ENV., LENGTH	ENV., LENGTH
Length Class (cm) Subset	*All BSB*	*0 – 14*	*14 – 20*	*20 – 45*	*All BSB*	*All BSB*
Season Subset	Spring and Fall	Spring and Fall	Spring and Fall	Spring and Fall	Spring	Fall
Occurrence						
R² Adj.	0.02	0.01	0.00	0.01	0.02	0.02
Deviance Explained	24.10	14.44	9.94	16.59	23.40	26.41
Calibration y-Intercept	0.00	0.00	0.00	0.00	0.00	0.00
Calibration Slope	0.77	0.88	0.90	0.91	1.00	0.95
AUC	0.93	0.85	0.83	0.90	0.92	0.94
False Positive Rate	0.26	0.28	1.00	0.74	0.25	0.19
False Negative Rate	0.08	0.18	0.00	0.03	0.11	0.09
Abundance						
R² Adj.	0.06	0.02	0.03	0.04	0.05	0.05
Deviance Explained	26.61	12.66	26.36	20.93	21.77	14.86
Calibration y-Intercept	-1.82	0.54	0.44	1.25	-0.63	-0.13
Calibration Slope	1.63	0.92	0.91	0.66	1.14	1.04
R_p	0.32	0.14	0.20	0.19	0.25	0.26
R_{sp}	0.27	0.18	0.20	0.22	0.26	0.26
RMSE	9.93	11.94	16.58	11.02	11.61	2.57
AVE	-0.38	-0.21	0.02	0.48	-0.05	0.04

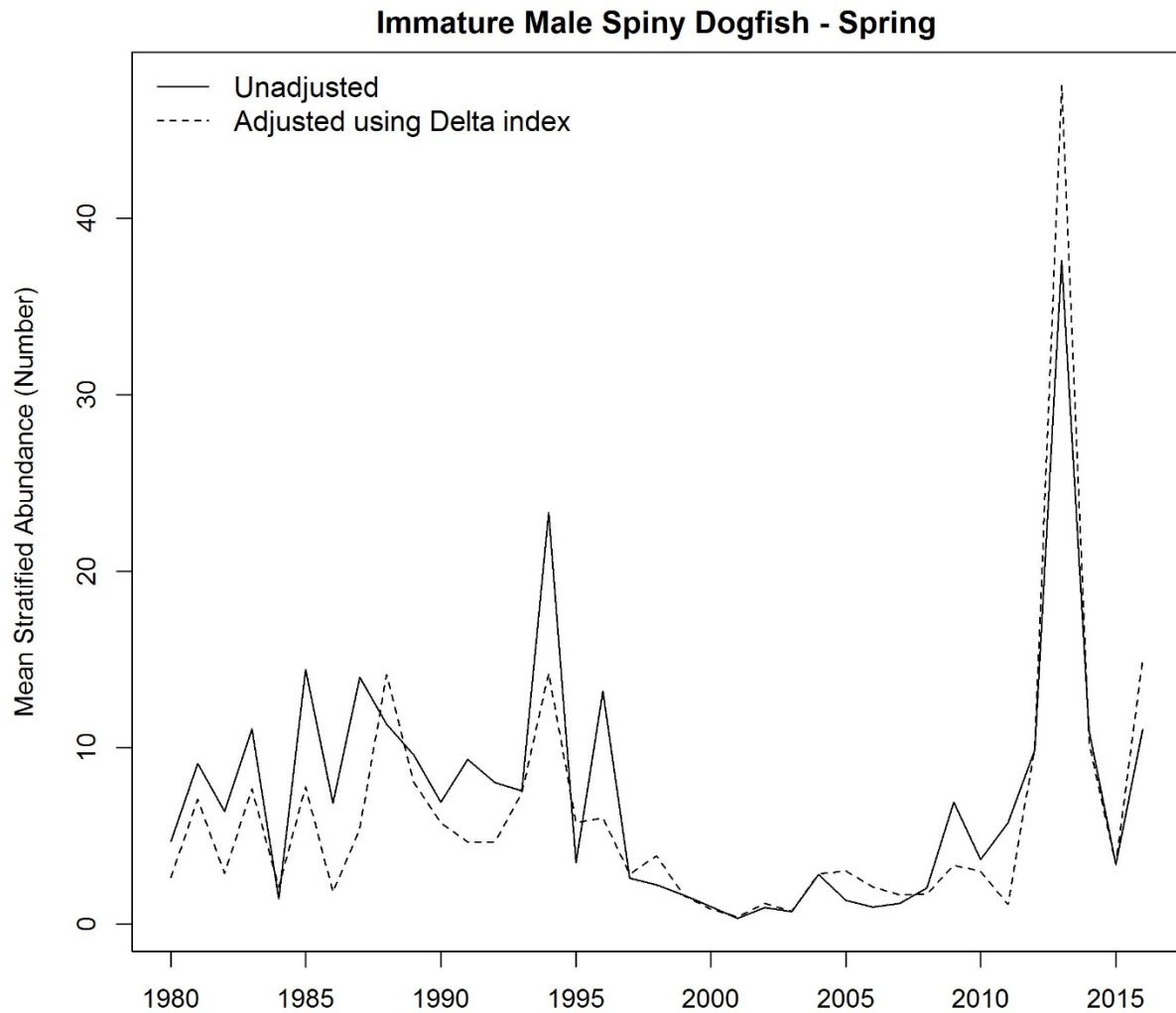**Figure 1**. Mean delta-index (averaged within each spatial cell across years 1968-2016) and associated standard error for neonate spiny dogfish (≤ 26 cm TL).
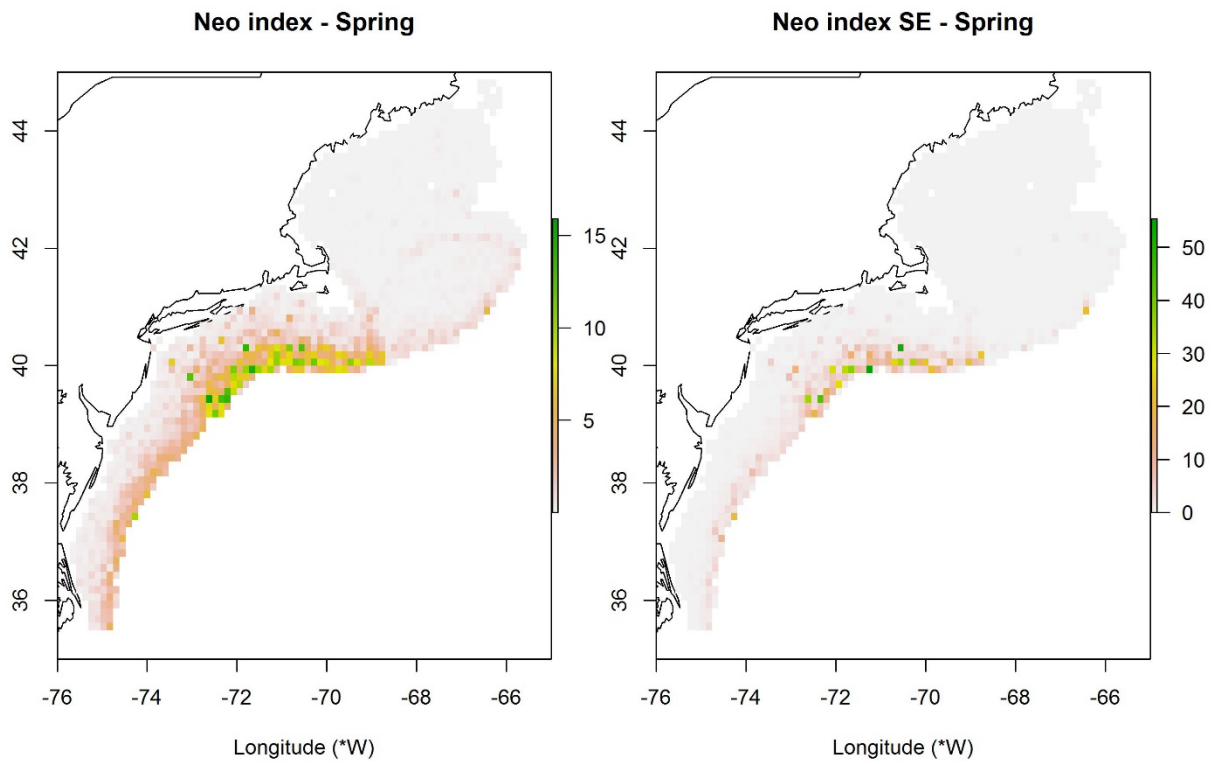
Figure 2. Mean delta-index (averaged within each spatial cell across years 1968-2016) and associated standard error for neonate spiny dogfish (≤ 35 cm TL).
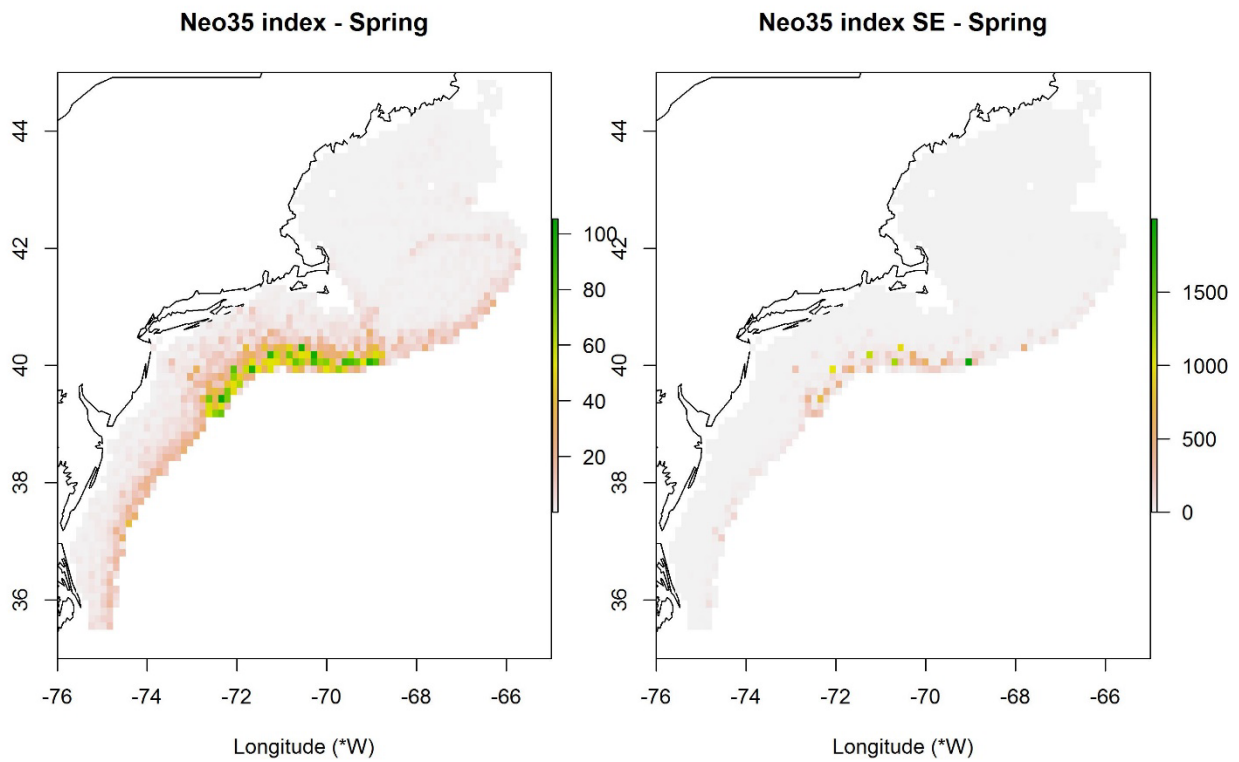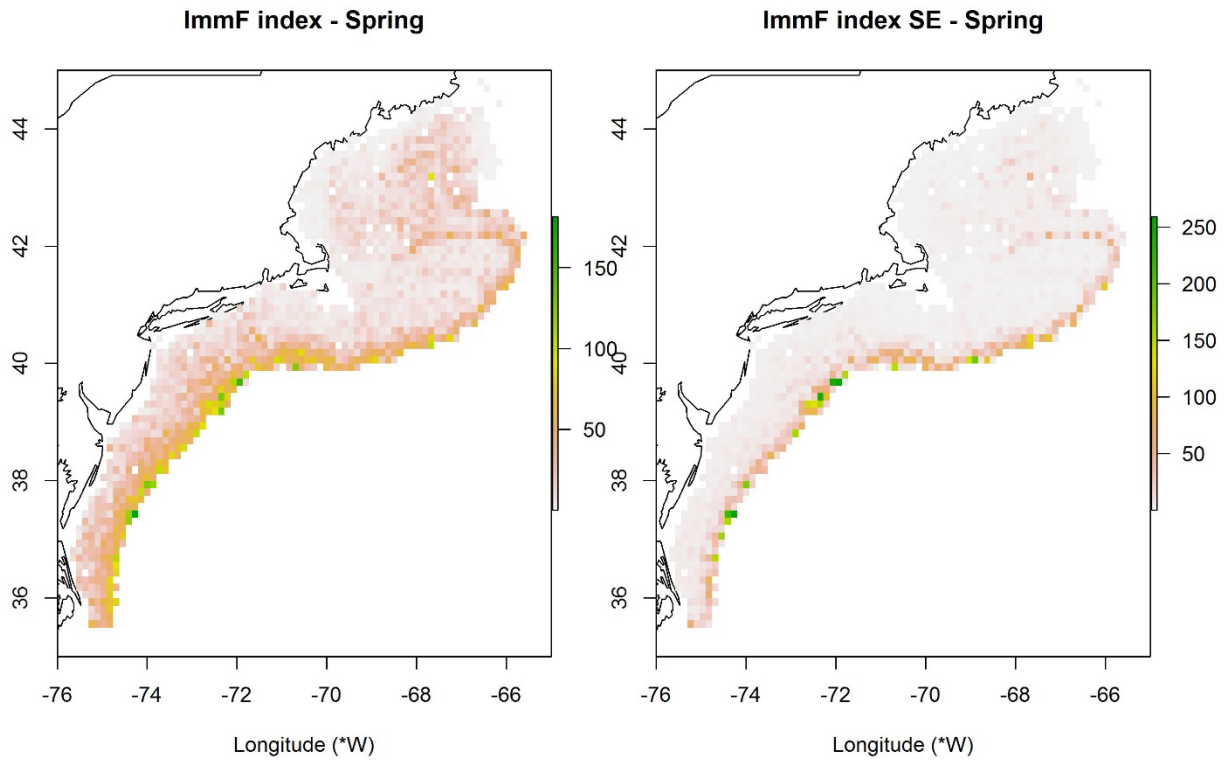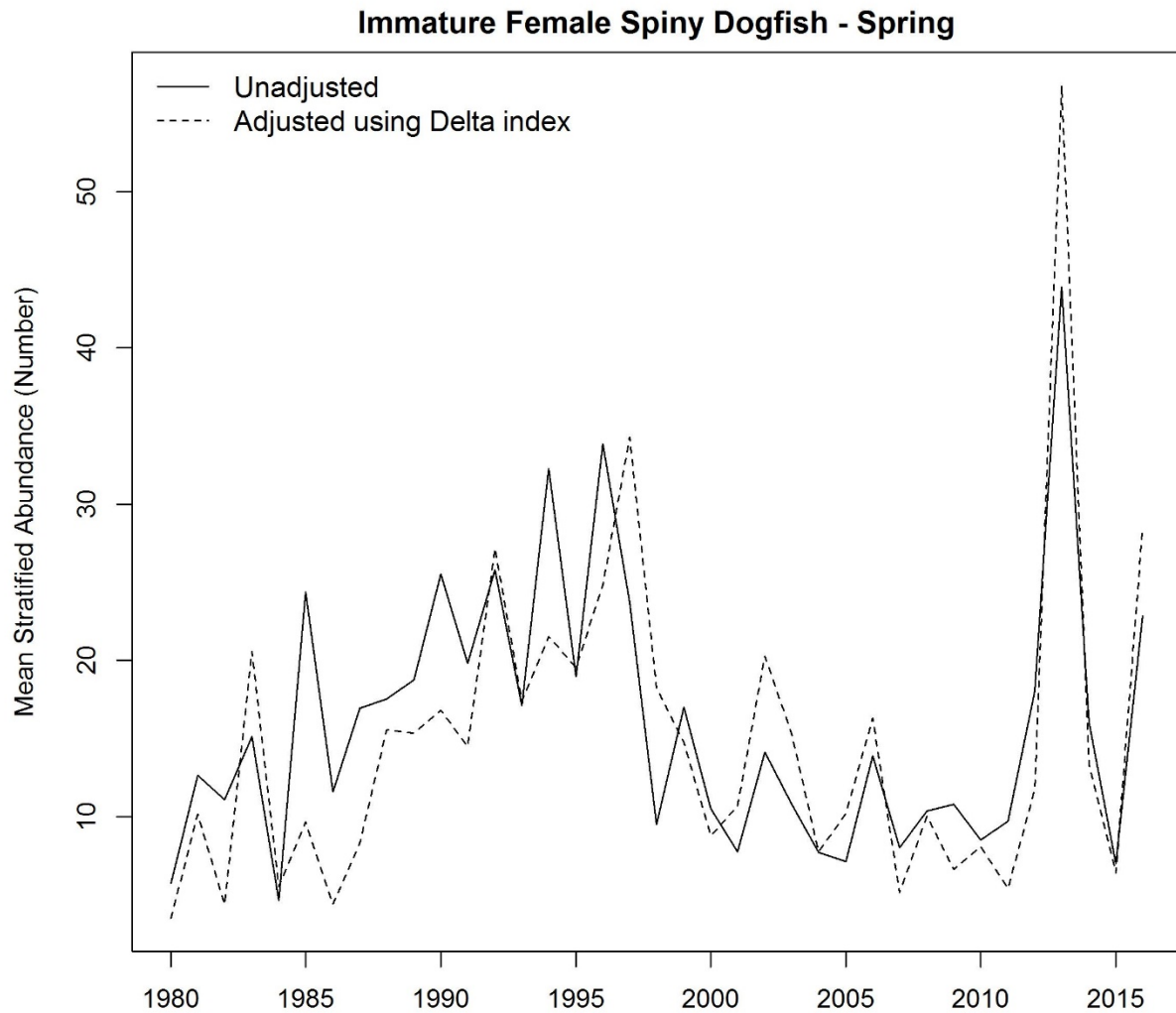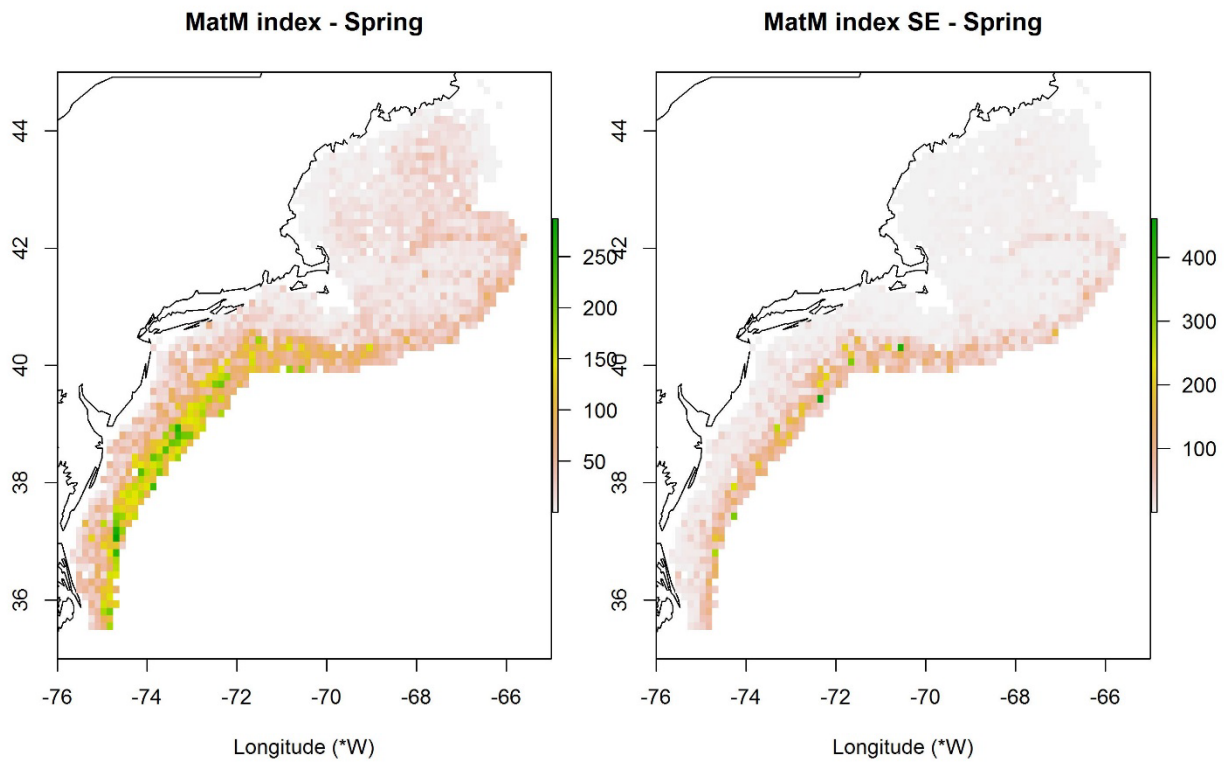
Figure 3. Comparison of mean stratified abundance (number) using the delta index to predict the numbers of neonate spiny dogfish (≤ 35 cm TL) between 1968 and 2016. The unadjusted mean stratified abundance (number) is shown for comparison.
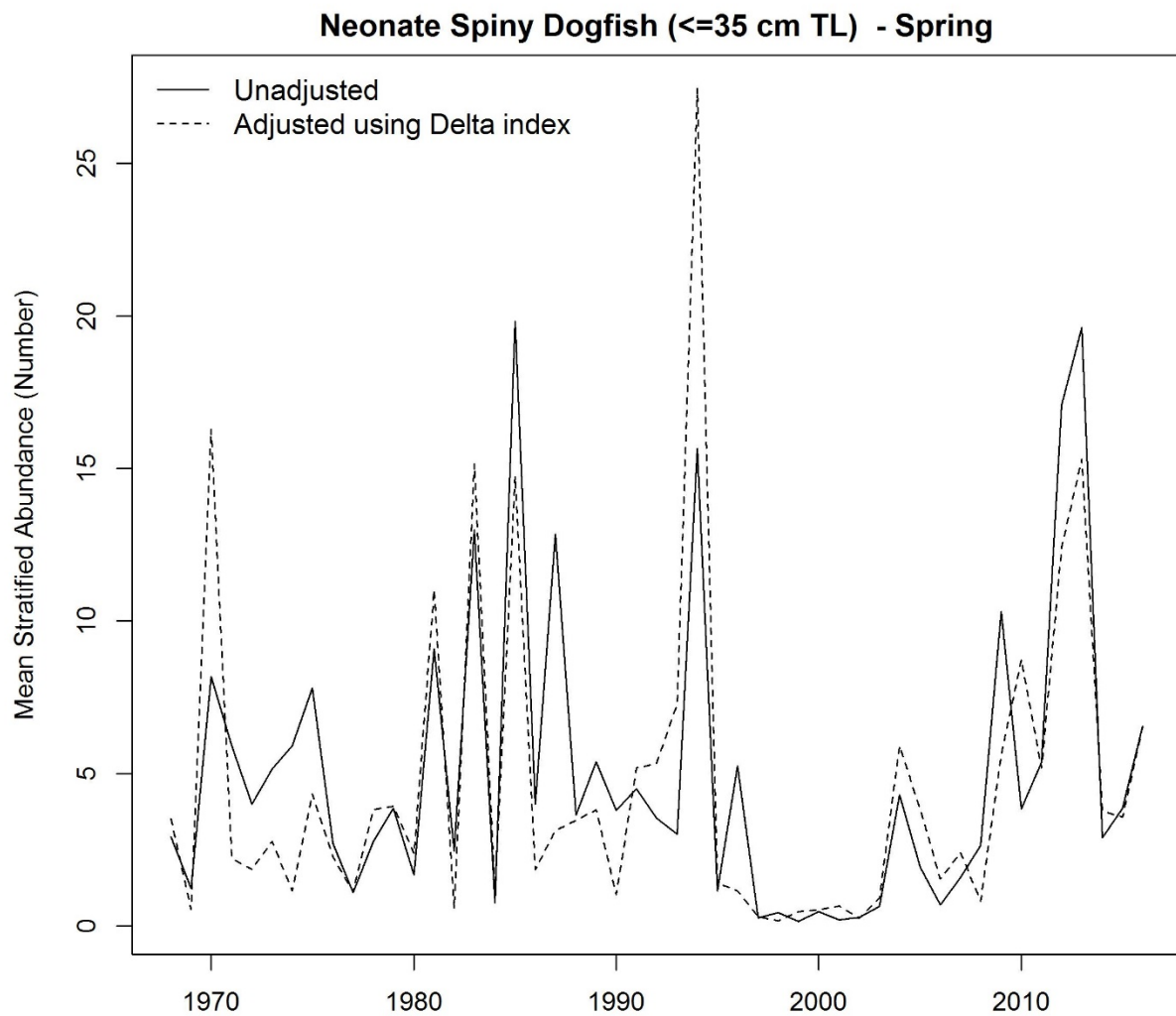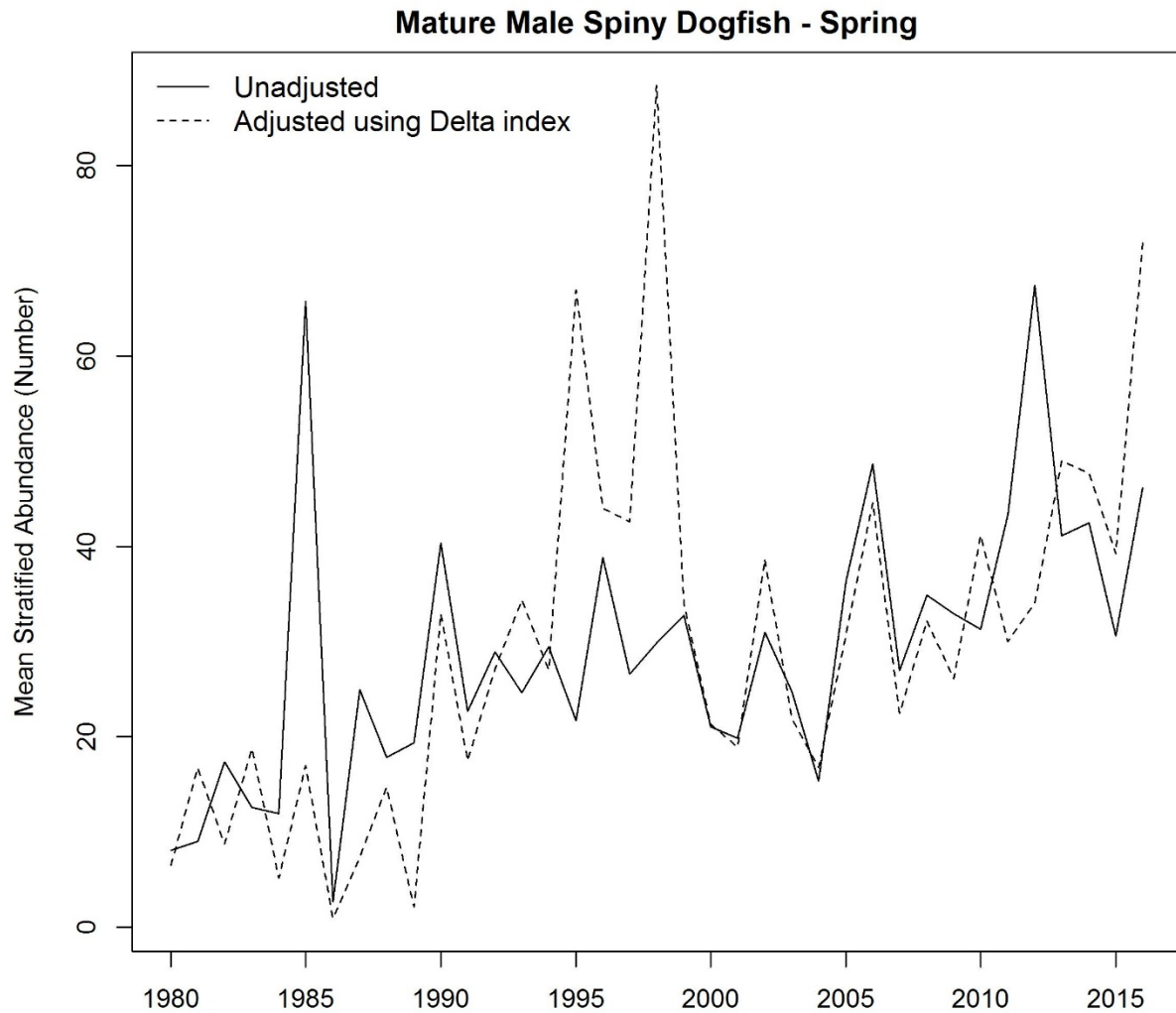
Figure 4. Mean delta-index (averaged within each spatial cell across years 1980-2016) and associated standard error for immature male spiny dogfish (26 cm TL < TL < 60 cm TL).
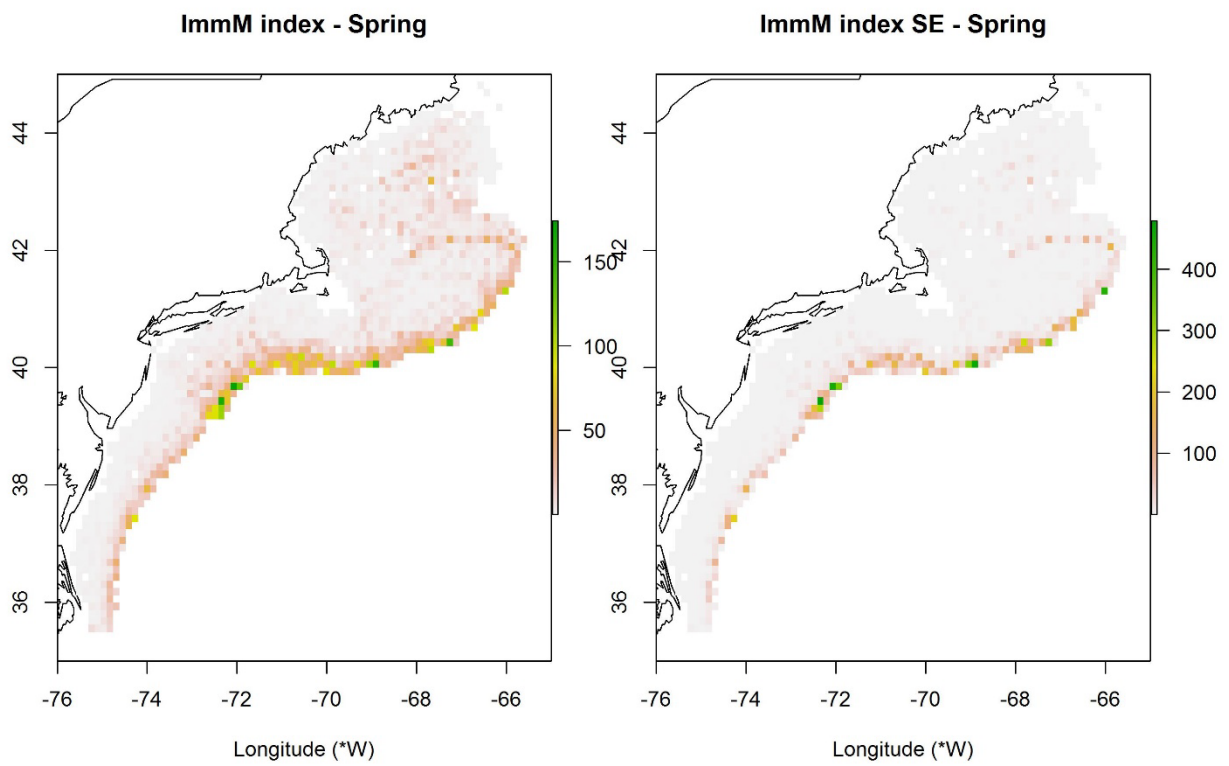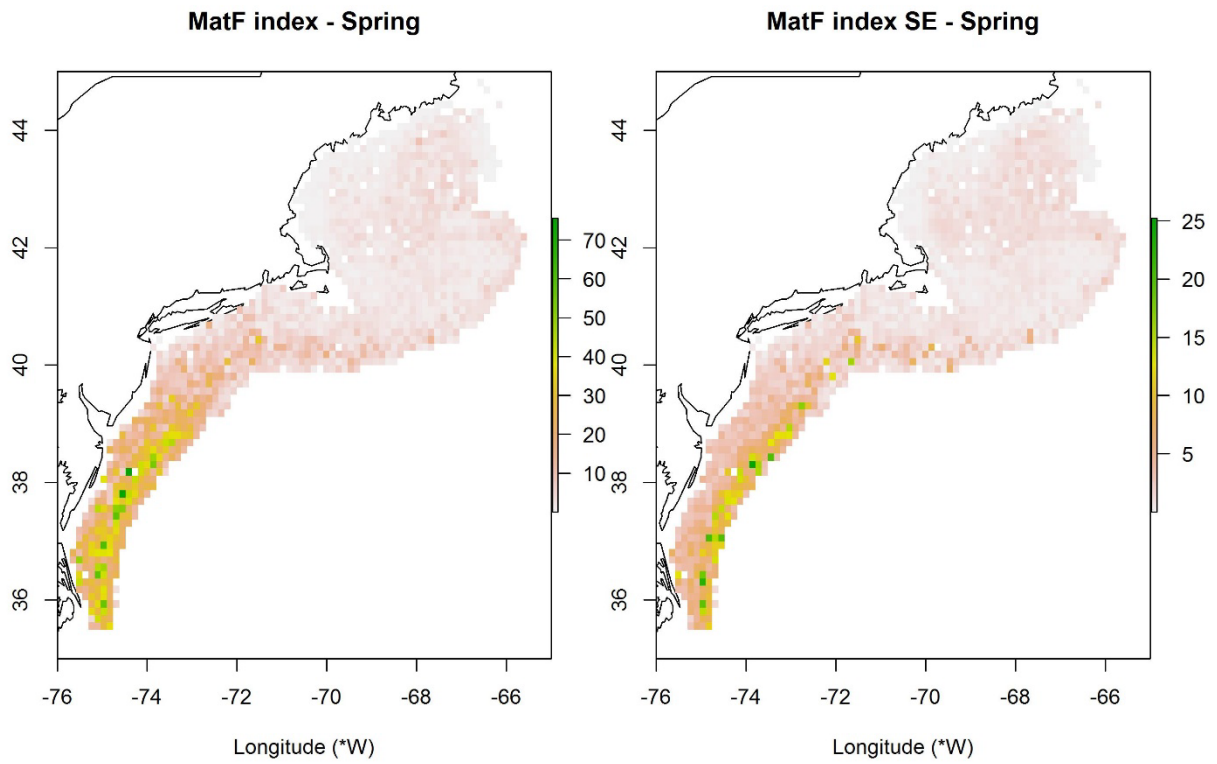
Figure 5. Comparison of mean stratified abundance (number) using the delta index to predict the numbers of immature male spiny dogfish (26 cm TL < TL < 60 cm TL) between 1980 and 2016. The unadjusted mean stratified abundance (number) is shown for comparison.


Immature Male Spiny Dogfish - Spring

Figure 6. Mean delta-index (averaged within each spatial cell across years 1980-2016) and associated standard error for immature female spiny dogfish (26 cm TL < TL < 80 cm TL).

Figure 7. Comparison of mean stratified abundance (number) using the delta index to predict the numbers of immature female spiny dogfish (26 cm TL < TL < 80 cm TL) between 1980 and 2016. The unadjusted mean stratified abundance (number) is shown for comparison.

Figure 8. Mean delta-index (averaged within each spatial cell across years 1980-2016) and associated standard error for mature male spiny dogfish (≥ 60 cm TL).

Figure 9. Comparison of mean stratified abundance (number) using the delta index to predict the numbers of mature male spiny dogfish (TL $\geq$ 60 cm TL) between 1980 and 2016. The unadjusted mean stratified abundance (number) is shown for comparison.

Figure 10. Mean delta-index (averaged within each spatial cell across years 1980-2016) and associated standard error for mature female spiny dogfish (≥ 80 cm TL).

Figure 11. Comparison of mean stratified abundance (number) using the delta index to predict the numbers of mature male spiny dogfish (TL ≥ 80 cm TL) between 1980 and 2016. The unadjusted mean stratified abundance (number) is shown for comparison.

35
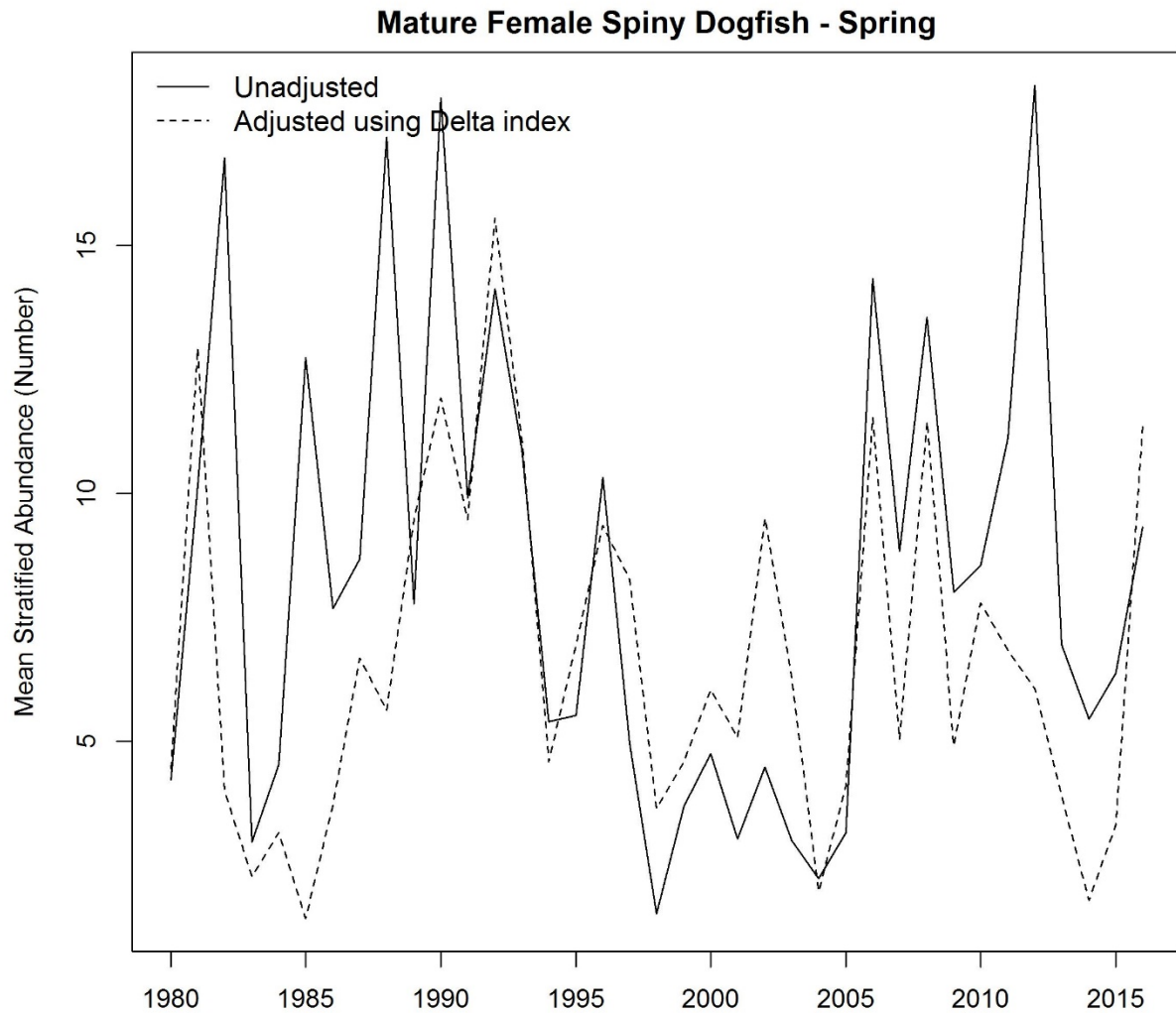
Figure 1. CDFs of Summer Flounder distribution with respect to Bottom Temperature (^{o}C) for the survey (available habitat; black dots), all Summer Flounder in the survey (occupied habitat; grey dots), and each of the length class (0-30 cm, purple dots; 30-40 cm, blue dots; and 40-70 cm fish, green dots) in the NEUS LME for spring and fall (1968-2015) assessed from the survey. Years that the data is taken from and the n number of data points are listed above each plot. The x-axis shows the range of the environmental variables in question, and the y-axis is the probability of occurrence from 0 to 1.

The Distribution of Summer Flounder over Bottom Temperature (0C)
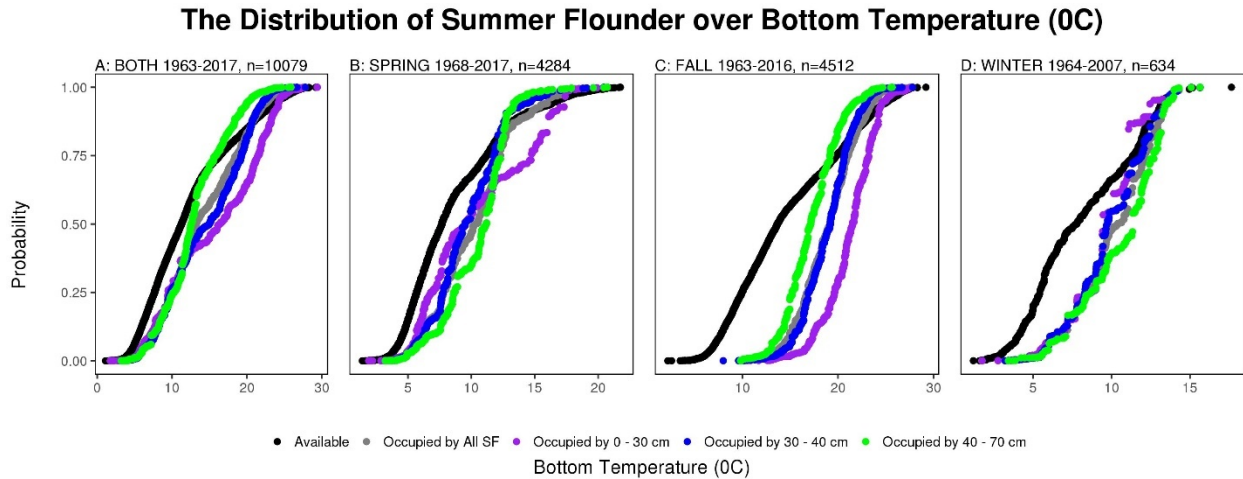
Figure 13. CDFs of Summer Flounder distribution with respect to Rugosity (TRI) for the survey (available habitat; black dots), all Summer Flounder in the survey (occupied habitat; grey dots), and each of the length class (0-30 cm, purple dots; 30-40 cm, blue dots; and 40-70 cm fish, green dots) in the NEUS LME for spring and fall (1968-2015) assessed from the survey. Years that the data is taken from and the n number of data points are listed above each plot. The x-axis shows the range of the environmental variables in question, and the y-axis is the probability of occurrence from 0 to 1.

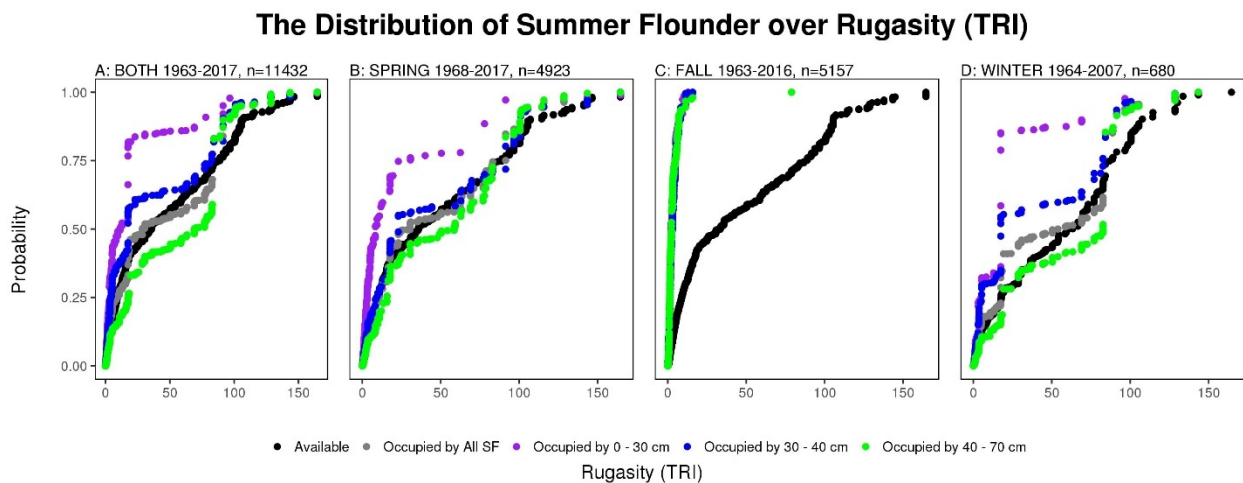The Distribution of Summer Flounder over Rugasity (TRI)

36

Figure 14. Mean delta-index (averaged within each spatial cell across years) for all summer flounder with length and season as a covariate (left panel), age 2-6 adult fish (last column) in the NEUS LME, all length in fall using length as a covariate (middle panel), and all lengths in spring using length as a covariate (right panel)
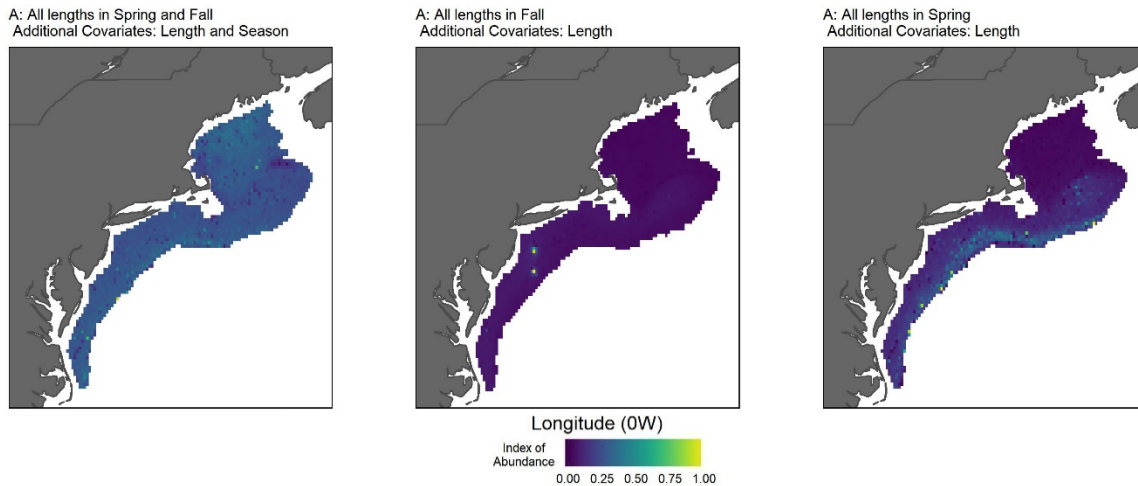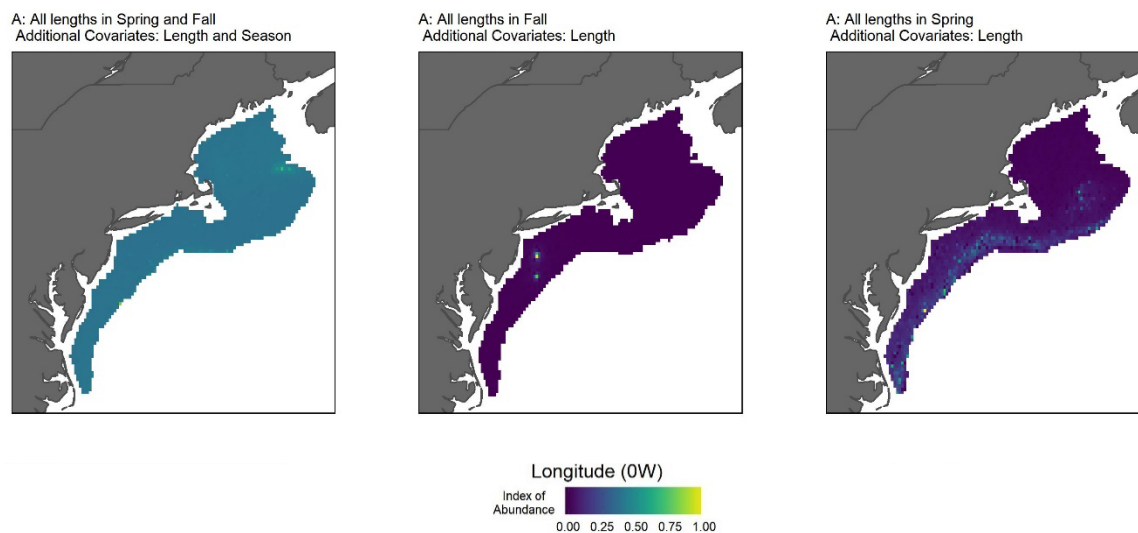

Figure 15. Standard Error of mean delta-index (averaged within each spatial cell across years) for all summer flounder with length and season as a covariate (left panel), age 2-6 adult fish (last column) in the NEUS LME, all length in fall using length as a covariate (middle panel), and all lengths in spring using length as a covariate (right panel)

Figure 16. Mean delta-index for all summer flounder with length and season as a covariate (left panel), all lengths in fall using length as a covariate (middle panel), and all lengths in spring using length as a covariate (right panel)
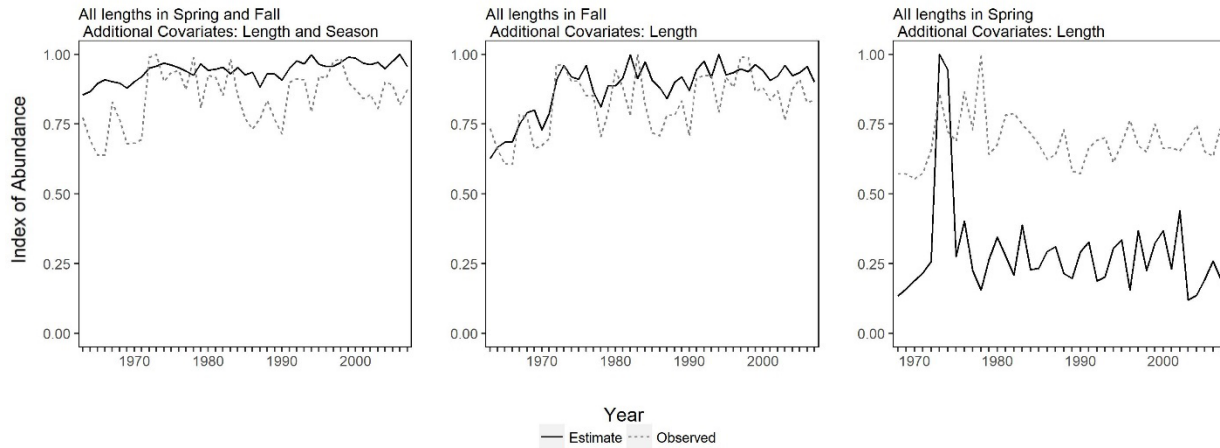
Figure 17. CDFs of Black Sea Bass distribution with respect to Bottom Temperature (^{o}C) for the survey (available habitat; black dots), all Black Sea Bass in the survey (occupied habitat; grey dots), and each of the length class (0-14 cm, purple dots; 14-20 cm, blue dots; and 20-45 cm fish, green dots) in the NEUS LME for spring and fall (1968-2015) assessed from the survey. Years that the data is taken from and the n number of data points are listed above each plot. The x-axis shows the range of the environmental variables in question, and the y-axis is the probability of occurrence from 0 to 1
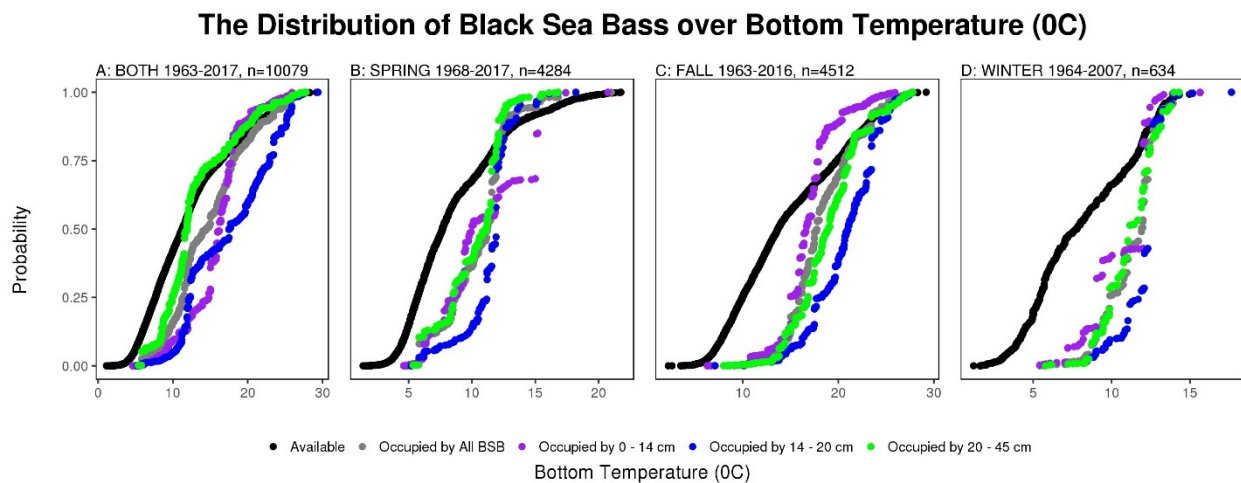

The Distribution of Black Sea Bass over Bottom Temperature (0C)

Figure 18. CDFs of Black Sea Bass distribution with respect to Rugosity (TRI) for the survey (available habitat; black dots), all Black Sea Bass in the survey (occupied habitat; grey dots), and each of the length class (0-14 cm, purple dots; 14-20 cm, blue dots; and 20-45 cm fish, green dots) in the NEUS LME for spring and fall (1968-2015) assessed from the survey. Years that the data is taken from and the n number of data points are listed above each plot. The x-axis shows the range of the environmental variables in question, and the y-axis is the probability of occurrence from 0 to 1.
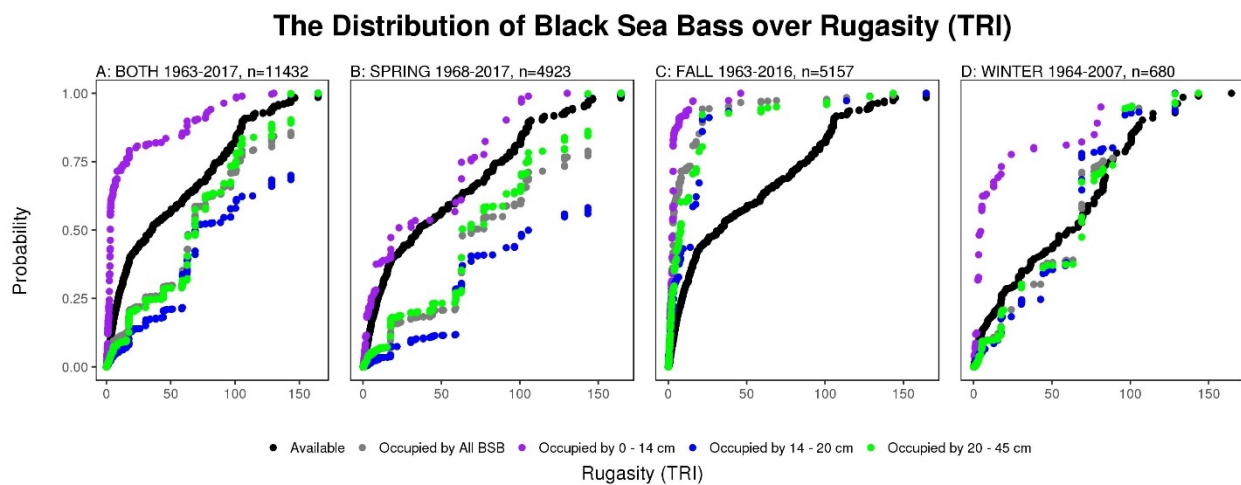

The Distribution of Black Sea Bass over Rugasity (TRI)

39

Figure 19. Mean delta-index (averaged within each spatial cell across years) for each model of Black Sea Bass described in Tables 1 and for both spring and fall seasons combined (first panel), spring (middle panel), and fall (last panel) and all Black Sea Bass (first column), 0 – 14 cm age 1 fish (second column), 14 – 20 cm age 2 fish (third column), 20 – 45 cm age 2-6 adult fish (last column) in the NEUS LME.
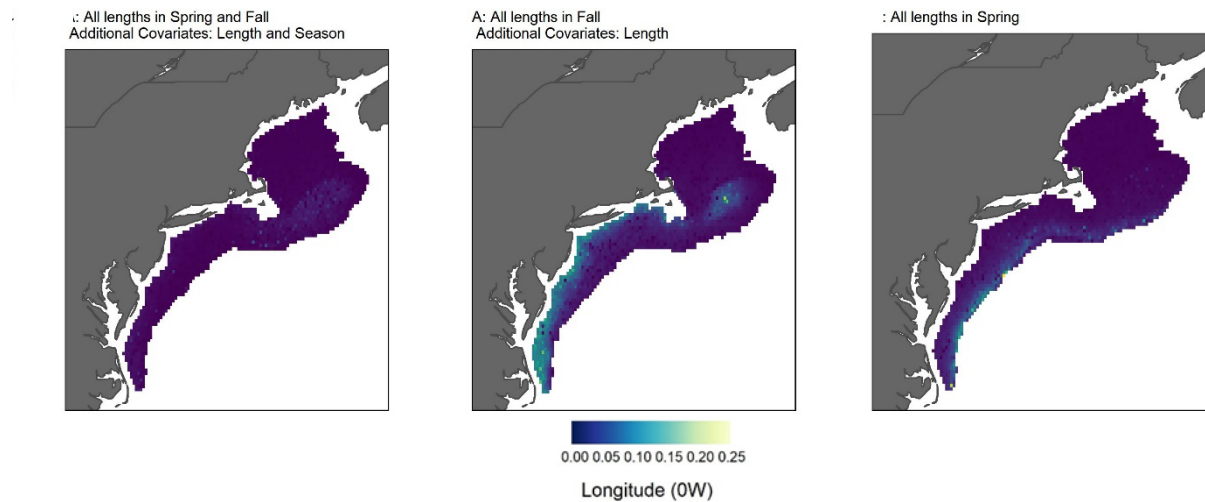

Figure 20. Standard Error of the Mean delta-index (averaged within each spatial cell across years) for each model of Black Sea Bass described in Tables 1 and for both spring and fall both spring and fall seasons combined (first panel), spring (middle panel), and fall (last panel) and all Black Sea Bass (first column), 0 – 14 cm age 1 fish (second column), 14 – 20 cm age 2 fish (third column), 20 – 45 cm age 2-6 adult fish (last column) in the NEUS LME.
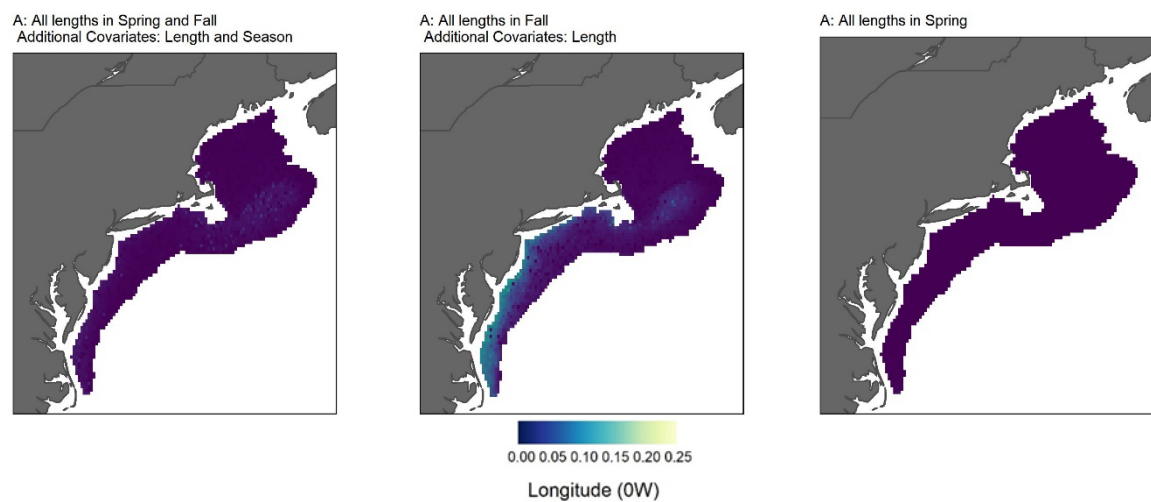
Figure 21. Adjusted mean delta-index (averaged within each spatial cell across years) (black lines) and the unadjusted mean stratified abundance (grey dashed lines) for each model of Black Sea Bass described in Tables 1 and for both spring and fall seasons combined (first panel), spring (middle panel), and fall (last panel) and all Black Sea Bass (first column), 0 – 14 cm age 1 fish (second column), 14 – 20 cm age 2 fish (third column), 20 – 45 cm age 2-6 adult fish (last column) in the NEUS LME.