

Final report to the Mid Atlantic Fisheries Management Council Collaborative Research Program: *Collaborative development of a winter habitat model for Atlantic Mackerel, “version 2.0”, for the identification of “cryptic” habitats and estimation of population availability to assessment surveys and the fishery.*

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Executive Summary

The goal of our industry-science collaborative study was to develop a habitat model to accurately describe winter and early spring distributions of trawlable juvenile and adult Atlantic mackerel. We then applied the model to a) develop estimates of the availability of the mackerel population to the spring NOAA North East Fisheries Science Center bottom trawl survey which has provided the principle index of population condition for the US stock assessment since the late 1970s. We provided habitat based availability indices to inform survey catch-ability for the 2017 stock assessment. We also used the

model to *b*) develop a quantitative inference about the characteristics of overwintering habitat outside the range of the NOAA survey that could be used to develop a collaborative survey. Our work was guided by the hypothesis that Atlantic mackerel distributions during winter and spring, and thus availability to the spring NEFSC survey and winter fishery, are primarily determined by the development and distribution of overwintering habitat which may be changing in the Northwest Atlantic in response to anthropogenic climate change.

A review of literature describing habitat preferences of mackerel throughout the Atlantic, analysis of existing fishery dependent, fishery independent and environmental data, and collaborative field work within the active winter fishery indicated that overwintering habitat for mackerel was best described at the scale of the northwest Atlantic by bottom temperatures ranging from 7-9°C. However, real time modeling and monitoring within the active winter fishery revealed that mackerel were not caught in preferred thermal habitat unless it had been connected to suitable habitat to the northeast along the fall and winter migration route connecting the mid-Atlantic Bight to summer feeding habitats in the Gulf of Maine. Thus, habitat connectivity along the migration route appeared to determine of patterns in fishery catch and mackerel habitat occupancy. We therefore constructed and evaluated a thermal habitat model that explicitly accounted for movement constraints along the fall migration route. US fishery dynamics and distributions of fish in winter and spring fishery independent bottom trawl surveys in the US and the Nova Scotian Shelf, Canada were associated with projections of this habitat model. We applied the model to develop estimates of the population availability to the spring NEFSC bottom survey that we presented in a working paper at the 2017 stock assessment. We estimated that the spring NEFSC survey sampled approximately 69% (2.5 & 97.5% quantiles = 45% & 89%) of winter habitat available within the model domain from 1980 through 2016. The habitat model also indicated that a persistent band of potential winter habitat for mackerel may exist on the continental slope outside the domain of the NEFSC survey in salinities ranging from 35‰ to 36‰ and depths ranging from approximately 350 to 500 Meters. Temperatures, depths, and salinities we identified in the projections were remarkably similar to deep overwintering habitats adjacent to continental shelves on west coast of the United Kingdom and Nova Scotia, Canada where commercial concentrations are known to occur.

We also developed analyses presented in an additional working paper for the 2017 assessment, testing the underlying hypothesis that mackerel distributions during the spring NEFSC survey and availability to the winter fishery are primarily determined by the evolution of overwintering habitat in the Northwest Atlantic which may be changing in response to climate change. We compared the results of identical analyses of the spatial structure of trawlable juvenile and mature mackerel in the NEFSC survey to empirically measured and modeled winter thermal habitat from 1968-2015. We also examined the relationship between fishery landings, and indicators of fish and habitat distributions during the spring survey. The analysis indicated that centers of biomass for immature and mature fish shifted progressively northeast at an average rate of over 10 $km\ y^{-1}$ from 1980-2016. Before 2000, mature fish were often distributed 150 km southwest of immature fish in the southern part of the MAB. After 2000, mature and immature fish

overlapped strongly, the northeast shift was more rapid and fish were collected farther into the northern Gulf of Maine than in the past. The northward shift and increase in overlap between mature and immature fish was accompanied by apparent dispersal of fish over larger areas and an increase the frequency of occurrence of fish in NEFSC survey samples. In contrast, fishery landings were high earlier in time when fish were more concentrated farther to the southwest in the mid-Atlantic. The distribution of measured and modeled thermal habitat used by juvenile and adult Mackerel for overwintering also shifted to northeast, but later in time (1990) and at a half the rate of the fish ($\sim 5 \text{ km y}^{-1}$). Our analyses did support our hypothesis that fishery landings are related to winter habitat evolution and concentration of fish to the southwest in the mid Atlantic Bight. It did not, however, support the hypothesis that fish distributions in the spring NEFSC survey are primarily determined by overwintering habitat availability. The shift in mature fish distributions occurring in the 2000s corresponded to the period when larvae and eggs abundances on the mid Atlantic Bight Spawning/Nursery ground, which was historically important for population recruitment, dramatically declined. Small pelagic fishes, like mackerel are particularly flexible and opportunistic in their use of migration pathways that allow them to link habitats critical to the completion life history stages and processes while minimizing energetic costs and predation risk. We now speculate that winter distributions of mackerel in the NEFSC survey are primarily determined by locations of viable spawning and nursery grounds and secondarily by overwintering habitat that does not currently appear to be limiting. Distributions of mature mackerel in the spring NEFSC survey may have shifted northeast because the mid Atlantic Bight Spawning/Nursery ground is not viable and fish are now overwintering farther north in closer proximity to viable spawning and nursery grounds in the Gulf of Maine.

1.0 Overall Project Objectives:

In an effort to investigate a) net efficiency, availability and catchability of Atlantic mackerel to the NEFSC trawl survey and b) the abundance and/or distribution of Atlantic mackerel beyond the depth range of current NEFSC trawl surveys, we proposed to:

- 1) Develop an environmentally informed and time varying estimates of the availability of Atlantic mackerel to fishery independent surveys used to inform models in upcoming stock assessments, and
- 2) Use the analysis and models developed in #1 to frame a quantitative hypothesis that can be used to design an efficient, cost effective, state of the art industry based field survey of cryptic habitat and potential mackerel aggregations outside the domain of fishery independent surveys and the current fishery.

2.0 Performance Summary:

The performance of this project related to the proposed tasks was made possible through significant collaboration among science, management and industry partners familiar with the mackerel fisheries and its assessment. The project began with a kickoff meeting held on June 9, 2016 to review: a) the overall project objectives including broad outlines of final products; b) the NOAA NEFSC Study Fleet and ROFFS™ modeling

efforts; and c) the availability of fishery and fishery independent data as well as ocean observations and numerical ocean model output that can be used to calibrate and evaluate a version 2 model useful for estimating population availability. The approaches to modeling and field evaluation were discussed in the context of model applications. A second meeting was held among CO-PIs on January 13, 2017 to continue to refine and develop the habitat models. Much of the work reported here was developed and reviewed by a transdisciplinary working group of experts for *Atlantic Mackerel Population Ecology and the Fishery* that was supported and led by the NEFSC cooperative research branch(lead by CoPI Manderson) and which met in December of 2015 and 2016 prior to the Atlantic mackerel stock assessment. Throughout the project, we worked closely with industry participants to develop analyses of Atlantic mackerel migration and habitat use and the fishery to determine linkages between the ecology of the population, the fishery including vessel and processing capacities, markets, and constraints including regulatory influences. Products from this specific project were developed and presented in two working papers at the 2017 Atlantic mackerel assessment data (May 2017), modeling (July 2017) and SAW/SARC meetings (Nov 2017). They are referenced in the Assessment documentation and appendices (<https://www.nefsc.noaa.gov/saw/reports.html>).

The project tasks were organized to gather background information on ecology and existing models (tasks 1 and 2), further model development (Task 3), and application of refined models (Tasks 4 and 5). For the purpose of this final report, we summarize the performance in these general categories of the work flow.

2.1 Background information (Tasks 1 and 2):

We formally evaluated NEFSC Cooperative Research Program and ROFFSTTM and habitat models as part of the development of the 2nd generation habitat model used to develop products for the 2017 stock assessment. We worked with 6 large fishing vessels in the NEFSC study fleet active in the directed mackerel fishery to evaluate 1st and 2nd generation models using a model “nowcasting” approach.

We assembled and reviewed scientific and industry based information describing characteristics of mackerel habitats (>200M) with special reference to winter habitat, including deep water in the North East Atlantic as well as the North West Atlantic Ocean. Following a thorough literature review, this included a fact-finding mission in mid-September 2016 to Iceland (Co-PIs Moore, Bright, Manderson) to investigate the northeast Atlantic mackerel fishery and the recent outbreak of fish in Iceland and the west Coast of Greenland. Activities in Iceland included a lecture on the northeast Atlantic mackerel fishery and habitats presented by scientists and industry experts at the Icelandic Marine Research Institute (a department of the Ministry of Fisheries) in Reykjavik, a tour of HB Grandi (one of Iceland’s largest and most successful vertically integrated fishing companies, producing groundfish and pelagics), and Hampidjan (one of the world’s most innovative pelagic trawl manufacturers). In addition, Co-PIs Bright, Manderson, and Moore traveled to Seydisfjordur to meet with the captain of a 230 meter pelagic trawler for in-depth discussions about mackerel habitat ecology, ecosystem clues to locating and catching mackerel. We also participated in a tour of the HB GRANDI pelagic processing plant, and meetings with management and fishing Masters of SILDARVINSSLAN, another leading pelagic fishing and processing company based in Neskaupfjordur. The

following week one of the CO-PIs (Manderson) attended the ICES annual science conference in Riga, Latvia and made contact with several prominent EU scientists working on NE Atlantic mackerel. The PI's participated in a ICES ASC session on pelagic habitat and contributed to the manuscript "Pelagic habitat: exploring the concept of good environmental status" (Dickey-Callas et al., 2017). Co-PI Manderson also presented a paper entitled "Collaborative now-casting of seascape dynamics to develop models for accurate estimates of past and future availability of fish to fisheries and fisheries independent surveys" which articulated the approach being taken in the project in the ICES ASC session "Seasonal-to-decadal prediction of marine systems: opportunities, approaches, and applications."

We summarize the results of our review in three parts: Part 1) review of scientific literature describing Atlantic mackerel behavior and habitat ecology throughout the Atlantic relevant to the interpretation of spring NEFSC bottom trawl survey; Part 2) we use analysis of spatial indicators to describe changes in the spatial structure of immature and mature mackerel in the NEFSC bottom survey from 1968 to 2016. We applied the same indicators to habitat defined by *in situ* temperatures measured during the surveys to determine whether changes in habitat distributions as defined by temperature matched the observed changes in fish distributions. We then move on to model development and application.

2.1.1: A review of *Atlantic mackerel behavior and habitat ecology relevant to catchability and interpretation of the NEFSC spring bottom trawl survey*

The NEFSC spring bottom trawl surveys occur from March through May, with most tows completed in March (23%) and April (71%). We therefore hypothesized that the availability of mackerel to the NEFSC survey is determined primarily by behaviors associated with the timing and location of late fall and winter migration, overwintering habitat, and spring migration.

North West (NW) Atlantic mackerel range from Newfoundland, Canada to Cape Hatteras, North Carolina. The species also occurs in the Northeast (NE) Atlantic from the west coast of Greenland to the Gulf of Cadiz. Currently there is no evidence of significant mixing of NW and NE Atlantic mackerel (Nesbo et al. 2000, Rodríguez-Ezpeleta et al. 2016; reviewed by Jansen and Gislason 2013). Mackerel are a fast swimming pelagic fish (individual cruising speed ~ 3.5 body lengths per second [$BL\ s^{-1}$]; burst speed $\sim 18\ BL\ sec^{-1}$; school speeds of $\sim 6\ m\ s^{-1}$) that occupy habitats from the nearshore continental shelf to the continental slope (He and Wardle 1988, Wardle and He 1988, Godø et al. 2004). Mackerel can also traverse deep ocean habitats (Astthorsson et al. 2012, ICES 2014a). Habitat preferences vary by life history stage, life history process and season. Physiological requirements and rates of many important specific mackerel life history stages and processes appear to be met and controlled through behavioral habitat selection for abiotic and biological properties and processes in the water column. Seawater temperature appears to be particularly important (Castonguay et al. 1992, Reid et al. 1997, Bruge et al. 2016, and many others). The complex pelagic habitat ecology of mackerel is reflected in highly plastic patterns of migration, geographic distribution, schooling, and life history event schedules (Neill 1984, Walsh et al. 1995, Reid et al. 1997, Bruge et al. 2016). Throughout recorded history Atlantic mackerel have exhibited dramatic fluctuations in local abundance. Some of the earliest fishery gear restrictions were

imposed in the US during the 17th century in response to the disappearance of mackerel in coastal Massachusetts waters (Stansby and Lemon 1941, Hoy and Clark 1967). In recent years and on both sides of the North Atlantic mackerel have exhibited dramatic changes in geographic distribution and productivity attributed to changes in ocean temperature with anthropogenic climate change (Overholtz et al. 2011, Astthorsson et al. 2012, Radlinski et al. 2013, Jansen et al. 2016). These impacts included recent distribution shifts observed in the NOAA/NEFSC spring bottom trawl survey that have been also associated with changes in seawater temperature (Overholtz et al. 2011, Radlinski et al. 2013).

North West Atlantic mackerel are believed to be composed of two migratory contingents: a southern contingent that historically spawned along the south side of Long Island and the western Gulf of Maine in April and May and a northern contingent that spawns in the Gulf of Saint Lawrence during July (Sette 1943, 1950, Ware 1977, Morse 1980). When the animals reach spawning grounds they have low somatic fat reserves (3-5% by weight). This poor condition, which results from the energetic demands of spring migration and the mobilization of lipids from somatic tissues to gametes, can produce significant mortality on spawning grounds (Grégoire 2006). After spawning, the southern contingent uses summer feeding habitats in the coastal waters of the Gulf of Maine and Georges Bank. From October through December, the southern contingent aggregates to feed in the southern Gulf of Maine where a late fall fishery occurs (Sette 1950, Bright WM Pers Comm.). Somatic fat peaks during this late fall period (20 to >30% by weight) when fish are most valuable in international markets (Grégoire and Lévesque 1994, G Goodwin, Seafreeze LTD Pers Comm). As winter progresses, the fish in western Gulf of Maine move along the continental shelf to the southwest into Southern New England and the Mid-Atlantic Bight where they have supported an important winter fishery since the 19th century (Pierce 1934). Typically the largest fish migrate close to the coast and, during some winters, these fish can occur as far to the southwest as Cape Hatteras (See Axelson et al., 2017). A portion of the northern spawning contingent spends the summer in Canadian waters on the Nova Scotia shelf, the northern Gulf of Saint Lawrence and Newfoundland. Some young fish that spend the summer in Canadian waters move to deep water (~200 meters) overwintering habitats including areas on the outer edge of Nova Scotia Shelf (Sette 1950, Grégoire et al. 2014). Older fish of the northern contingent moves south to mix with the southern contingent in the Gulf of Maine during the summer and late fall. These northern contingent fish are also believed to migrate into the southern New England-Mid Atlantic Bight region during the winter.

During winter and early spring on both sides of the Atlantic mackerel occur in high concentrations in relatively cold bottom water ranging from approximately 5°C - 7°C (Giedz 1988, D'Amours and Castonguay 1992, Jansen et al. 2015). The fish become progressively lean during the winter and feeding activity is presumed to be low. The fish may occupy cold water to conserve energy through the winter when primary productivity is low. In the northwest Atlantic Fish begin to migrate northeast in the early spring along multiple pathways including the shallow nearshore continental shelf and inner edge of the continental slope (Sette 1950, Christensen and Clifford 1980, Axelson 2017). The speed and direction of migration appears to be temperature dependent and dominant migration pathways can shift between nearshore and offshore (Reid et al. 1997). In the northwest Atlantic fish are believed to follow the 7°C isotherm northeast to arrive on spawning

grounds in the spring and early summer (Hoy and Clark 1967, Ware and Lambert 1985). Mackerel are also reported to use downstream circulation to conserve energy during long distance migration (Sette 1950, Ware and Lambert 1985, Castonguay and Gilbert 1995, Reid et al. 1997, Nøttestad et al. 2016).

This literature review indicates that the habitat ecology relevant to the spring NEFSC bottom trawl survey is complex. The review and observations in the active fishery suggest that the distribution of fish during availability and availability to the Spring NEFSC survey that occurs during the winter-spring ocean transition is be a function of the development of relatively cold water 5-7°C during the late fall and winter before the survey takes place. This water can provide pathways to access the mid-Atlantic Bight and an energy saving overwintering refuge. Because the NEFSC survey occurs during the winter-spring ocean transition period availability and detectability may also be affected by the timing of a behavioral shift from a relatively strong association with bottom water and possible a degree of torpor during overwintering to high speed pelagic migration to spawning grounds during the spring.

A note on the detectability of mackerel in bottom trawls

The fast-swimming pelagic lifestyle and schooling behavior of Atlantic mackerel has significant impacts on the detectability of the fish in bottom trawls used in fishery independent (FI) surveys and the degree to which indices derived from them are proportional to population size. FI surveys use random sampling, relatively small demersal trawls towed at slow speeds for short durations that select slower swimming, small juvenile fish and larger fish in poor condition (Slotte et al. 2007). Since the Atlantic mackerel are fully pelagic and meet ecological requirements by selecting water column features including those allowing them to avoid predators, net efficiency (=detectability) appears to be low and variable and has been estimated to range from 0.009 to 0.0248 (Massé et al. 1996, Harley et al. 2001, DFO, 2008). During the winter, mackerel are associated with cold bottom water on both sides of the Atlantic Ocean and exhibit diving behavior in response to approaching trawlers (Slotte et al. 2007). As a result, Jansen et al. (2015) concluded that winter trawl surveys can provide useful indices of juvenile recruitment for stock assessments as long as the data are carefully interpreted. Their analysis of combined fishery hydroacoustic and trawl data indicated that bigger schools of mackerel are more closely associated with the seabed than smaller schools. On the basis of this finding Jansen et al. (2015) concluded that net efficiency was positively density dependent and that square or cube root transformation of bottom trawl survey data was required for developing indices of juvenile recruit abundance useful for population assessments (ICES 2014b). However, mackerel exhibit complex schooling behavior that may be related to changes in the biotic and abiotic environment and/or population size (Glass et al. 1986, Reid et al. 1997, Petitgas et al. 2001). Stratified random bottom trawl surveys do not measure the three-dimensional structure of schools of pelagic fish, including volumes and concentrations of fish within volumes (Jech and McQuinn 2016). The uncertain relationship between abundance in the trawl survey and population size and condition as a result of variations in availability and detectability has been discussed throughout the history of US stock assessments. (Isakov, 1979; Overholtz and Parry. 1986).

2.1.2: Analyses of changes in the spatial structure of NE Atlantic Mackerel and thermal habitat during the Spring NEFSC bottom trawl survey from 1968 to 2016.

Methods: To analyze the spatial structure of Atlantic mackerel collected in the spring NEFSC bottom trawl survey we divided fish into immature and mature size classes. The maturity classes were divided at 25 cm total length based on bootstrapped logistic regression of size and maturity data collected on the NEFSC survey (Appendix 1).

We applied survey-based spatial indicators to spring NEFSC bottom trawl survey data to identify changes in location (center of gravity, global index of collocation of mature and immature fish) and space occupation (inertia, isotropy, positive area, spreading area, and positive area: spreading area ratio, microstructure and number of patches) of immature and mature Atlantic mackerel from 1968-2015 (Table 1, Woillez et al. 2007, Woillez et al. 2009). Null densities and the shape of the study domain do not affect these indicators. We chose a support size of ~20 km (~10 nautical miles, nm) which is close to the median nearest neighbor distance between stations in the spring NEFSC survey. We also chose ~100 km (50 nm) as the limit of sample influence for the calculation of the microstructure index. Our focus in the analysis is centered on relative changes in indicator values over time rather than absolute values, because indicators are dependent on parameter values. To account for changes in the spatial patterns of sampling over time we also developed indicators for the center of gravity, inertia, isotropy and positive area of the NEFSC survey stations. We used the same parameter values for all of the spatial indicator calculations.

Results: Many of the spatial indicators of location, space use and occupation for immature and mature Atlantic mackerel varied systematically over time with long term trends in frequency of occurrence (Fig. 1) and abundance (see below).

Frequencies of occurrence of immature and mature Atlantic mackerel in the NEFSC spring bottom trawl survey ranged from less than 3% in the late 1970s and early 1980s to over 19% in 2012. A secondary peak occurred in 2000-2001. The highest frequencies of occurrence occurred in 2012-2013 (Fig. 1).

Centers of gravity (CG) for immature and mature fish shifted to the northeast over time and distance of CGs from Cape Hatteras was correlated with changes in frequencies of occurrence (Fig. 2; Rho immature fish 0.533, $p=0.0001$; mature fish 0.457, $p=0.001$). Centers of gravity (CG) for fish were probably not influenced by changes in the survey as CGs for the survey varied little over time. There was a slight decrease in the survey CG in the early 1980s when a relatively large number of stations were sampled south of Cape Hatteras. The survey CG was also relatively high in 2014 when the southern mid-Atlantic Bight was not sampled.

The CG of immature fish shifted at an average rate of ~ 10.8 km yr⁻¹ toward the northeast from 1980 to 2016 (SD=2.62 km yr⁻¹, $p=0.0002$). Mature fish shifted to the northeast at a slightly more rapid rate of 14.7 km yr⁻¹ (SD= 2.803, $p=8.2e-06$). While the long-term trend in CGs for both maturity classes was to the northeast the progression was variable. Centers of gravity were farthest southwest for both maturity classes in the 1960s, late 1970-early 1980s, 1993-1994, 2004-2005 and 2010-2011. Centers of gravity were farthest northeast during the springs of 1975, 2000, 2007, and consistently from 2012-2016. Prior to the late 1990s fish were rarely collected in the Gulf of Maine during the survey. From 2007 to 2016, both maturity classes were common in the northern Gulf of Maine adjacent to the mouth of the Bay of Fundy.

The spatial overlap of immature and mature fish in the survey was variable but collocation scores were consistently high (≥ 0.8) from 2000 to the 2016 (Fig. 3). During 10 of the 11 years when collocation scores were < 0.8 earlier in the series, the median centers of gravity for mature fish was 160 km southwest of the CG for immature fish (range = -9 km to 423 km). This pattern is consistent with published work and fishery observations indicating that larger fish migrate longer distances and that the nearshore runs of large fish that moved southwest into the southern Mid Atlantic Bight disappeared around 2000 (Nottestad et al. 1999; see Axelson et al. 2017). Fish older than age 3 were also rare in the survey after 2000.

Inertias (\sim variance) around centers of gravity were variable and often high when centers of gravity for fish were farthest from Cape Hatteras. (Figs 3,4). The isotropy of fish was only slightly lower than the isotropy for the survey, indicating that mackerel distributions were generally aligned with the principal southwest-northeast axis of the survey (Fig 5).

Estimates for the area surveyed were stable over time with two exceptions (Figs. 6 & 7). The area estimate for the survey was smallest during 2014 when the southern part of the Mid-Atlantic Bight was left unsampled. Estimates of approximate area surveyed were highest during the early to mid 1980s when large numbers of samples were collected south of Cape Hatteras.

Indicators measuring patterns in the area occupied by mature and immature mackerel increased gradually from 1980 to the present in a manner that matched frequency of occurrence and the northeastward movements of centers of gravity (Figs 6,7). Areas occupied by immature fish were always larger than areas occupied by mature fish. From 1977-1983 only about 2% of the area surveyed was occupied by immature fish, while adult fish occupied only 1% of the area. Area occupancy reached secondary peaks for immature fish in 2000 (19% of the area surveyed), and for mature fish in 2001 (16% of the area surveyed). Area occupied then declined to approximately 10% for the two size classes from 2002-2008. Since 2008 immature and mature fish have occupied \sim 23% and 15% of the area surveyed.

Spreading area (SA), which weights area occupied by catch densities, exhibited trends similar to positive areas, but increased at rates that were \sim 10% of the rate of increase of area occupied (Fig. 6). PA:SA ratios were variable, but the faster rate of increase in the area of presence (PA) than in the area occupied weighted by densities (SA) was evident in the trend in the index. This suggests that fish occupied new areas at relatively small school sizes and/or densities. This interpretation is supported by trends in the microstructure index that indicated that heterogeneity in catch densities at spatial grains less than 50 nm gradually decreased from 1980 onward (Fig. 8). This pattern was relatively strong for mature mackerel.

The number of large patches containing $>10\%$ of mackerel ranged from 1 to 4 for immature fish and 1 to 3 for mature fish (Fig. 9). The indicator was variable. However, mackerel occurred at significant densities in more than one patch more frequently after 1991.

Analysis of changes in thermal habitat location and areas

Methods: For analysis of thermal habitat in the spring NEFSC survey we identified temperature associations of immature and mature mackerel using single factor

quotient analysis and bottom temperatures measured *in situ* (Fig 16, Table 4 see also section 2.2.2 below). Mature and immature mackerel were more abundant in temperatures ranging from 5.5°C to 9.5°C than expected by chance in the spring NEFSC survey. Quotients and weighted average temperatures computed annually indicated that this temperature association did not change over the years of the spring survey.

We classified survey stations on the basis of whether bottom temperatures measured *in situ* were within (=1) or outside (=0) the “preferred” temperature range (5.5C- 9.5C). To identify changes in the location and surface areas of thermal habitat, we applied the same spatial indices and support sizes used above to the classified stations.

Results: Thermal habitat available during the surveys shifted to the northeast but later in time and at a slower rate than distributions of Atlantic mackerel. Centers of gravity for preferred temperatures began to shift persistently northeastward in 1990 at an average rate of 5.0 km y⁻¹ (+/-1.2 km y⁻¹; P=0.0004). CGs for thermal habitat during the survey were northeast of CGs of mackerel from 1968 to 1997 (Fig. 10). CGs for thermal habitat were south of CGs for immature mackerel periodically from 2000-2016. Thermal habitat was located to the south of mature mackerel CGs in 2007, 2012, and 2014.

The area of thermal habitat was variable (Fig. 11). Habitat areas were approximately four times larger (2.5% & 97.5 % quantiles 1.51, 20.69) than areas occupied by immature mackerel and 7 times larger than areas occupied by mature mackerel (2.5% & 97.5 % quantiles 2.43, 77.89).

Differences in the speed and timing of the northeast shift in thermal habitat and the large areas of thermal habitat when compared to shifts in CGs and areas occupied by fish indicated mackerel distributions may have been affected by winter habitat availability but winter habitat was probably not the dominant factor driving northeastward shifts in late winter and spring distributions of fish.

2.1.3: Principal components analysis of spatial indices for mackerel and thermal habitat and their relationship to abundance and size structure in the NEFSC survey and landings.

Methods: We performed principal components analysis (PCA) on the time series of spatial indicators to construct composite, orthogonal indices of the spatial structure of mackerel distributions that we could relate to indices of abundance and size structure during the survey and US landings. PCA was performed using all spatial indicators for mackerel and thermal habitat described above. Indices were re-scaled to have a unit variance before PCA was performed.

To identify significant relationships between indices of abundance developed from the NEFSC spring bottom trawl survey, US fishery landings, and the indicators of spatial structure we applied generalized additive modeling and a backward selection approach to select among the first five principal components that accounted for 80% of the variation. We extracted indices of abundance and size structure as well as fishery landings from the Atlantic mackerel Update assessment for 2017 (https://static1.squarespace.com/static/511cdc7fe4b00307a2628ac6/t/5720e48dab48de3e8ab30892/1461773454206/mackerel_data_update_2016.pdf).

Backward selection was performed using the technique of multi-model inference using AICc for low sample sizes to compute evidence ratios (Burnham and Anderson 2002). The best model was identified as the one with the lowest evidence ratio. Partial

deviance plots of the best models were inspected to determine whether effects of independent variables on dependent variables were more than marginal. We considered effects marginal when two SE confidence bands included zero throughout the data range. We used the BIOENV procedure (Clarke and Ainsworth 1993) to identify changes in the size structure of mackerel collected in the NEFSC survey that were correlated with changes in the spatial structure of the population as represented by the principal components. This approach allowed us to identify the subset of PCs that produced a Euclidean distance matrix with the highest Spearman correlation to a Bray-Curtis dissimilarity matrix derived from abundances of fish in 1 cm size classes in each year of the spring bottom trawl survey.

Results: Five principal components accounted for nearly 80% of the variance in the spatial indicators (Table 2). Principal component #1 (PC1) accounted for 37% of the variance and was defined by area of occupation, frequency of occurrence, spreading areas, distances of centers of gravity from Cape Hatteras for immature and mature fish, the PA:SA ratio for mature fish and thermal habitat area. Correlations of these indices with PC1 were all higher than 0.62. Inertia, number of patches, microstructure were all negatively correlated with PCA 2 which accounted for an additional 18% of the variance. PC3 was negatively related to the PA:SA ratio for immature fish. Spreading area for mature fish, the PA:SA ratio for mature fish, and habitat area were also correlated with PC3 but less so than with PC1. PC 4 & 5 accounted for less than 7% of the variance. The index of collocation of mature and immature mackerel was negatively related to axis four while the distance of the center of gravity for thermal habitat was positively related to this axis. As PC5 scores increased, the center of gravity for habitat shifted southwest and the number of patches increased.

GAM models that included PC1 explained NEFSC survey indices of abundance by weight and number (Table 3). In both cases the indices of abundance increased as the indices of area occupied increased and the center of gravity for mackerel shifted to the northeast with increasing PC1 scores (Fig. 12). While the evidence ratio for the model for the survey index by number were slightly lower when PC3 and PC5 were included, effects were marginal based on inspection of partial deviance plots. The effect of PC2 on the index of abundance by weight was also marginal. The index of abundance by weight was slightly higher in the middle of the range of PC5 scores. Dissimilarities in annual patterns of size structure for mackerel in the survey were also correlated with PC1 ($r^2=0.3381$, $P<0.001$) but not the other PCs (Fig. 13). Large sizes of fish occurred in the survey during springs when the area occupied was relatively small and CGs were relatively near to Cape Hatteras.

In contrast with survey abundance indices, landings of mackerel in the US fishery, typically largest in Southern New England and the Mid Atlantic Bight during the winter and early spring, were high when the area occupied by mackerel was small and center of gravity was located to the southwest during the NEFSC spring survey (high PC1 scores) (Fig 14). Landings also decreased as PC3 increased. Landings tended to be highest during years when both the PA:SA ratio and microstructure index for immature fish were high.

Our review suggests that the structure of mackerel distributions in the NEFSC spring survey has changed since the 1980s. Areas occupied and frequency of occurrence for immature and mature fish increased as centers of gravity shifted northeast. Mature fish, which often occupied areas well to the southwest of immature fish before 2000, have shifted northeast at a faster rate and now show higher overlap with immature fish. We note that larval mackerel became rare in the mid Atlantic bight in zooplankton surveys during the mid 2000s and thus there is evidence for reduced spawning in the region (Richardson et al., 2017). These changes have accompanied decreases in aggregation and the heterogeneity of mackerel catch densities at relatively fine scales. Mackerel may become more dispersed with small schools and perhaps lower densities of fish occupying new areas. These changes have been accompanied by increases in indices of abundance and size truncation within the survey. In contrast, US fishery landings which are typically high during the winter, were highest during years when mackerel were aggregated in smaller areas located southwest in the mid-Atlantic Bight during the NEFSC survey. These results indicate that stratified random bottom trawl surveys are likely to be useful for measuring the numbers of schools of mackerel. However, since they do measure school volumes or concentrations of fish within volumes the relationship between bottom trawl survey abundance indices and population size are probably complex and non-intuitive.

During the survey, changes in the location and area of preferred winter thermal habitat occurred later and more slowly than changes in mackerel distributions. Shifts in winter distributions of Atlantic mackerel in US waters have often been reported and are usually attributed to changes in bottom water temperature (Sette 1950, Taylor et al. 1957, Anderson and Almeida 1977, Overholtz et al. 2011). The results we present here indicate that spatial distributions of mackerel in the NEFSC bottom trawl survey are not a simple function of contemporaneous shifts in thermal habitat occupied by trawlable juveniles and adult animals during the winter and spring.

2.2: Mackerel Model v2.0 and application to the 2017 Stock Assessment (Task 3 and 4):

2.2.1. Rational and relevant results:

Catchability of juvenile and adult Atlantic mackerel in spring NEFSC bottom trawl surveys has been an important source of uncertainty throughout the history of US population assessments. Analyses indicate that mackerel have shifted distributions as a result of changing habitat conditions, particularly ocean temperatures (Overholtz et al. 2011, Radlinski et al. 2013, Bruge et al. 2016, Henderson et al. 2017). Systematic habitat shifts can cause changes in a population's availability and thus catchability in fishery independent surveys used to inform population assessments (Link et al. 2011). Systematic shifts are one potential cause of retrospective patterns that have appeared in recent Atlantic mackerel assessments (Deroba et al. 2010).

Indices of age specific mackerel abundance measured in the NEFSC spring bottom trawl survey conducted from March through April for nearly 5 decades have been used to inform assessments. The spring survey, conducted when bottom temperatures on the Northeast shelf are coldest (Richaud et al. 2016), describes the abundance of trawlable age classes of mackerel during the overwintering period, and the beginning of spring migration.

To provide an environmentally explicit proxy for population availability to spring NEFSC bottom trawl surveys we developed model-based estimates of proportions of available winter habitat for trawlable juveniles and adults in the northwest Atlantic. We developed the model using habitat analysis and collaborative field research conducted by NEFSC cooperative research staff and industry partners using a model nowcasting approach within the active fishery.

2.2.2. Habitat analysis: Specific methods and results

Methods: To develop a baseline winter habitat for juvenile and adult mackerel we used collections of fish and environmental data measured *in situ* and by satellite during the spring NEFSC survey. Abundance per tow was calculated for fish divided at 25 cm total length, the size of maturity for 50% of fish based on analysis of size at maturity Appendix 1. The habitat characteristics considered included surface and bottom temperature and salinity, along with bottom depth measured *in situ*. We also used MODIS_Aqua satellite measurements to derive primary productivity, frontal gradient strengths and used different optical wavelengths for deriving colored organic matter (A443) and particulate organic carbon (POC) available from (<http://basin.ceoe.udel.edu/thredds/dodsC/Aqua1DayAggregate.nc>) (Blondeau-Patissier et al. 2014). We extracted median values for satellite data aggregated at a daily time step from 2003-2016 within 2000 meter (~1 nm) diameter buffers surrounding each survey sample. Nearly 5000 samples were collected during the MODIS period. Of these only 31% to 45 % could be matched to satellite measurements due to cloud interference.

We first applied single factor quotient analysis (van der Lingen et al. 2001, Bernal, 2007) to identify significant associations of mackerel with ranges of specific environmental variables. We then determined the relative importance of significant variables using the method of (Thuiller 2013, Thuiller et al. 2016) which compares relative out of sample prediction accuracy of 10 fold cross validated GAMs. Here we only analyzed samples complete for all significant habitat variables.

Results: Quotient analysis indicated that mackerel associations with depth and bottom and surface temperature and salinity were greater than expected by chance (Table 4). We did not detect significant associations of mackerel with any of the ocean features measured by MODIS based satellite (Chlorophyll, colored organic matter (A443), particulate organic carbon (POC) and the strengths of optical fronts.

Prediction accuracy was two fold higher for bottom temperature than for the other significant variables (Fig. 15). Associations of mackerel with the other variables occurred over relatively broad ranges, were relatively uninformative, or conflicted with fishery information (Table 4). While fish were collected in a specific depth range in the NEFSC survey, fishery catches of mackerel occur in the shallow nearshore as well as deep water near the outer edge of the continental shelf and shelf slope sea (Axelson et al. 2017). Preferred sea surface temperatures were nearly identical to preferred bottom water temperatures, as expected on the shelf during the spring survey when the ocean is well mixed. Fish were associated with all but low estuarine salinities. We believed that incorporating variables other than bottom water temperature in the model would constrained it from projecting winter habitat into areas and times fish are known to occur.

Mature and immature size classes of mackerel were positively associated with nearly identical bottom water temperatures ranging from $\sim 5.5^{\circ}$ to 9.5°C . (Fig. 16). This range is similar to winter thermal habitat preferences reported for fish throughout the Atlantic (Giedz 1988, D'Amours and Castonguay 1992, Jansen et al. 2015). Fishery reports, comparison of mackerel sizes in fall and subsequent spring surveys, and annual cycles of tissue fat content (Grégoire and Lévesque 1994) suggest that during winter, mackerel are strongly associated with cold bottom water, don't grow significantly and are relatively inactive including showing reduced feeding activity. Mackerel may become hypometabolic in winter habitats in order to conserve resources for extensive spring migration and spawning. If this is the case a thermal habitat model may be sufficient for developing a first order approximation of overwintering habitat dynamics for large juvenile and adult Atlantic mackerel.

2.2.3. Collaborative model evaluation & refinement with the winter trawl fishery

Methods: We collaborated with members of the winter trawl fishery to evaluate and refine the winter habitat model developed above using two approaches. In both we used bottom temperatures from a data assimilative operational numerical ocean model to project estimates of winter temperatures preferred by mackerel in space and time on the continental shelf in Southern New England and the Mid-Atlantic Bight (Wilkin and Hunter 2013)

(http://tds.marine.rutgers.edu/thredds/dodsC/roms/espresso/2013_da/avg/ESPRESSO_Real-Time_v2_Averages_Best).

We used habitat hindcasting to determine whether fishery catches of mackerel greater than 1,000 lbs and recorded by fishery observers or electronically by captains in the NEFSC fishery study fleet were made within or outside preferred habitat. We only analyzed catches made during winter which we defined as the period from January 1 through April 15. We applied an *exact binomial test* to determine the strength of association of fishery catches with thermal habitat classified as preferred, cold, and warm based on the quotient analysis of the NEFSC spring trawl survey. Null expectations for the tests were developed by calculating the proportion of temperatures within the model domain in each thermal habitat class from January 1 through April 15 in 2014-2017.

We also evaluated the model in the field by observing the fleet, providing habitat nowcasts to several NEFSC study fleet captains ($N=5$) throughout the winter fishing seasons of 2014-2015 and 2016-2017, and by observing fishing operations in the field. To evaluate and improve habitat nowcast accuracy several modifications, including the substitution of continuous thermal responses, were tried during the two years based on suggestions and observations of individual industry collaborators and the lead scientist. Data from vessels with access to model nowcasts were not included in the *exact binomial tests* applied in the first approach.

Results: From January 1, 2014 to April 7, 2017, 132 fishery tows producing over 1000 lbs of mackerel were made within 10 km and 12 hours of bottom temperatures hindcast using the ROMS (Table 5; Fig 17). Frequencies of tows were much higher than

645 expected in the preferred habitat and much lower than expected in colder water.
646 Frequencies of catch in warmer water were rare but not different than expected based on
647 model based estimates of the relative availability of warmer water during the winter.

648 Active field research with NEFSC study fleet collaborators and observation of
649 habitat and fleet dynamics confirmed that fish were observed and catches were made in
650 bottom water temperatures ranging from 5°C - 10°C (Fig. 18a,b) However, the fishery
651 field research revealed that mackerel were not caught in preferred thermal habitat unless
652 that habitat had been connected in the past to suitable habitat to the north and east along
653 the winter migration route. Thus, habitat connectivity along the migration route appeared
654 to be an important determinant of geographic patterns of winter catches and habitat
655 occupancy.

656 657 658 **2.2.4. Development of a winter habitat model accounting for habitat connectivity**

659 *Methods:* To develop a winter habitat model accounting for habitat connectivity
660 we used daily estimates of bottom water temperature from an implementation of ROMS
661 that had a domain covering the path of the Gulf Stream and the northeast US continental
662 shelf (Kang and Curchitser 2013). The model has horizontal grain of approximately 7 km
663 (720 x 360 grid points), 40 vertical levels and a minimum depth of 10m. Its bathymetry is
664 derived from the 1 min resolution Shuttle Radar Topography Mission (Farr et al. 2007).
665 Oceanic boundary forcing and initial conditions are determined by reanalysis data of
666 Simple Ocean Data Assimilation v3.0.0 (Carton and Giese 2008). The Coordinated
667 Ocean-ice Reference Experiments (CORE.v2) dataset supplies the model with air
668 temperature, sea level pressure, humidity, wind, solar radiation, and precipitation.
669 Modern Era Retrospective Analysis for Research and Applications (MERRA) reanalysis
670 (Rienecker et al. 2011) is also used. Bias associated with inadequate representation of
671 cloud cover in MERRA was dealt with by correcting short-wave radiation. This 50-year
672 (1958–2007) NW Atlantic ROMS hindcast simulation and its validation is described in
673 Kang and Curchitser 2013, Kang and Curchitser 2015, and Kang et al. 2016.

674
675 For our application, we extracted data from the portion of the ROMS domain
676 north of 34°N where bottom depths were < 1000 meters (Fig. 18). We selected this area
677 based on reported distribution limits of Atlantic mackerel (Froese 2017). Comparison of
678 bottom temperatures measured *in situ* and those extracted from ROMS at spring survey
679 samples indicated that modeled bottom temperatures had a warm bias of ~0.45° C.
680 Therefore, we applied a -0.45°C correction to estimates of temperature ranges preferred
681 by mackerel during the winter and late fall (see below). We used Lambert equal area
682 projection for all grid calculations.

683 We constructed environmentally explicit estimates of late fall spatial distributions
684 of fish for each year to constrain the daily development of winter habitat in our model
685 (e.g. Fig. 19). We defined fall distributions based on environmental conditions identified
686 with single factor quotient analysis of mackerel catches made from October 1- December
687 31 in 15 state and federal fishery independent surveys included in the NOAA Northeast
688 US Essential Fish Habitat Geodatabase. These conditions were applied to ROMS output
689 on December 1 for the years 1979-2014 to describe late fall mackerel distributions.

ROMS bottom temperatures for each day from December 2 to the end of the NEFSC spring bottom trawl survey in the subsequent year (1980-2015) were classified to develop grids of preferred (=1, 5-10°C, with bias adjustment) and avoided winter habitat (=0, <5°C, >10°C). Connectivity grids were also developed for each day by identifying and aggregating pixels of preferred habitat adjacent to the previous days habitat beginning with December 1 late fall distributions. We multiplied each day's winter habitat grid by its connectivity grid to eliminate thermal habitat that had developed noncontiguously. These computations were carried out for each successive day through the end of the NEFSC spring bottom trawl survey in each year. Habitat grids defined by preferred temperatures and connectivity constraints for the days of the NEFSC spring survey from 1981-2015 were used to compute annual estimates of the proportion of thermal habitat sampled in each survey using the equation below (e.g. Fig. 18).

The proportion of available thermal habitat surveyed (ρ_H) was calculated in a manner that accounted for the survey design using the following equation:

Equation 1

$$\rho_H = \sum_{k=1}^n \frac{Area_{k,j} * \frac{HSI_{k,j}}{Area_{total}}}{\sum_{k=1}^n Area_{k,j} * \frac{HSI_{k,j}}{Area_{total}}}$$

Here the habitat suitability value (HSI ; 0 or 1) for sample k , occurring at location j on day i is extrapolated to the area sample k represents in the survey (e.g. Fig. 18). This is achieved by dividing the *Area of the strata* (km^2) in which sample k occurs by the total number of samples (n) in the strata. This area is then multiplied by sample k 's HSI (0-1). The habitat suitability weighted area of sample k is then divided by the sum of HSI values for all locations $j=1..n$ within the model domain for the day of sampling (i) multiplied by the surface areas of all ~pixels in the model. The surface area of model pixels is ~49 km^2 ($Area_{total}$) as defined by the resolution of the ROMS bottom temperature hindcast. The result is the proportion of the total habitat suitability weighted area available in the model domain represented by sample k . The total proportion of available habitat suitability sampled on a survey (ρ_H) is then the sum of the proportion of available habitat suitability sampled for each station in the survey ($k=1..n$).

Results: The quotient analysis of fall collections included in EFH GEO database indicated that mackerel were positively associated with latitudes north of 41.8, depths from 40 - 160 meters and bottom water temperatures ranging from 9°C to 13°C. To develop potential late fall distributions of mackerel on December 1 we selected areas of the ROMS with latitudes > 41.5, depths < 160M and temperatures ranging from 9°C to 13°C. The -0.45°C model bias adjustment was applied to the temperature range.

The final winter habitat model incorporating thermal habitat connectivity along fall and winter migration pathways was used to estimate that an average of 69% (2.5 & 97.5% quantiles = 45% & 89%) of habitat available within the model domain was sampled by the NEFSC survey between 1980 and 2016 (Fig. 19). The model based estimates did not vary systematically over the time period.

2.2.5. Evaluation of whether shifts in mackerel distributions are explained by changes in modeled or measured winter habitat distributions

Methods: To determine whether mackerel distribution shifts were explained by measured or modeled shifts in winter habitat we computed centers of gravity and area occupied by modeled habitat using the methods of (Woillez et al. 2007, Woillez et al. 2009) as described in detail in Manderson et al. (2017). We analyzed the model data using the exact same constraints used in the analysis presented in Manderson et al. (2017) and in section 2 above. We then compared time series of centers of gravity and area occupied by fish and measured and modeled habitat, visually and with cross correlation function analysis (CCF).

Results: Centers of gravities and areas of habitat hindcast by the model for the survey were reasonably similar to habitat classified based on temperatures measured *in situ* (Fig. 20). They were most similar from 1990-2000, and relatively dissimilar before and after that period. The model did not capture the gradual northeastward shift of winter habitat (5 km y^{-1}) defined by *in situ* temperatures that began in 1990. However, the rapid northeastward shifts ($11\text{-}15 \text{ km y}^{-1}$) in mackerel distributions from 1980 to 2016 were not matched in either measured or modeled winter habitat. We found only a weakly significant correlation (0.334) at a time lag of 0 between centers of gravity for mackerel and winter habitat defined by *in situ* temperatures in CCF analysis. Furthermore, the areas occupied by mackerel were relatively small when compared with winter habitat areas suggesting that other factors constrain distributions

We propose two alternative but non-mutually exclusive hypotheses that could account for this result. First winter habitat may indeed primarily control distributions of juvenile and adult mackerel in the spring survey but our model poorly defines it. Literature describing thermal habitat preferences during the winter for Northwest and Northeast Atlantic mackerel as well as our habitat analysis and field evaluations using the habitat nowcasting approach suggest that this is probably not the case. Alternatively, changes in habitat conditions required for successful completion of other important life history processes, such as spawning and larval development which incentivize specific migration patterns may be the primary drivers of mackerel distribution shifts. Atlantic mackerel eggs and larvae have become relatively rare on historically important Mid-Atlantic Bight spawning and nursery grounds since 2005 (Richardson et al., 2017). This along with the change in the migration of large fish in the early 2000s are circumstantial evidence supporting this alternative hypothesis which is consistent with the mixed school feedback mechanism for pelagic schooling fish proposed by Bakun (Bakun 2001, Bakun and Cury 1999).

Task 3.0 Design a cost effective and efficient industry based survey of habitats outside the domain of fishery independent surveys using the 2nd generation model as a quantitative hypothesis.

3.1 Background

Empirical evidence supports the inference that Atlantic mackerel could occur in significant concentrations during the winter on the deep Mid Atlantic Bight continental shelf and slope. In the United Kingdom mackerel became rare on the shelf in the 1990s as their southern migration pattern shifted from an inshore route taken in late summer-early fall to an offshore, early winter migration (Walsh et al. 1995, Reid et al. 1997). Fish were discovered in commercial concentrations in deep shelf and slope water at temperatures ranging from 8°-9°C and salinities > 35‰. Age 0, 1 and 2 fish spawned in Canadian waters overwinter on the Nova Scotia shelf in areas where temperatures range from 7– 10°C and bottom depths are ~ 200 -250 meters (Grégoire et al. 2014). Model projections that we used to estimate proportions of winter habitat surveyed on the NEFSC bottom trawl survey in section 2 identified this Scotian shelf overwintering ground. From the 1930s through the early 1980s, the dominant southward migration pathway for Atlantic mackerel from the Gulf of Maine into the mid-Atlantic Bight during the fall was reported to be located along the outer continental shelf and slope. Oscar Sette developed this paradigmatic view of migration (Sette 1950), which was supported in early ICNAF and US population assessments (Anderson and Paciorek 1980). It continues to be the dominant view. Further, Atlantic mackerel occur as by-catch in the winter longfin squid fishery prosecuted at depths ranging from 150 to 210 meters along the outer edge of the mid MAB continental shelf (Fig. 22). By-catches are usually highest in the late winter and early spring when the squid fishery is executed at the deepest depths. While most of the US mackerel fleet does not target fish in deep water offshore, a few specialists report catching commercial quantities of mackerel near the edge of the continental shelf in the late winter-early spring (Axelson et al., 2017). They report particularly high concentrations in the vicinity of Wilmington Canyon and Baltimore Canyon areas off New Jersey, and from Veatches Canyon to Lydonia Canyon off New Southern England (Fig 21).

3.2 Methods:

We used our model to determine whether and where thermal habitat preferred by mackerel during the winter is most likely to occur at depths > 150 meters on the outer edge of the continental shelf and shelf slope sea. This region is sparsely sampled by the directed fishery and the spring NEFSC bottom trawl survey which samples to depths of 350 meters. Mackerel are fast swimming schooling fish that can occupy the entire water column. Nevertheless we focus on habitat associated with the seabed because trawling near or close to the bottom during winter remains the most effective method for sampling juvenile and adult mackerel in the fishery and fishery independent surveys (Jansen et al. 2015, Axelson et al. 2017). Atlantic mackerel lack swim bladders and can be detected with sounders using frequencies of 200 KHz or higher. High frequency sounders have ranges less 150 meters. As a result, currently available hydroacoustic technology with transducers mounted on surface ships cannot be effectively used to detect and survey mackerel at depths greater than approximately 150 meters.

We develop our analysis using temperatures ranging from 7°C to 9°C. Temperatures lower than 7°C and higher than 9°C appeared to be avoided based on quotient analysis (Fig. 16). This is also the approximate range of temperatures mackerel occupy during the winter in both Canadian and UK waters (Walsh et al. 1995, Reid et al. 1997, Grégoire et al. 2014). We developed our analysis using Espresso ROMS, a data

assimilative numerical ocean model, (<http://www.myroms.org/espresso/>), for several reasons. First, in our fishery field work we have found it to be accurate with respect to a number of water column properties including water temperature within the limits of model resolution ($\sim 7 \text{ km}^2$ & 1 day) because it assimilates near real-time meteorological and ocean observations (see <http://www.myroms.org/espresso/> Wilkin and Hunter 2013). Further the model projects oceanographic properties daily from May 20, 2013 to the present. This allowed us to summarize possible spatial characteristics of deepwater overwintering habitat for mackerel using nearly 5 years of ocean model output. The limitation of using Espresso ROMs is that its domain extends from the coastal zone south of Cape Hatteras to Cape Cod and offshore to New England canyons and the Gulf Stream but does not include the Gulf of Maine (Fig. 23). While two other numerical ocean models include the Gulf of Maine, one does not cover the entire mid-Atlantic Bight, while the second is new, untested by us, and extends back only to November, 2017.

We used the Espresso ROMs to develop daily projections of thermal habitat associated with the seabed in shallow (≤ 150 meters) and deep water (>150 meters) from June 2013 – April 10, 2018. We examined the series of daily habitat projections and used the daily grids to calculate statistics describing the properties and dynamics of potential winter habitat for mackerel within the model domain.

3.3 Results & Discussion

Analysis of projections of deep water thermal habitat from the output of the ROMs assimilative ocean model indicated that temperatures between $7\text{-}9^\circ\text{C}$ occurred on the continental slope at depths ranging from approximately 350 to 500 Meters where salinities ranged from 35‰ to 36‰ (Fig. 22, 23). While “winter” water on the shelf showed strong spatial and temporal variability at seasonal time scales (Fig 23, 24), the thin band of potential habitat adjacent to the shelf on the slope persisted in approximately the same location throughout the year.

During late summer and fall (September-December), overwintering temperatures preferred by mackerel appear to be only available on the slope because fall turnover associated with atmospheric cooling and mixing by storms eliminates temperatures in the suitable range from the seabed on the continental shelf. ROMs projections indicate that deep water overwintering habitat may cover a median of 5000 km^2 of slope seabed (2.5%-97.5% quantiles= $4000 - 7000 \text{ km}^2$). These estimated surface areas are relatively consistent throughout the year with a low annual variance (Fig. 24). In contrast overwintering habitat on the shelf has high seasonal and interannual variance.

Overwintering habitat then begins to form in shallow water in the northern part of the Mid-Atlantic Bight when the water cools in response to late fall/early winter storms. The shelf habitat continues to develop in response to winter storms to form a continuous band of suitable temperatures that often extends from New England to Coastal Virginia and may cover a median of $32,500 \text{ km}^2$ of seabed (2.5%-97.5% quantiles= $12,500 - 52,626 \text{ km}^2$). Fishery catches occur across the extent of this band once it has crossed the Hudson Canyon shelf valley based on daily observations in the fishery. As coastal and mid shelf water continues to cool below 7°C through February, March and April, the band of preferred shelf habitat translates offshore into deeper water and fragments near the shelf break. In the early spring the remaining shelf habitat occurs just inshore of the

869 persistent band of slope habitat. The thermal habitat preferred by mackerel during the
870 winter on the slope is ~15% of the size of overwintering habitat on the shelf when shelf
871 habitat is at its maximum.

872 Our analysis used a data assimilative numerical ocean model to project thermal
873 habitat and to develop a speculative inference about the possible existence and
874 characteristics of deep water overwintering habitat for mackerel on the MAB continental
875 slope. Several lines of evidence support our inference. First, mackerel occupy deep water
876 areas on the continental shelf and slope in United Kingdom and Canada that have
877 temperatures, salinities and depths very similar to those we identified here (Walsh et al.
878 1995, Reid et al. 1997, Grégoire et al. 2014). The outer edge of the MAB continental
879 shelf has long been viewed a primary migration pathway between the Gulf of Maine and
880 mid-Atlantic Bight overwintering areas by US scientists and fishermen (Sette 1950,
881 Axelson et al. 2017). Several US fishermen target mackerel near submarine canyons on
882 the edge of the shelf where the mackerel also occur as by-catch in the winter longfin
883 squid fishery. Finally the foreign fleets targeted Atlantic mackerel in the vicinity of
884 submarine canyons along the outer edge of the MAB continental shelf during the 1960s
885 and early 1970s (Chuksin 2006).

886 Our analysis of deep water overwintering habitat for mackerel could be used to
887 guide the design of efficient exploratory offshore survey. A conservative approach
888 would be define continental slope strata based on model output with a slightly broader
889 temperature/depth range and distribute sampling across the strata. The survey should be
890 conducted once winter conditions are fully established on the shelf (late January,
891 February), but before the shelf habitat translates offshore to potentially mix fish
892 overwintering on the shelf with those that may occupy slope water throughout the winter.
893 Because the acoustic properties of mackerel limit the usefulness of shipboard acoustics to
894 depths <150 meters, a survey designed to develop biomass estimates would probably
895 need to rely on bottom trawls. To supplement and inform a bottom trawl survey, fishery
896 hydroacoustics could be deployed on autonomous underwater vehicles to overcome
897 detection range issues associated with high frequency transducers mounted on the hulls of
898 surface ships.

899 Based on the analysis we presented in *section 2.1* and a review of the literature on
900 schooling and school structure in pelagic fishes (e.g. Petitgas et al. 2001) allocating trawl
901 samples to the survey strata is not straight forward, particularly if the goal is to develop
902 biomass estimates as indicators of population condition. The spatial characteristics and
903 dynamics of Atlantic mackerel aggregations appear to be complex at multiple levels of
904 organization. As discussed earlier, fish occur in variable densities within schools that can
905 be homogeneous or heterogenous with respect to size and age (See also Axelson 2017).
906 Schools then vary in number and volume. Multiple schools can then aggregate into larger
907 shoals that also vary in number and volume. If the relationship between hierarchical
908 schooling behavior and population condition is nonlinear, abundance indices developed
909 from a traditional stratified random trawl sampling will not reflect population condition
910 in a simple manner. For example, if large schools fragment into small schools that
911 disperse at threshold population sizes because school fragmentation and dispersal confers
912 survival advantages at low population size, a decrease in the frequency of 0 counts in a
913 traditional random sampling scheme could result in abundance indices that actually
914 increase when population size falls below the threshold associated with the shift in

915 schooling behavior. If this is the case, a survey approach permitting the development of
916 accurate estimates of the statistical distributions of numbers of schools and shoals and
917 their volumes as well as estimates of individual fish densities within schools is required.

918
919 We believe we have developed a relatively strong inference about habitats that
920 could support overwintering mackerel on the Mid-Atlantic Bight continental slope in
921 close proximity to the shelf break. The thermal conditions appear to be suitable and it is
922 likely that food is available as a result of proximity to primary and secondary productivity
923 associated with canyons and the shelf break (Gawarkiewicz et al. 2018). While the
924 structure and dynamics of the water column and seabed are complex in the area we don't
925 know whether adequate predation refugia is also available. It is also the case that habitat
926 can be high in quality and still be unoccupied due to spatial and other constraints.
927 Overwintering habitat on the slope and elsewhere could appear to be unoccupied in
928 bottom trawls survey if Atlantic mackerel are unavailable to bottom trawls because they
929 are using pelagic habitat.

930 It is also the case that marine animals also use migration between a diversity of
931 functionally important habitats to complete complex life histories in ways that are not
932 overly costly with respect to energy use and predation risk (McQUINN 1997, Secor
933 2015). Small pelagic fishes, whose fitness is influenced by hydrography rather than
934 geography, are particularly flexible in their use of migration pathways that allow them to
935 link habitats critical to life history stages and processes; habitats that can be ephemeral
936 short to long time scales (days to decades). The literature suggests that Atlantic mackerel
937 have used outer continental shelf and slope sea habitats in Mid-Atlantic Bight as an
938 important migration pathway or as overwintering habitat in the past when the MAB
939 spawning and nursery grounds also produced most of the recruits in the northwest
940 Atlantic Ocean (Sette 1943). However, large fish appeared to cease migrating into the
941 MAB in large numbers by 2000 (our study), the MAB spawning and nursery ground
942 collapsed in the mid 2000s, and fish appear to be spawning only in the Gulf of Maine and
943 Canada (Richardson et al., 2017). Meanwhile the Gulf Maine is warming at a rapid rate
944 (Saba and al. 2015). If current warming trends continue greater quantities of
945 overwintering habitat are likely to become available in the Gulf of Maine nearer to viable
946 spawning and nursery grounds in the Gulf of Maine and Canada. Overwintering in the
947 Gulf of Maine in close proximity to high quality spawning and nursery grounds could
948 confer an energetic and survival advantage to fish and reduce the frequency of fish
949 overwintering in the MAB until the quality of spawning and nursery grounds improves in
950 the MAB.

Table. 1 Spatial indicators summarizing changes in spatial distributions of immature and mature Atlantic mackerel in the spring NEFSC bottom trawl survey over time (Woillez et al. 2007, Woillez et al. 2009). Indicators were also calculated for the survey to account for changes in the survey, and CG and positive area were calculated for thermal habitat.

Indicator	Interpretation
Center of gravity (CG)	Mean location of distribution (Kilometers from Cape Hatteras, NC)
Inertia (I)	Spatial dispersion around CG (nm)
Global index of collocation (GIC)	Similarity in spatial occupation patterns of immature (≤ 25 cm) and mature (> 25 cm) size classes of fish
Isotropy	Elongation of population in space
Positive area (PA)	Area (nm ²) occupied by each maturity classes
Spreading area (SA)	Area occupied by maturity classes weighted by catch densities (nm ²)
Degree of aggregation (PA/SA)	PA/SA measures how evenly population densities are distributed in the area occupied. When PA/SA = 1 population densities are spread evenly across the area. As PA/SA increases high density patches of small area occur within the broader area occupied.
Microstructure	Heterogeneity in catch densities below chosen lag scale (50 nm). 0=low, 1=high
Number of patches with >10% of density	Number of large patches of fish.

Table 2. Principal Components analysis of spatial indicators of Atlantic Mackerel distributions and thermal habitat during the spring NEFSC bottom trawl survey.

	PC1	PC2	PC3	PC4	PC5	PC6
Standard deviation	2.61	1.84	1.52	1.13	1.05	0.95
Proportion of Variance	0.36	0.18	0.12	0.07	0.06	0.05
Cumulative Proportion	0.36	0.54	0.66	0.72	0.78	0.83
<hr/>						
Contribution of variable						
Correlation of variable						
<hr/>						
Positive Area (I)	13.07	0.02	0.00	0.03	3.22	2.21
	0.94	0.03	0.00	-0.02	0.19	-0.14
Frequency (I)	12.88	0.00	0.02	0.17	3.51	2.64
	0.94	0.01	0.02	-0.05	0.20	-0.15
Positive Area (M)	11.54	0.00	0.00	3.81	0.12	6.08
	0.89	0.01	-0.01	-0.22	0.04	-0.23
Spreading Area (I)	9.66	0.10	8.82	0.57	0.63	0.12
	0.81	0.06	0.45	-0.09	0.08	0.03
Frequency (M)	9.10	0.48	0.93	2.74	0.01	0.12
	0.79	0.13	0.15	0.19	-0.01	-0.03
CG (M)	8.87	0.55	2.84	0.54	5.48	10.60
	0.78	0.14	-0.26	-0.08	-0.25	0.31
CG (I)	7.79	0.21	3.72	5.25	0.62	13.55
	0.73	0.08	-0.29	0.26	-0.08	0.35
Spreading Area (M)	7.39	0.93	10.18	0.17	3.12	2.98
	0.71	0.18	0.48	-0.05	-0.19	-0.16
PA:SA (M)	6.19	0.06	11.38	4.29	6.07	4.88
	0.65	-0.05	-0.51	-0.23	0.26	-0.21
Positive Area habitat	5.66	0.01	4.89	0.04	0.18	24.03
	0.62	-0.02	-0.34	0.02	-0.04	0.47
PA:SA (I)	1.77	0.19	20.63	5.39	0.38	10.37
	0.35	0.08	-0.69	0.26	0.07	-0.31
Inertia (M)	1.28	18.16	1.57	1.93	5.88	1.40
	0.30	-0.78	0.19	0.16	-0.26	-0.11
GCI	1.26	0.67	0.57	37.80	19.71	1.18
	0.29	-0.15	0.11	-0.70	-0.47	0.10
CG habitat	1.05	0.04	0.99	26.87	29.39	2.47
	0.27	-0.04	-0.15	0.59	-0.57	-0.15
Number Patches (I)	0.75	14.80	2.12	2.70	17.19	6.65
	0.23	-0.71	0.22	0.19	0.44	0.25
Microstructure (M)	0.64	16.34	8.90	1.38	0.13	2.13
	-0.21	-0.74	-0.45	-0.13	-0.04	-0.14
Inertia (I)	0.63	20.81	1.20	0.82	1.53	4.23
	0.21	-0.84	0.17	0.10	0.13	0.20

Microstructure (I)	0.24	11.91	14.09	5.06	1.06	0.02
	-0.13	-0.63	-0.57	-0.25	-0.11	-0.01
Number Patches (M)	0.23	14.70	7.17	0.45	1.75	4.34
	0.13	-0.70	0.41	0.08	-0.14	-0.20

Table 3. Results of generalized additive modeling (GAM) of the relationship between indices of abundance derived from the NEFSC bottom trawl survey and US landings and principal components derived from indicators of spatial structure of mackerel and thermal habitat during the survey (see Table 2). AICc is the Akaike Information Criterion corrected for small sample sizes

Dependent variable /independent variables	Residual Deviance	Deviance explained (%)	AICc	Log Likelihood	Δ AIC	Relative Likelihood	AIC Wt.	Evidence Ratio
<i>Abundance Index (N)</i>								
PC1+PC3+PC5	32947	39.3	448.9	-216.5	0.0	1.0	0.3	1.0
PC1+PC5	25233	53.5	449.1	-210.3	0.2	0.9	0.3	1.1
PC1+PC3	38543	29.0	449.8	-220.1	0.9	0.6	0.2	1.6
PC1+PC3+PC4+PC5	32830	39.5	450.9	-216.4	2.0	0.4	0.1	2.7
~1	54256	0.0	460.2	-227.9	11.3	0.0	0.0	279.6
PC3+PC5	46701	13.9	460.8	-224.5	11.9	0.0	0.0	380.1
PC1+PC2+PC3+PC4+PC5	14296	73.7	462.9	-197.3	14.0	0.0	0.0	1100.6
<i>Abundance Index (W)</i>								
PC1+PC2+PC5	739	42.2	281.2	-129.1	0.0	1.0	0.4	1.0
PC1+PC5	916	28.3	282.5	-134.1	1.3	0.5	0.2	1.9
PC1+PC2+PC4+PC5	708	44.6	283.6	-128.2	2.4	0.3	0.1	3.4
PC1+PC2	982	23.2	283.8	-135.7	2.6	0.3	0.1	3.6
PC2+PC5	908	29.0	285.1	-133.9	3.9	0.1	0.1	7.0
~1	1279	0.0	287.8	-141.7	6.6	0.0	0.0	27.1
PC1+PC2+PC3+PC4+PC5	571	55.4	292.1	-123.2	11.0	0.0	0.0	240.2
<i>US Landings</i>								
PC1+PC3	1.85E+12	30.3	1268.4	-626.9	0.0	1.0	0.5	1.0
PC1+PC2+PC3	1.80E+12	32.4	1270.0	-626.2	1.7	0.4	0.2	2.3
PC1+PC2+PC3+PC5	1.77E+12	33.3	1272.0	-625.9	3.6	0.2	0.1	6.1
PC1+PC2	2.02E+12	23.9	1272.5	-628.9	4.1	0.1	0.1	7.7
PC2+PC3	2.40E+12	9.8	1274.6	-632.8	6.3	0.0	0.0	22.9

~1	2.66E+12	0.0	1274.7	-635.2	6.3	0.0	0.0	23.2
PC1+PC2+PC3+PC4+PC5	1.76E+12	33.8	1275.1	-625.7	6.8	0.0	0.0	29.4

Table 4. Results of single factor quotient analysis relating the catch densities of immature (I) and mature (M) mackerel in the spring NEFSC trawl survey and environmental variation measured *in situ* or with MODIS satellite.

Variable	Maturity Class (N samples)	Location Measured	Significant Association	Range of association	Range of avoidance	Data Range
Depth	I (16972)	<i>in situ</i>	Yes	35-90	≤ 25	5-494 M
Depth	M (16972)	<i>in situ</i>	Yes	30-80	≤ 15	
Bottom Temperature	I (14525)	<i>in situ</i>	Yes	6-9	$\leq 5, \geq 11$	0-22.7°C
Bottom Temperature	M (7296)	<i>in situ</i>	Yes	6-9	$\leq 5, \geq 11$	
Bottom Salinity	I (7296)	<i>in situ</i>	Yes	33-34.5	$\leq 32, \geq 36$	23-37 PSU
Bottom Salinity	M (7296)	<i>in situ</i>	Yes	33.5-34	$\leq 33, \geq 36$	
Surface Temperature	I (14868)	<i>in situ</i>	Yes	6-8	$\leq 5, \geq 11$	0-23.8°C
Surface temperature	M(14868)	<i>in situ</i>	Yes	6-8	$\leq 5, \geq 13$	
Surface Salinity	I (7431)	<i>in situ</i>	Yes	33-34	$\leq 32, \geq 36$	16-36.5 PSU
Surface Salinity	M (7431)	<i>in situ</i>	Yes	33-34	$\leq 33, \geq 36$	
Solar elevation	I (17003)	Computed	No			-62.5-71.6°
Solar elevation	M (17003)	Computed	Marginal	10-15	-15--25	
Log Chlorophyll	I (1484)	Satellite	No			0.2-4.6
Log Chlorophyll	M (1484)	Satellite	No			
Log POC	I (2163)	Satellite	No			3.9-9.5
Log POC	M(2163)	Satellite	No			
Log A433	I (2163)	Satellite	No			-3.5-1.7
Log A433	M(2163)	Satellite	No			
Log Gradient Strength	I (1574)	Satellite	No			0-1.4
Log Gradient Strength	M(1574)	Satellite	No			

Table 5. Catches of mackerel in the winter fishery were significantly less likely in cold bottom water temperatures than expected and more likely than expected in preferred temperatures (*) based on exact binomial tests of frequencies of mackerel catches > 1000 lbs. The proportion of catches in warm bottom water was not different than expected. Preferred temperatures were those identified with quotient analysis. Bottom temperatures estimated for the ESPRESSO ROMS domain from Jan. 1 – April 13 in 2014-2017 were used to estimate catch temperatures and expectation (Wilkin and Hunter 2013).

Bottom temperature	Expectation within ROMS domain	Proportion of tows (N=132) (95% Confidence intervals)	P-value
5°-10°C*	0.2631	0.7121 (0.6269-0.7876)	2.2e-16
< 5°C	0.5829	0.0833 (0.0423-0.1442)	2.2e-16
>10°C	0.1540	0.2045 (0.1393-0.2835)	0.1162

Atlantic Mackerel:NEFSC spring survey

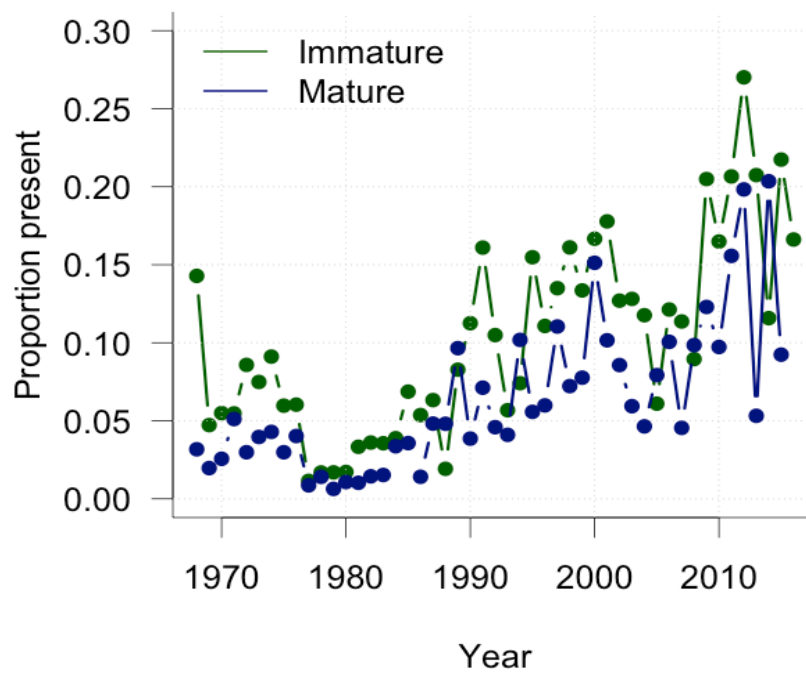


Figure 1. Frequencies of occurrence for immature (≤ 25 cm) and mature (> 25 cm) Atlantic Mackerel in the Spring NEFSC bottom trawl survey from 1968 through 2016

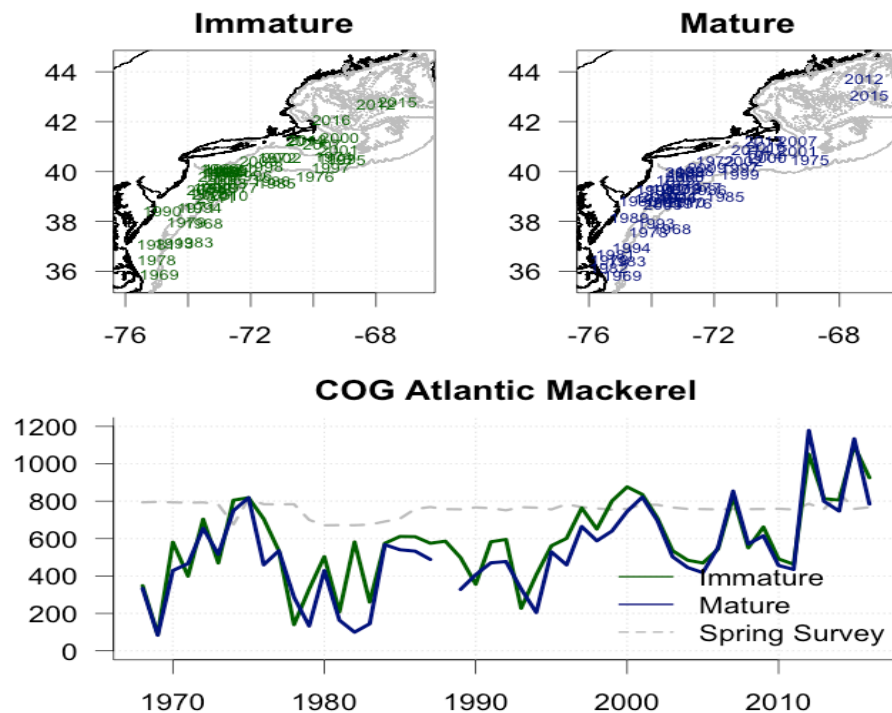


Figure 2. Centers of Gravity for immature (≤ 25 cm) and mature (> 25 cm) Atlantic Mackerel in the Spring NEFSC bottom trawl survey. Top. Maps of latitudes and longitudes of CGs. Bottom. Distance from Cape Hatteras (kilometers) of CGs for mature and immature mackerel and for the NEFSC survey

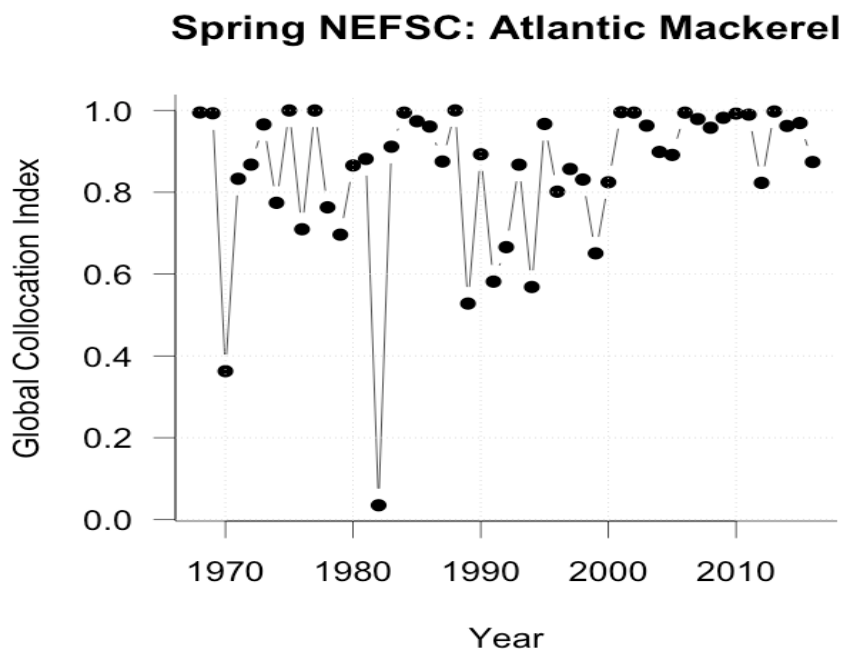


Figure 3. Collocation (GIC) of immature (≤ 25 cm) and mature (> 25 cm) Atlantic Mackerel was variable, but consistently high in the Spring NEFSC bottom trawl survey from 2000-2016. A GIC of 1 indicates perfect spatial overlap while lower values indicate less spatial overlap

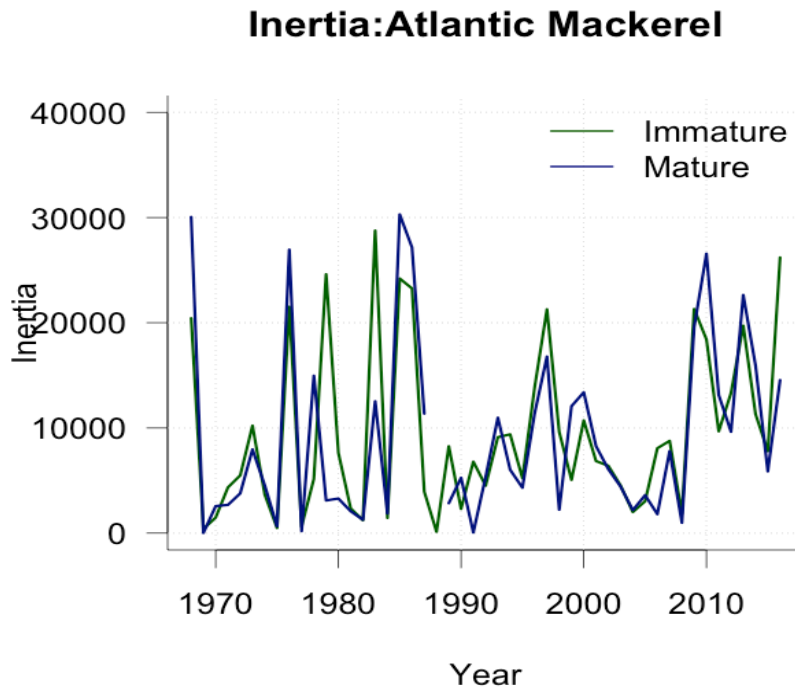


Figure 4. Inertia for immature (≤ 25 cm) and mature (> 25 cm) Atlantic mackerel was variable in the Spring NEFSC bottom trawl survey from 1968-2016.

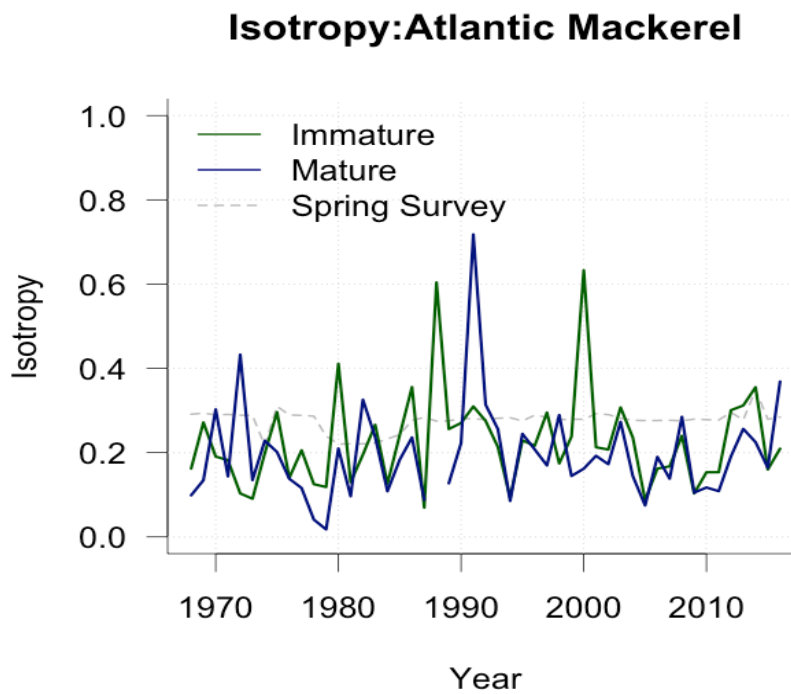


Figure 5. Isotropy for immature (≤ 25 cm) and mature (> 25 cm) Atlantic mackerel was variable and similar to stations in the Spring NEFSC bottom trawl survey from 2000-2016.

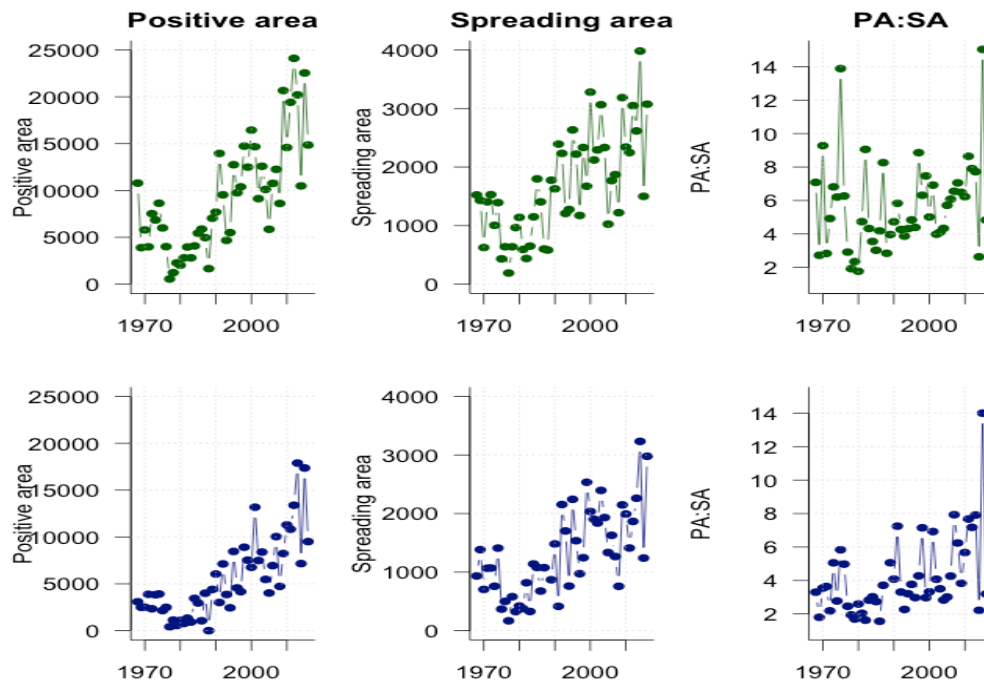


Figure 6. Indicators of area occupied for immature (≤ 25 cm; top panels) and mature (> 25 cm; bottom panels) Atlantic mackerel in the Spring NEFSC bottom trawl survey from 1968 -2016. Positive area (PA) only accounts for the presence of fish while spreading area (SA) takes into account catch density. The ratio of PA:SA is a global indicator of fish aggregation. When $PA:SA = 1$ fish densities are the same across the occupied area. As $PA:SA$ increases fish occur in high densities concentrations in areas smaller than areas where fish are just present.

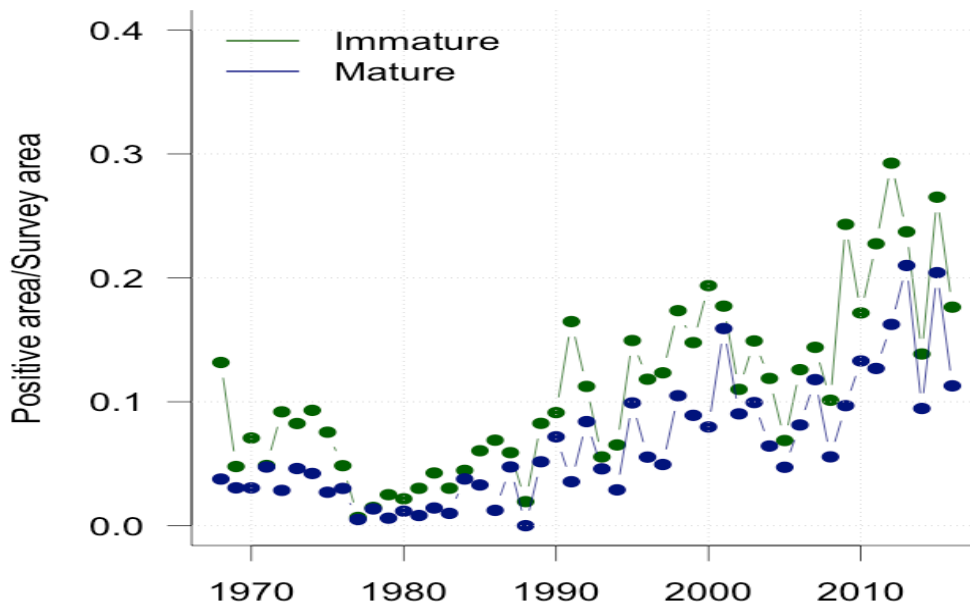


Figure 7. Positive area for immature (≤ 25 cm) and mature (> 25 cm) Atlantic mackerel in the Spring NEFSC bottom trawl survey (Fig. 6, left panels) standardized by area surveyed calculated using the same algorithm (Fig. 6)

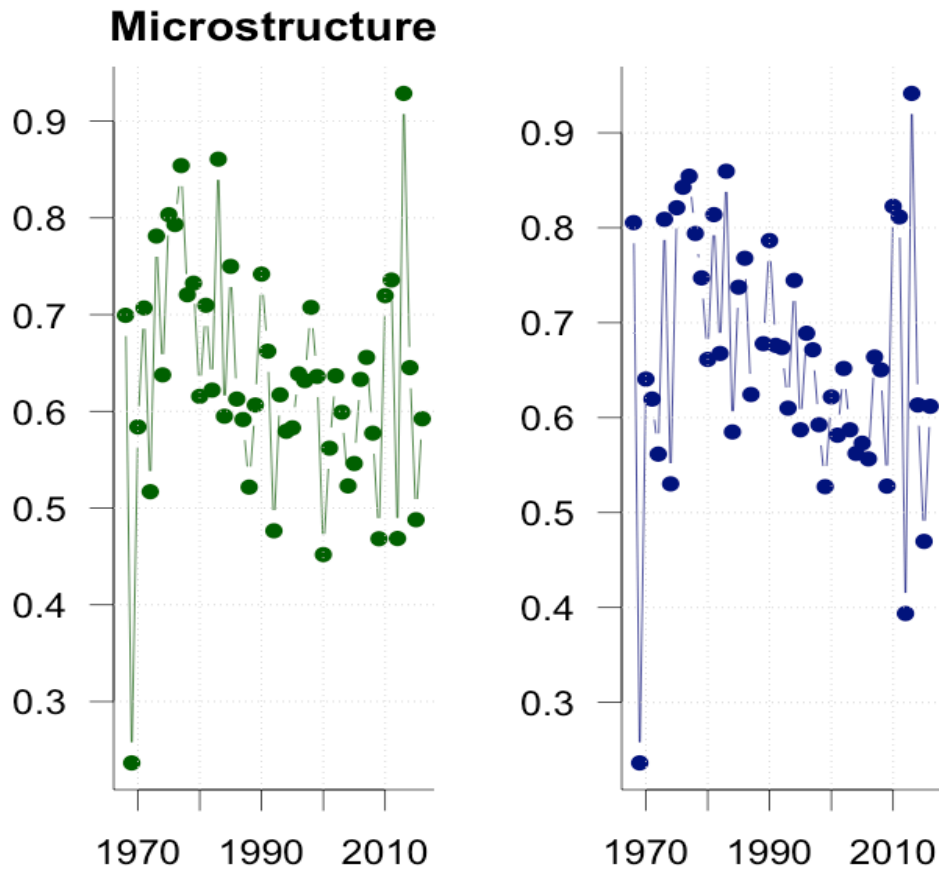


Figure 8. Trends in the microstructure indicators indicating that heterogeneity in catch densities for immature (≤ 25 cm; left) and mature (> 25 cm; right) Atlantic mackerel at spatial grains less than 50 nm declined over time in the Spring NEFSC bottom trawl survey from 1980 onward. When the indicator is 1 densities are heterogeneous. As the indicator decreases densities at grains less than 50 nm become more homogeneous.

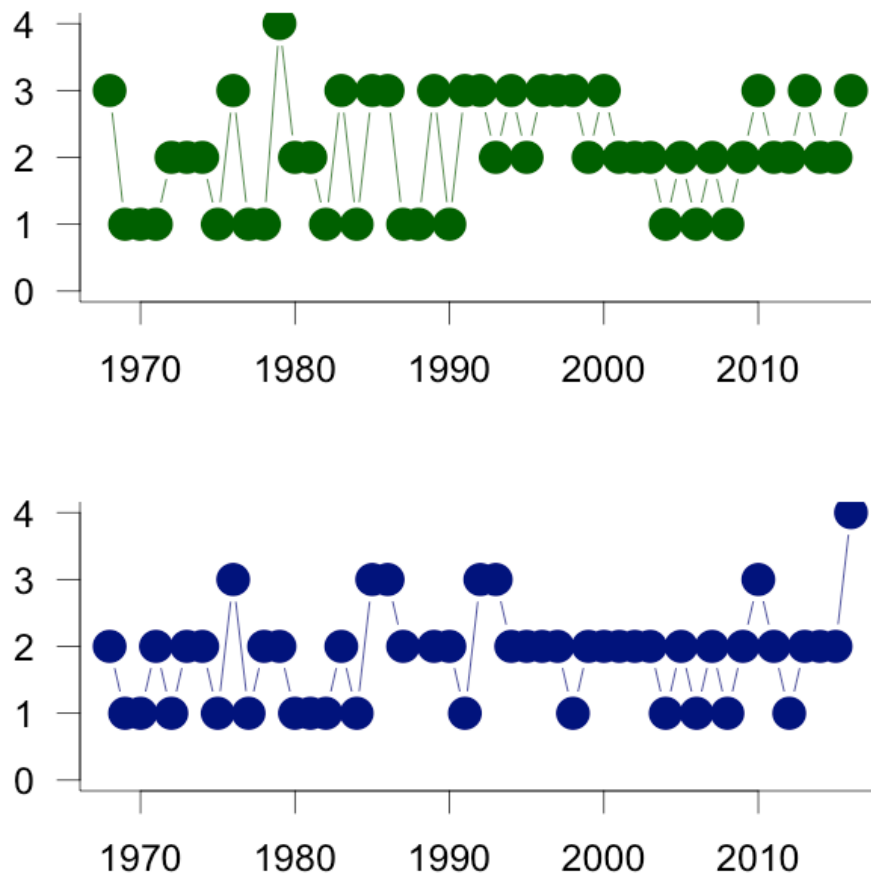


Figure 9. Number of patches with more than 10% of catch densities for immature (top) and mature (bottom) mackerel during the spring NEFSC trawl survey.

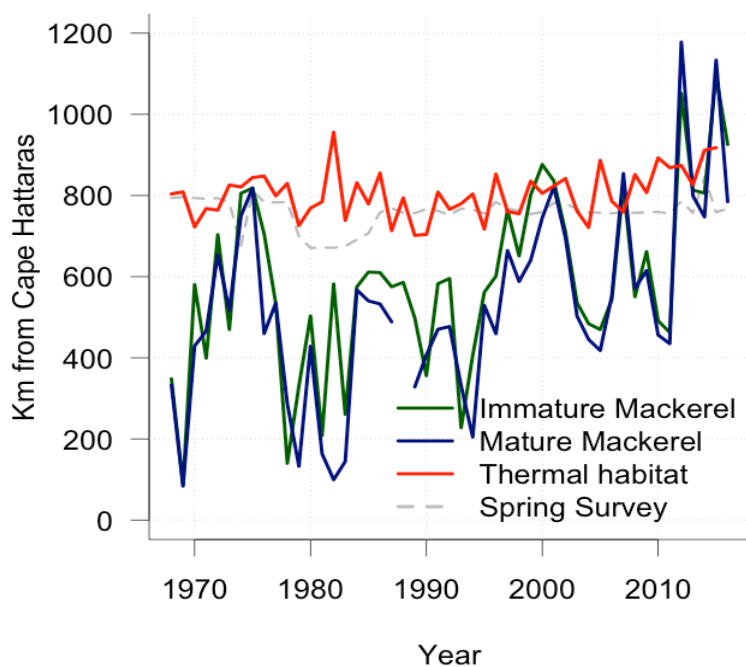


Figure 10. Center of gravity of thermal habitat preferred by Atlantic Mackerel (5.5C - 9.5C red line) compared to CGs for immature and mature mackerel and stations in the spring NEFSC bottom trawl survey.

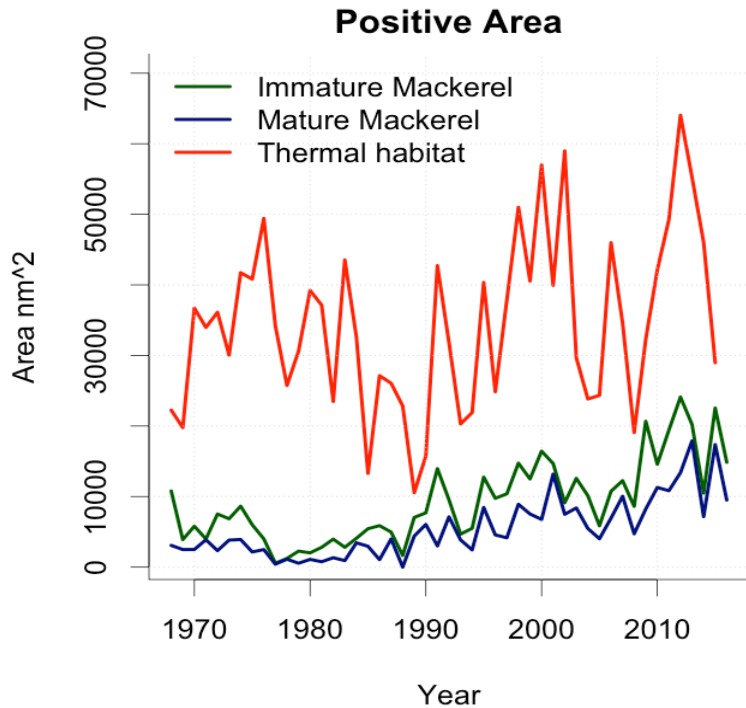


Figure 11. Positive areas for thermal habitat preferred by Atlantic Mackerel (5.5C - 9.5C red line) compared to PAs for immature and mature mackerel in the spring NEFSC bottom trawl survey.

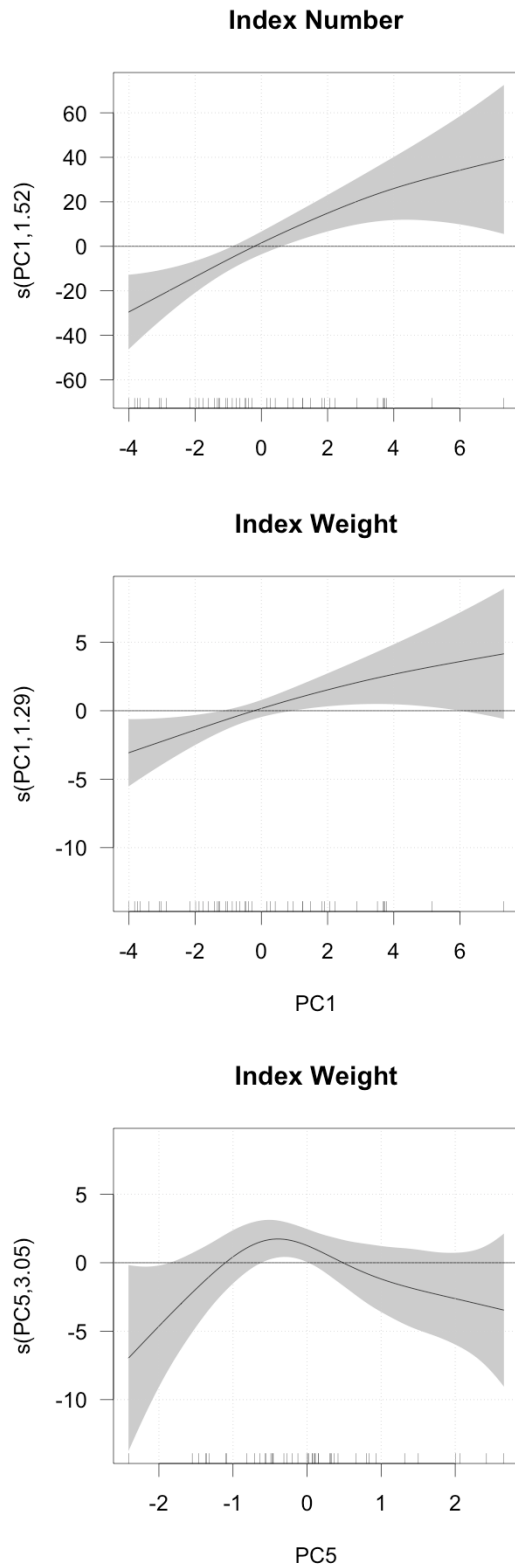


Figure 12. Deviance plots from generalized additive models of relationships of the index of abundance for Atlantic mackerel by number (top) and weight in the NEFSC survey with the first PCA for the spatial indicators (middle). Indices increased as the area occupied, frequency of occurrence and distance from Cape Hatteras increased. The relationship between PCA 5 (+correlated with number of patches, - correlated with distance of habitat CG from Cape Hatteras) and the index of abundance by weight is indicated at the bottom. The results of the PCA are described in Table 2, while the GAM results are described in Table 3.

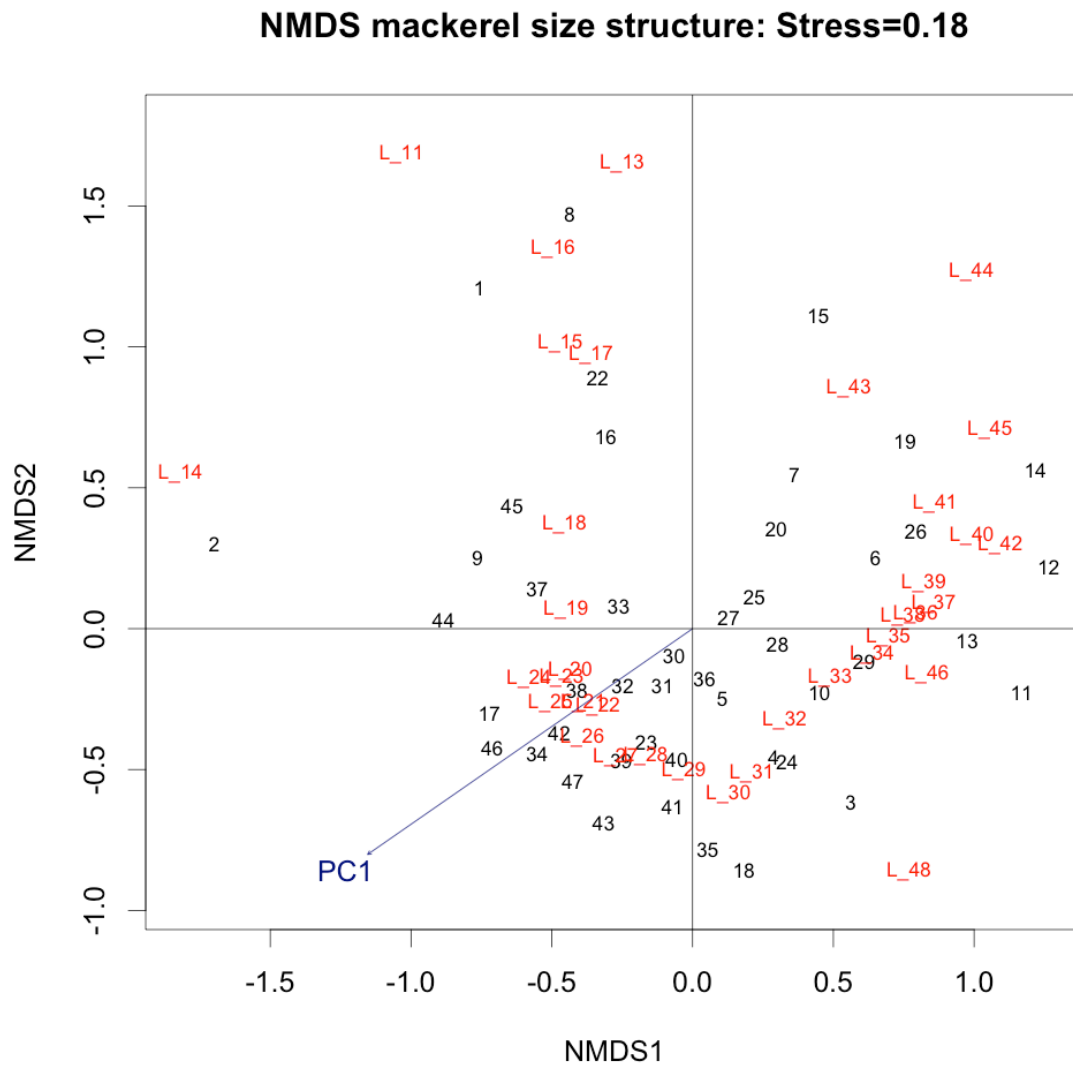


Figure 13. Nonmetric Multidimensional scaling plot of the relationship between size structure of fish collected in the NEFSC survey and the first principal component (blue arrow) of the spatial indicators, for which scores increased as areas of occupation and distance from Cape Hatteras increased. Red letters are length (L) classes in 1 cm intervals. Black numbers are year number from 1968. Only the first principal component was significantly correlated with changes in size structure using the BIOENV procedure.

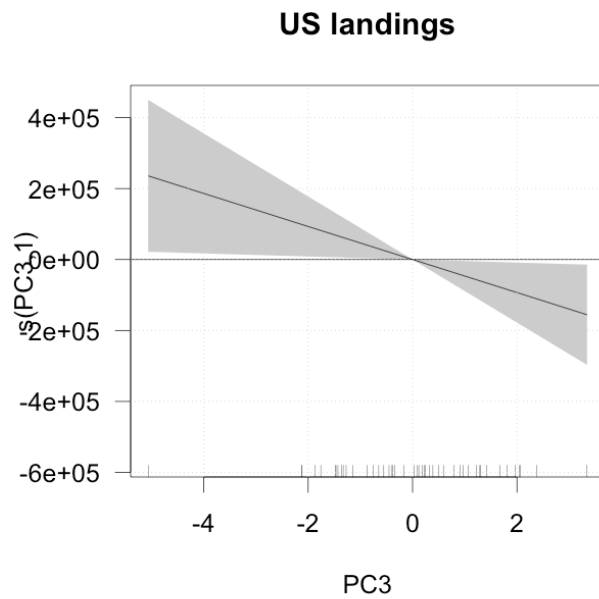
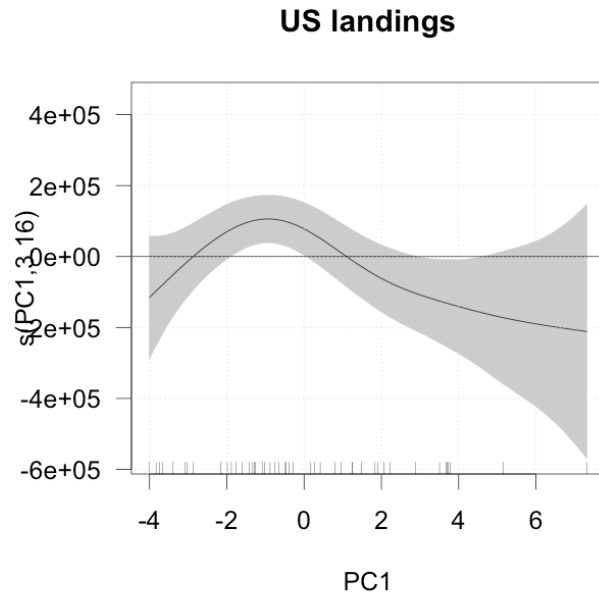
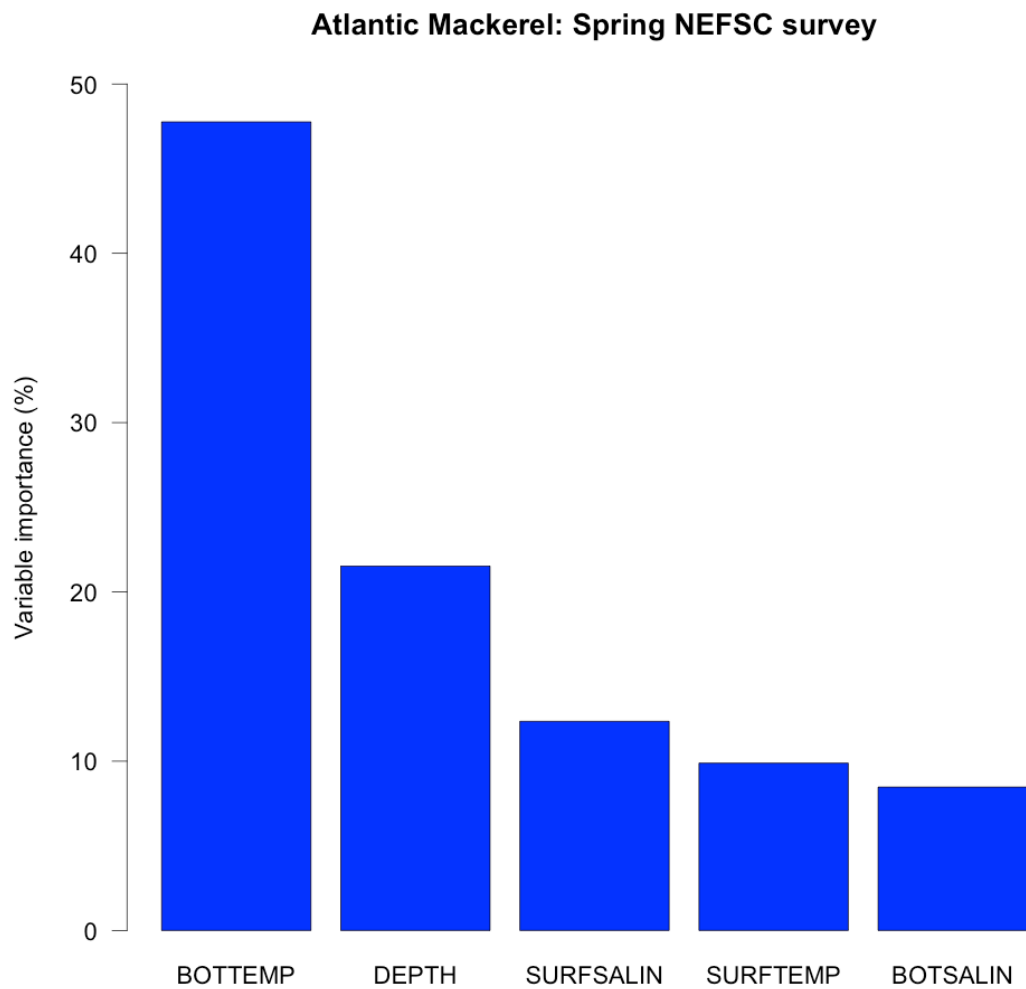


Figure 14. Deviance plots from generalized additive models of relationships between US landings of Atlantic mackerel and the first and third PCAs derived from spatial indicators of mackerel distributions and habitat during the spring NEFSC survey. Landings increased as the area occupied by mackerel decreased in the spring NEFSC survey and the center of gravity shifted southwest. The results of the PCA are described in Table 2, while the GAM results are described in Table 3.



Binomial GAM: 10 fold CV

Figure 15. Relative importance of habitat variables identified as significant in single factor quotient analysis applied to NEFSC bottom trawls survey collections of Atlantic mackerel. The analysis used the methods of Thuiller, 2013 and Thuiller, 2016, which compare correlations of observations with predictions from 10-fold cross validated GAMs.

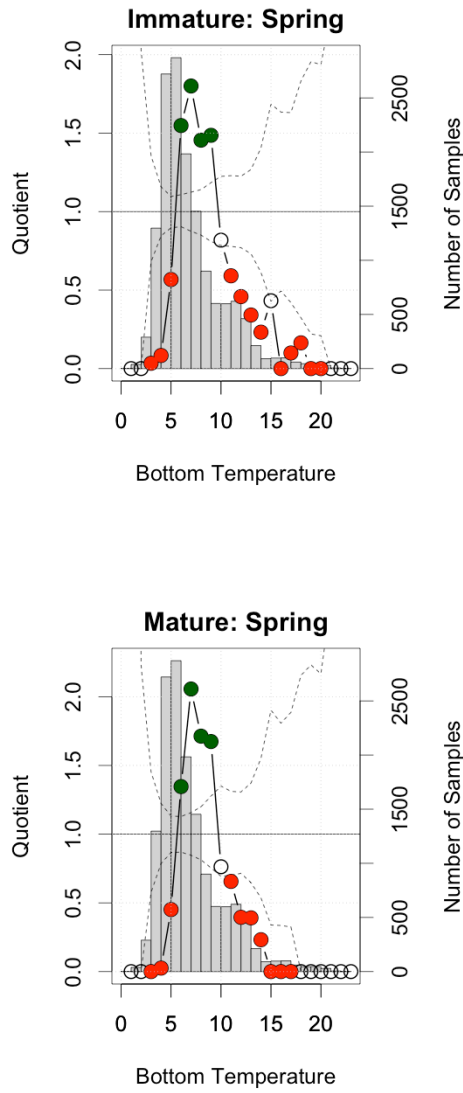


Figure 16. Single factor quotient analysis indicated that immature (top) and mature (bottom) size classes of Atlantic mackerel were positively associated with temperatures of 5.5-9.5°C and 5.7-9.5°C, (green dots) respectively during the spring bottom trawl survey. Dots indicate whether abundances in 1°C temperature bin were greater than (green; positive association), equal to (white, no effect) or lower than (red; avoidance) expected by chance based on randomization of the data (N=999). Dotted lines are 2 standard errors confidence bands for null quotients developed by data randomization. The histogram of bottom temperatures measured at the survey stations is indicated in grey.

Recorded winter catches: 2014-17

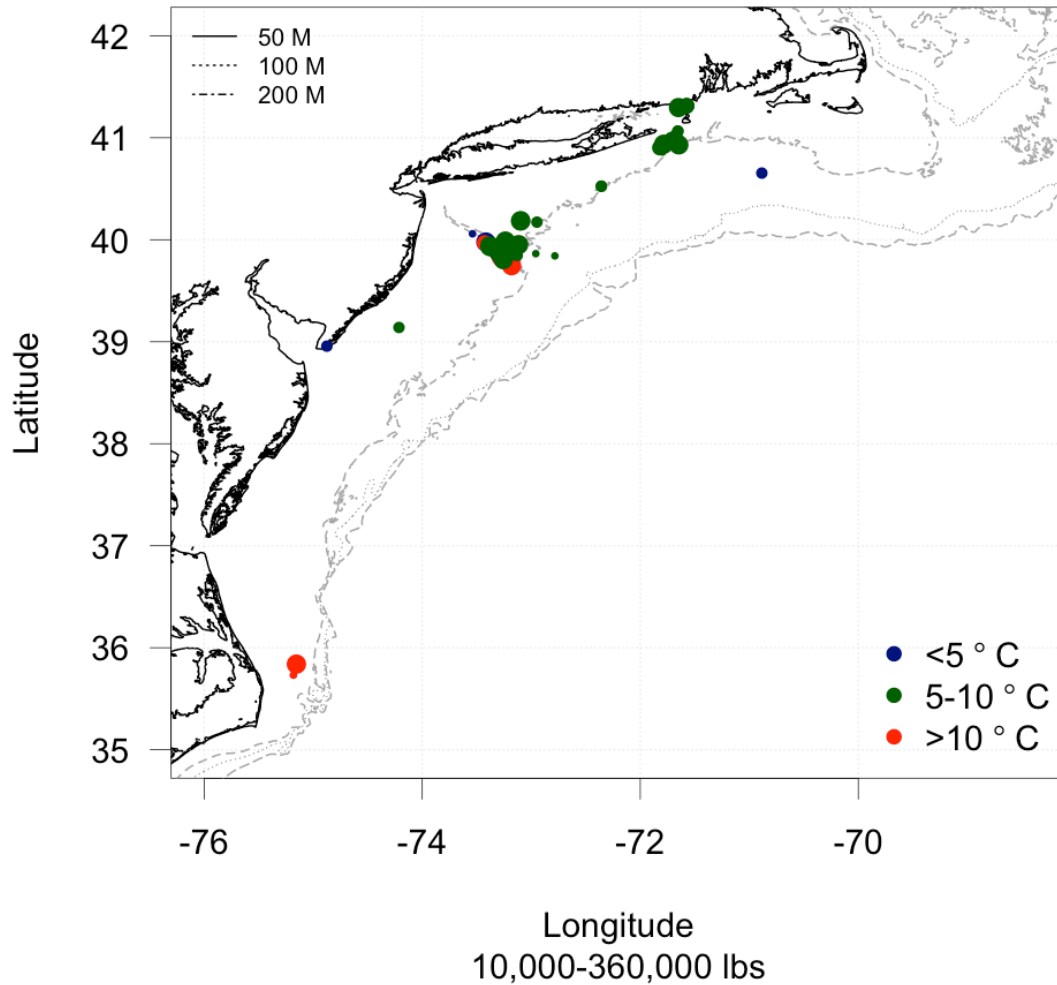


Figure 17. Locations and thermal habitat for fishery catches ($N=134$) of mackerel > 1000 lbs during the winter (January 1- April 15) from 2014 through 2017. Thermal habitat was classified based on the results of single factor quotient analysis (Fig 16) and water temperature hindcast by ROMS ESPRESSO within 10 km and 12 hours of tows. 8% of tows ($N=11$) occurred in bottom water colder than 5°C, 20% of tows occurred in bottom water warmer than 10°C and 71% ($N= 94$) occurred in the preferred temperatures (See Table 5).

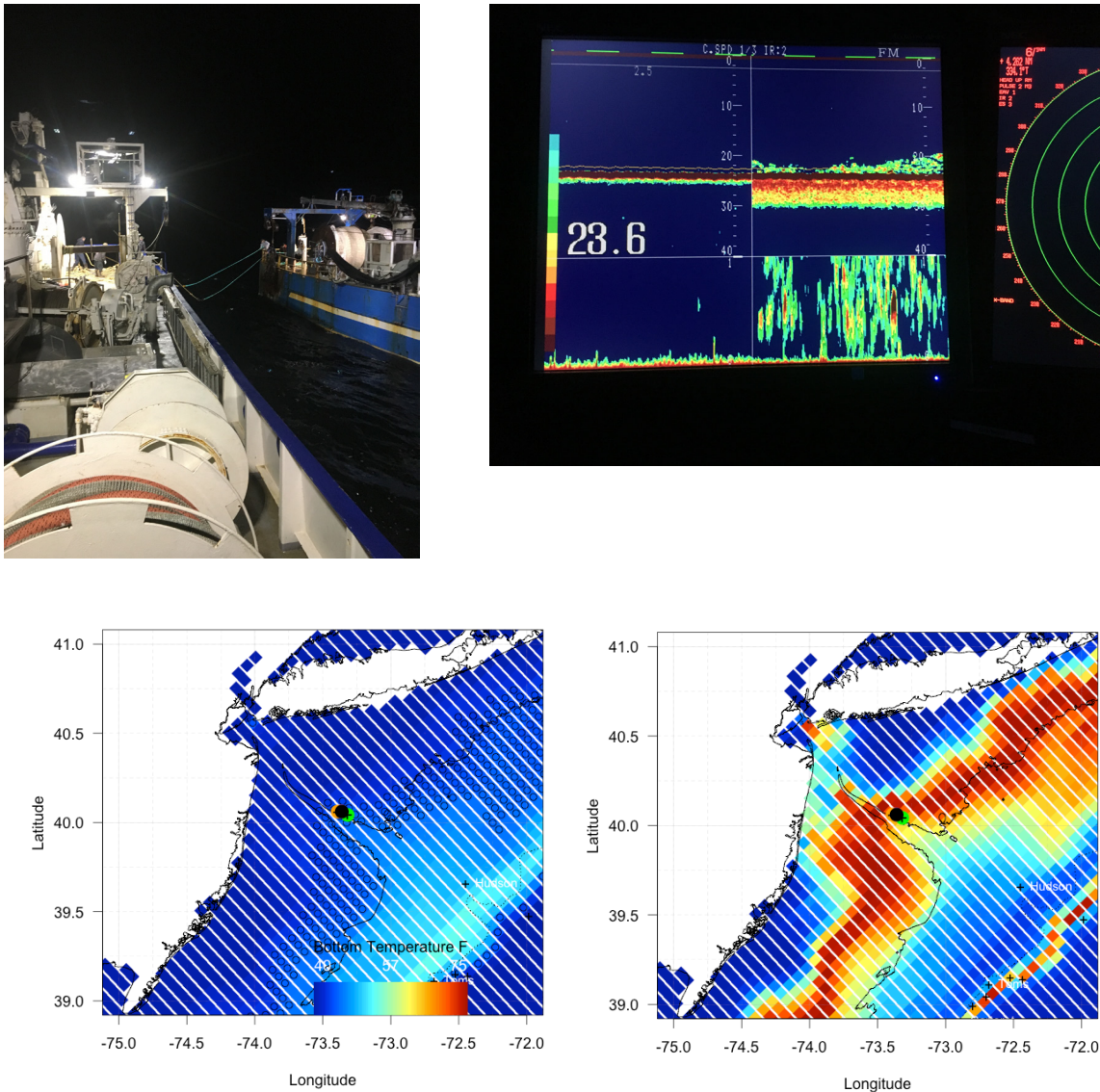


Figure 18a. Opportunistic field evaluation of the winter habitat model for mackerel on a commercial pair trawler targeting mackerel in mid-February in the Hudson shelf valley. **Top left.** Vessels passing net towing cables in preparation for the next tow. **Top right.** Mackerel detected in 200 khz fishery hydroacoustic unit. **Bottom left.** Locations of nighttime tows on real time bottom temperature output from the Espresso ROMS data assimilative numerical ocean model. Model temperatures and insitu temperatures measured at the net ranged between 5°C and 7°C and were similar. **Bottom right** locations of tows on thermal habitat model projected using Espresso ROMS bottom temperatures. Red is highly suitable thermal habitat while blue is unsuitable.

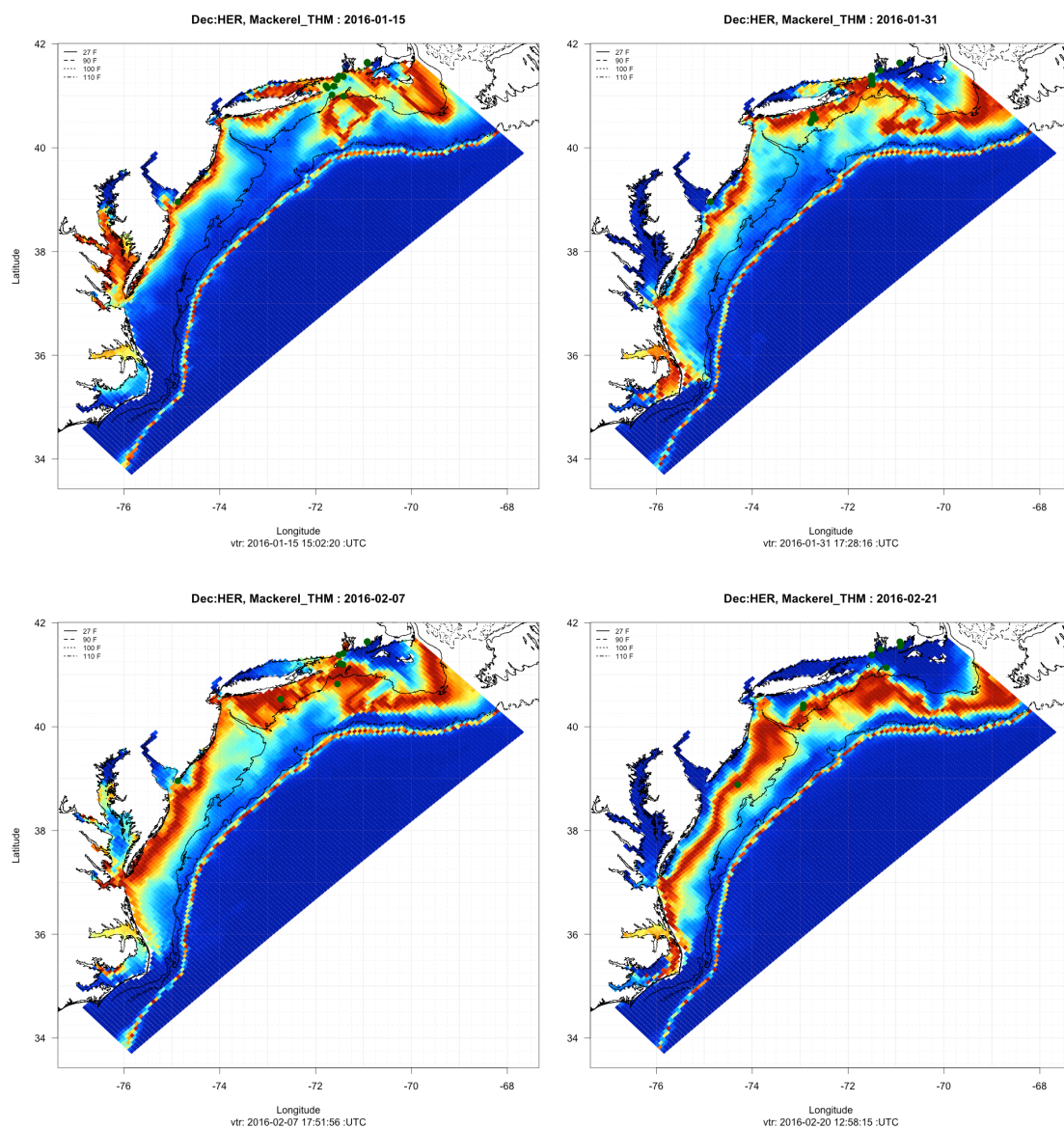


Figure 18b. Daily snapshots of vessels (green dots) declared into the Mackerel/Herring fishery during the winter 2016 on the winter habitat model projected using ROMS bottom temperatures. Red is suitable habitat, blue is unsuitable. **Top left.** Vessels fishing a patch of bottom habitat south of Block Island Sound that first developed on Nantucket Shoals during an early January Storm. **Top right & bottom left.** As the habitat continued to evolve and translate southwest vessels began to fish south of Long Island. **Bottom right.** Fishing does not occur south of the Hudson River valley until overwintering habitat bridged the valley. Fish were then reported in the recreational fishery as far south as the Virginia Capes. Daily modeling and fleet monitoring indicated that habitat connectivity was important in determining how far to the southwest the fishery and presumable mackerel were likely to occur.

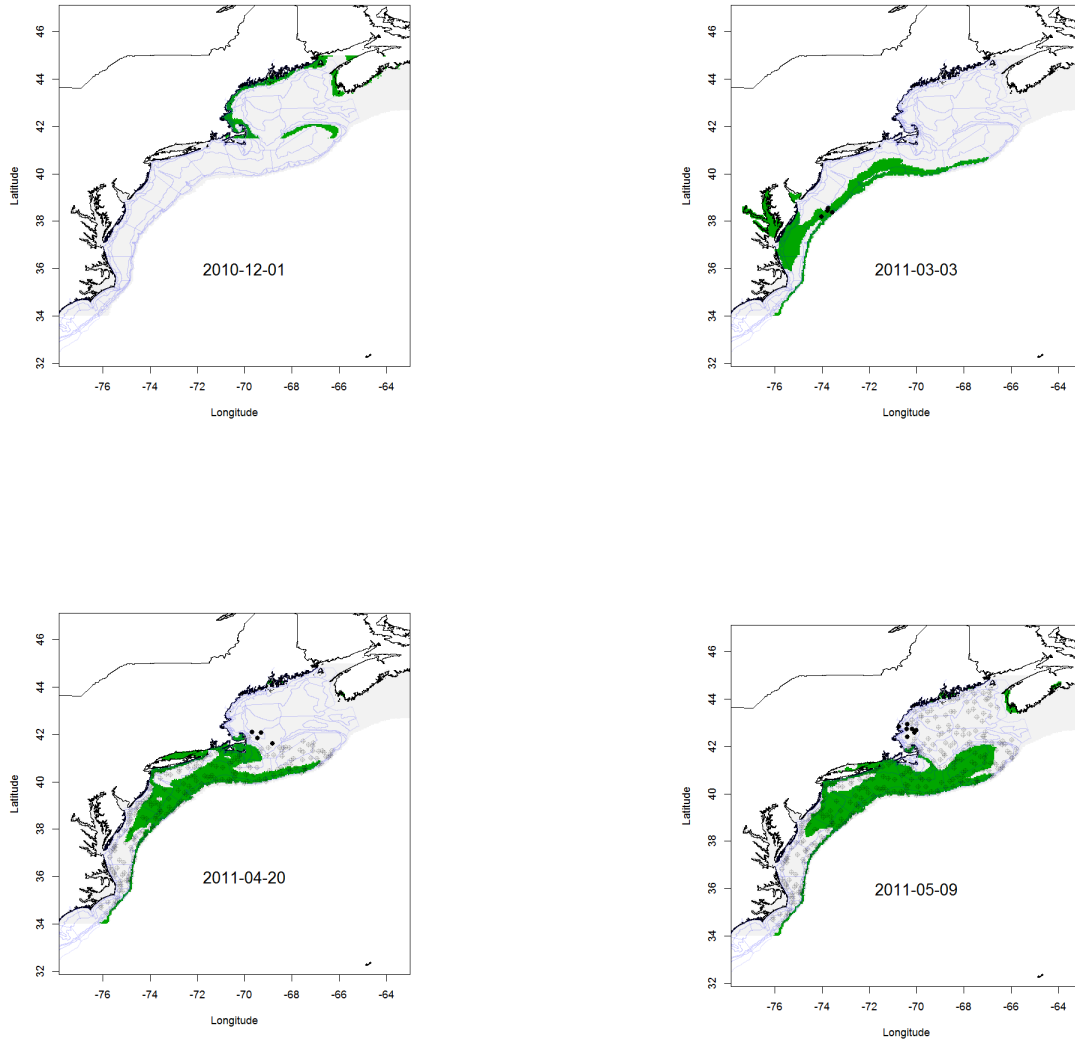


Figure 19. Portion of the NW Atlantic ROMS model domain used to develop the habitat model with movement constraints. (Top left) Initial fall distributions of Atlantic mackerel on December 1 2010 are defined by the green area where latitude is $> 41.5^\circ\text{N}$, depths $< 160\text{M}$, and bottom temperatures range from $8-12^\circ\text{C}$ (with model bias adjustment). Grids defined by the same conditions constructed for each year were used to set initial conditions to account for movement constraints associated with habitat connectivity along fall-winter migration pathways (See method). The remaining projections are selected daily estimates of preferred habitat (green) for the beginning (March 3), middle (April 20) and end (May 9) of the 2011 NEFSC bottom trawl survey. Closed circles are

survey samples taken on the day of the habitat projection while open circles are the samples completed before that date. Samples falling within the preferred habitat (Black dots within green areas) have an $HSI = 1$ while those falling outside are assigned and $HSI = 0$ in equation 1. Survey strata used in area calculations in equation 1 are depicted by blue lines

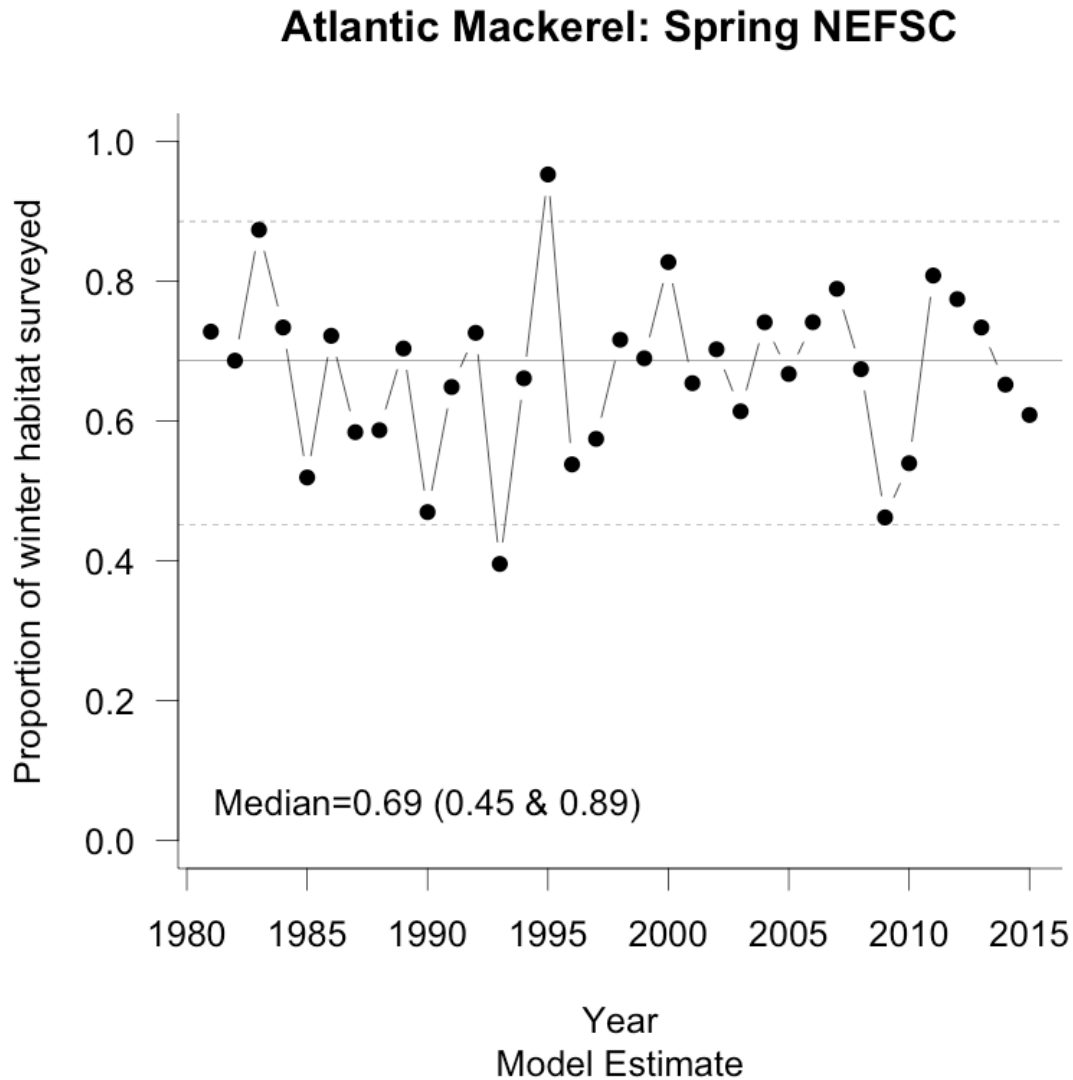


Figure 20. Model based estimates of the proportion of winter habitat surveyed in the spring NEFCS bottom trawl survey from 1980-2016 computed using habitat projections (e.g. Fig. 18) and equation 1. Estimates can serve as a ecologically informed proxy for availability that can be used to estimate catchability outside analytical assessment models.

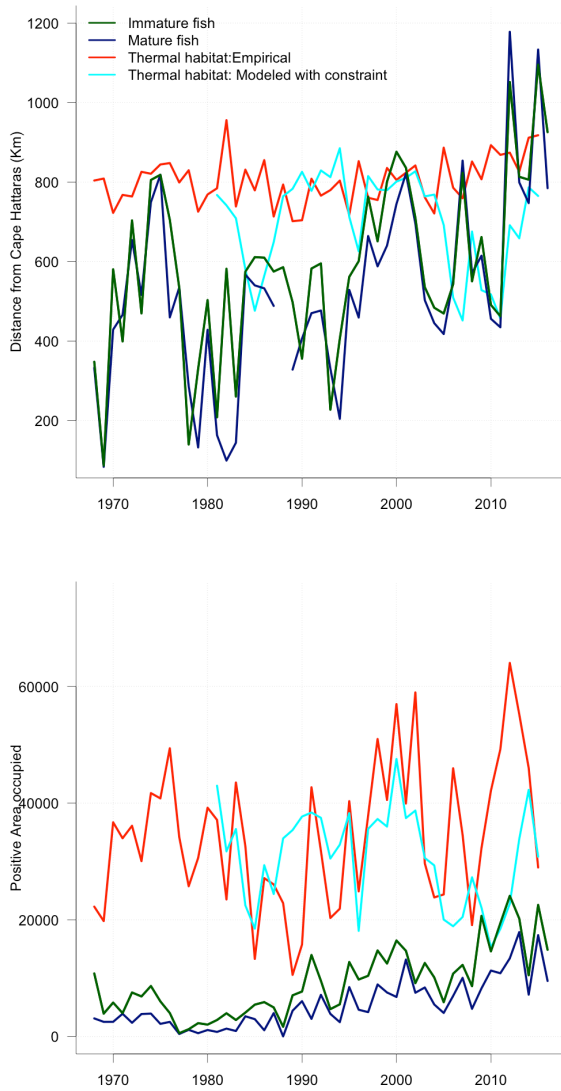


Figure 21. Distances of centers of gravity from Cape Hatteras (top) and relative areas of occupation (bottom) for juvenile and adult mackerel and habitat classified based on bottom temperatures measured in situ (empirical) and hindcast using the habitat model that incorporated movement constraints. Spatial indices were calculated using the methods of (Woillez, 2007; Woillez, 2009) as described in detail in (Manderson, 2017).

Fishery catches over 10,000 lb *Directed & by-catch*

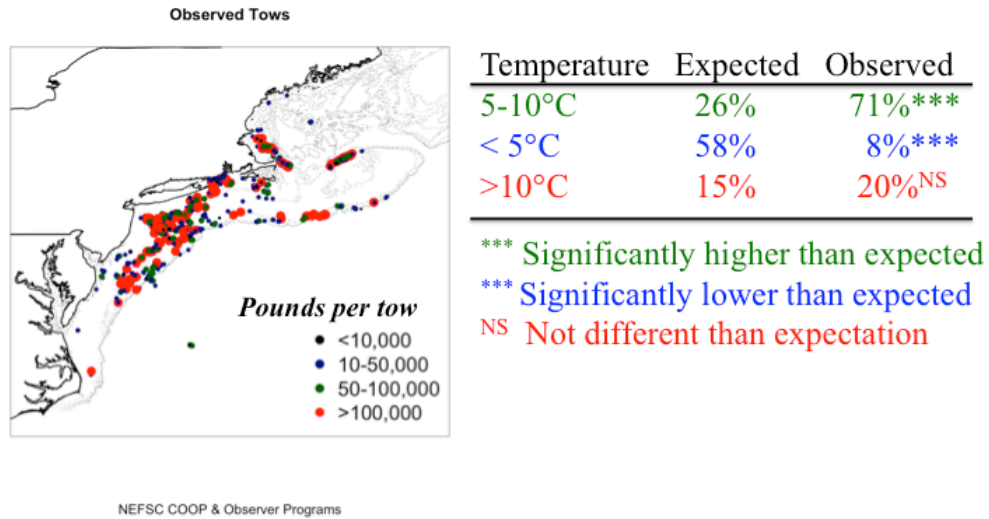


Figure 22. Catches of mackerel in the observer and study fleet programs in the directed fishery and as by-catch in the longfin squid fishery from September through April, including along the shelf break. The table on the right shows the results of exact binomial tests for associations of catches with bottom temperatures from the Expresso ROMS ocean model at the locations and times of catches. Catches were lower than expected by chance at model temperatures less than 5°C, associations were greater than expected by chance in temperatures from 5-10°C, Catches were not different from expected by chance at temperatures >10°C which were rare and occurred primarily during seasonal transitions.

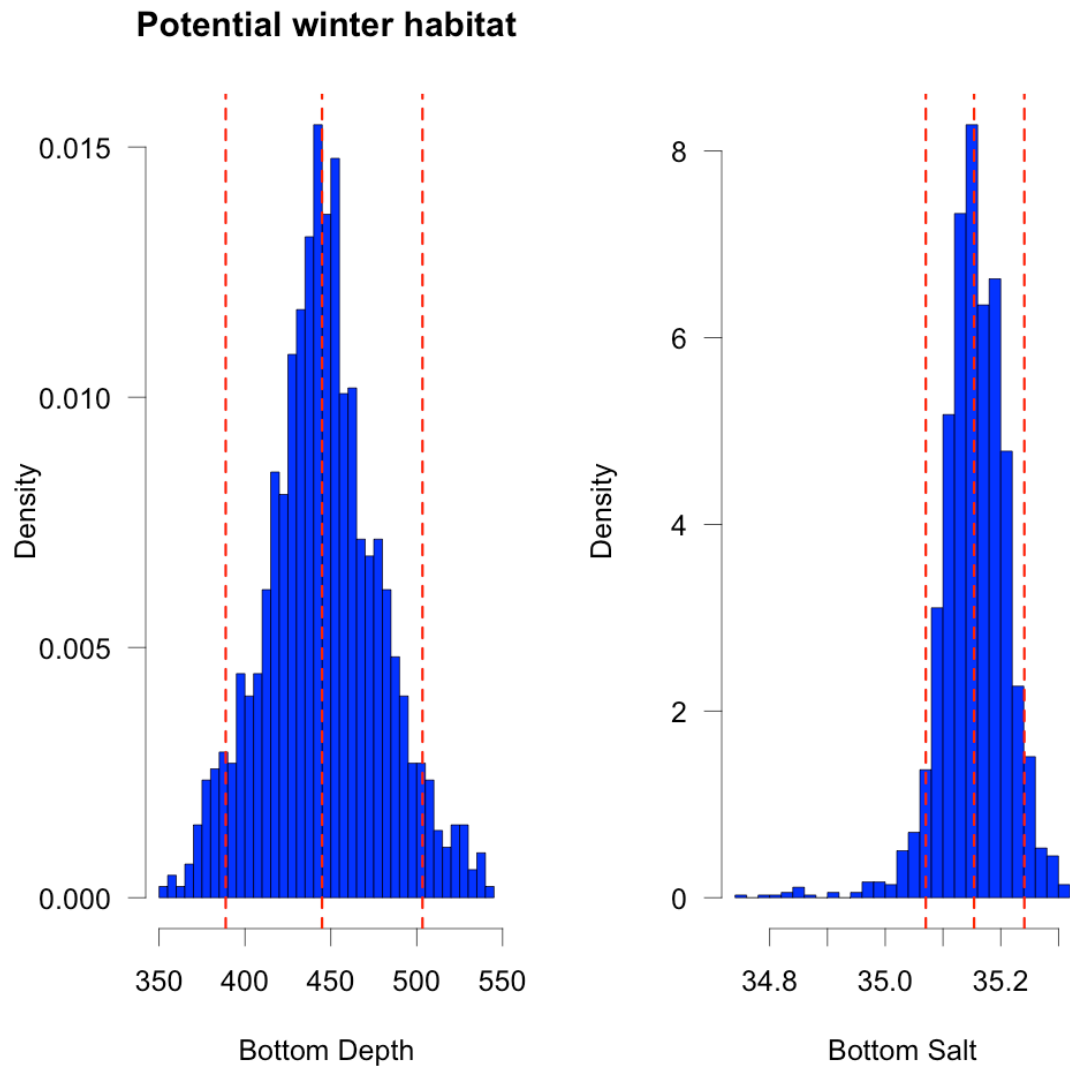


Figure 23. Range of bottom depths and salinities for water deeper than 150 meters with temperatures within the range preferred by mackerel during the winter (7-9°C) based on habitat projections using Espresso ROMS. Temperatures, salinities and depths are similar to those of habitats occupied by mackerel during the winter in Canada and the North East Atlantic (Walsh, et al. 1995, Reid, et al., 1997)

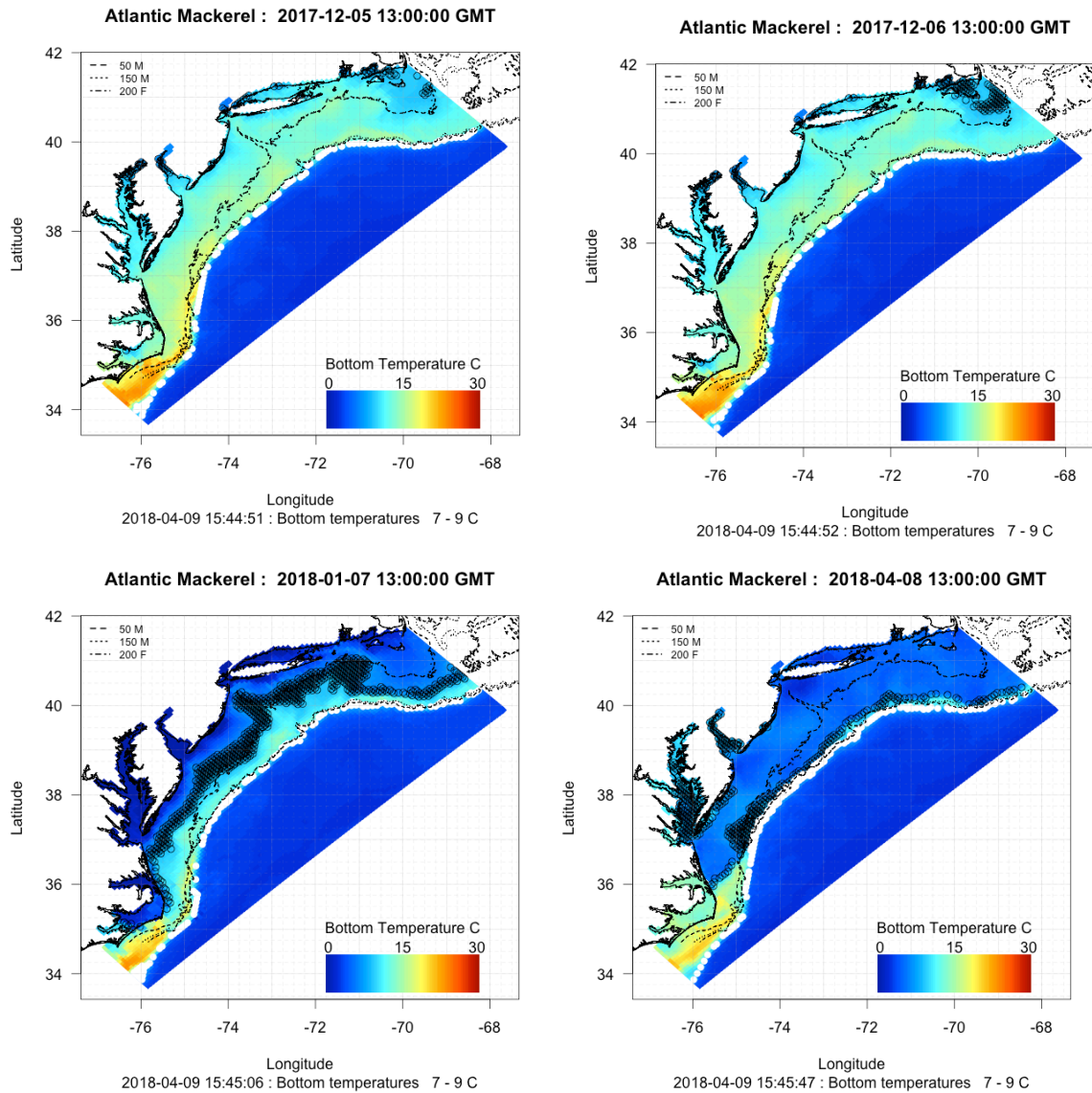


Fig 24. ROMs Projection of bottom temperatures from 7-9°C preferred by mackerel during winter highlighted with black circles in shallow water < 150 meters and white circles in deeper water. The band of slope water with temperatures of 7-9°C and salinities from 35-36‰ persists at 350-500 meters throughout the year (Fig. 22, 24). **Top left.** During the 2017-2018 winter season which was typical, water in the preferred temperature range was only available on the slope from early October through early December (Fig 23). **Top right.** Winter habitat began to develop on the shelf in early December around Nantucket shoals and Cape Cod in response to a winter storm. **Bottom left.** Mixing due to a prolonged and cold NE storm occurring after Christmas and through New Years, 2018 resulted in a band overwintering habitat that extended on the shelf from New England to Coastal Virginia. The winter mackerel fishery began in earnest on the MAB continental shelf immediately following this storm. **Bottom Right.** By

late April overwintering habitat on the continental shelf had translated offshore to the vicinity of the shelf break adjacent to slope water habitat.

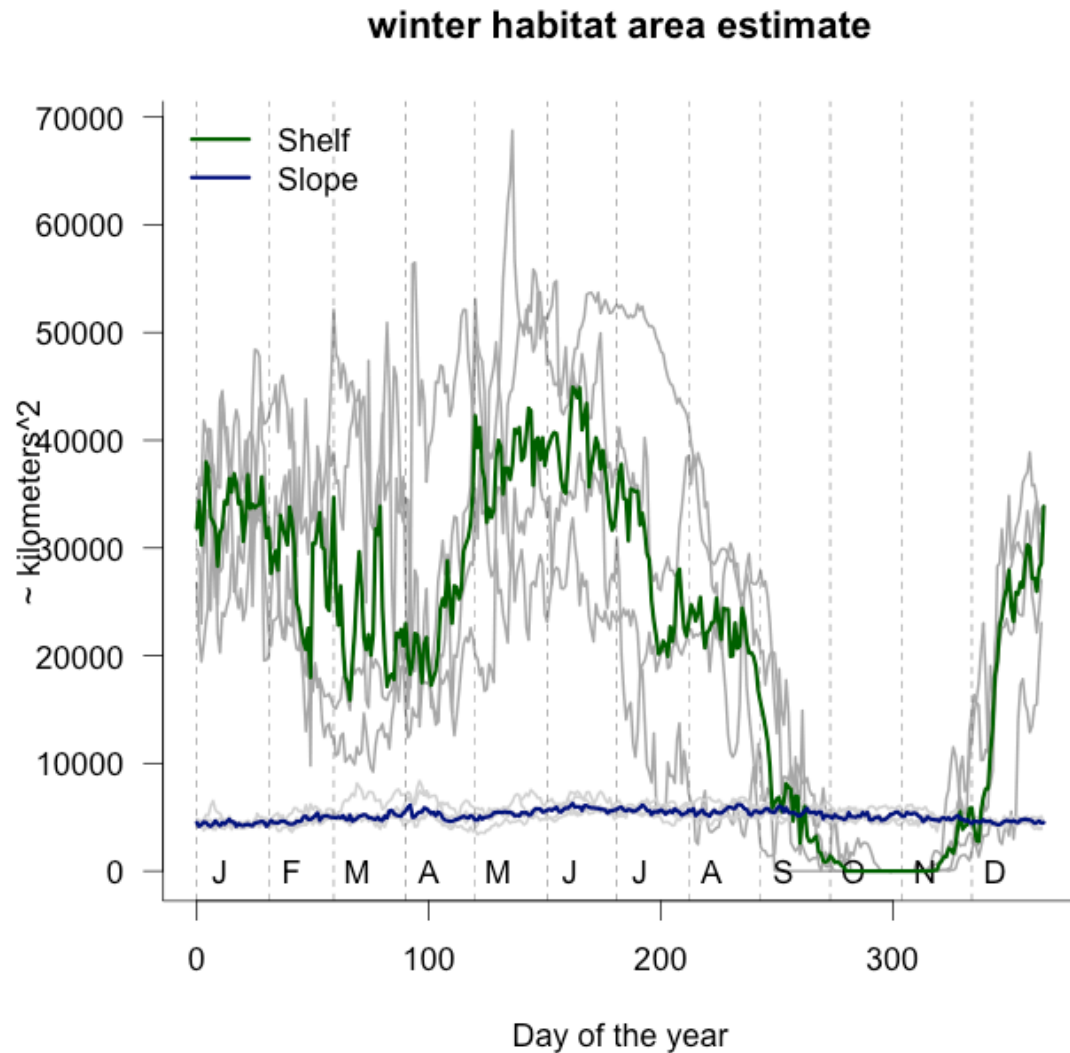


Figure 25. Surface area estimates of thermal habitat preferred by mackerel during the winter and associated with seabed based on daily Espresso ROMS projections (Fig. 23). Grey lines show yearly trajectories while colored lines show daily medians from 2013-the present for bottom depths <150 meters in green and for deeper water in blue. Winter habitat for mackerel was consistently available on the continental slope through out the year, while habitat on the continental shelf showed strong seasonal and interannual variability.

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Appendix 1:

Analysis of size at maturity to divide mackerel into immature and mature size classes

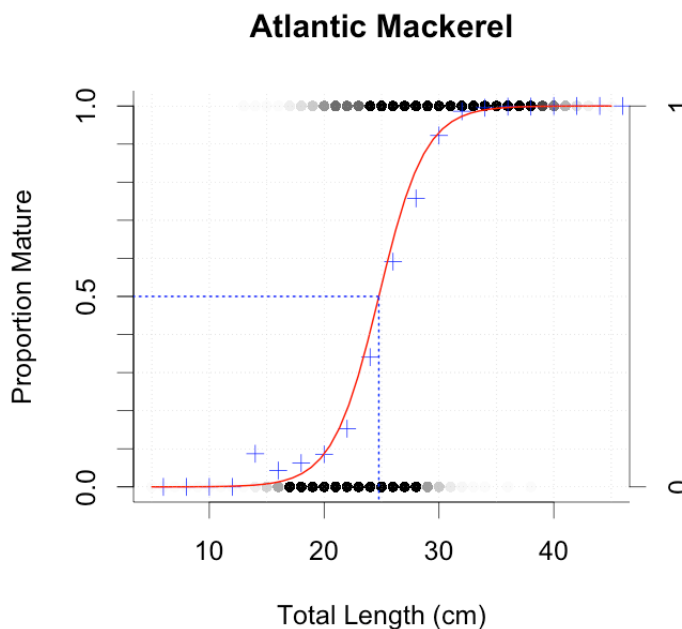
We used mackerel size and maturity data collected in the spring NEFSC bottom trawl survey and bootstrapped logistic regression to determine the length at 50% maturity and a threshold to classify immature and mature fish based on length. Differences in size at maturity between sexes were explored but proved not to be significant (length*sex interaction, $p=0.092$). The median length of 50% maturity (95% confidence intervals) calculated using bootstrapped regression ($N=1000$) was ~25 cm.

Bootstrapped coefficients

	Bootstrapped SD	50%	2.5%	97.5%
(Intercept)	0.173	-12.272	-12.612	-11.951
#LENGTH	0.007	0.496	0.483	0.508

Length at 50% maturity

50%	2.5%	97.5%
24.76	24.67	24.85



Appendix Figure 1. Logistic regression relating the maturity to body size for Atlantic mackerel collected in the spring NEFSC bottom trawl survey.