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ARTICLE

Impacts of Interannual Environmental Forcing and Climate Change on the Distribution of Atlantic Mackerel on the U.S. Northeast Continental Shelf

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Abstract
The Northwest Atlantic stock of Atlantic mackerel *Scomber scombrus* is distributed from Cape Hatteras to Newfoundland and migrates great distances on a seasonal basis. Atlantic mackerel are sensitive to changes in temperature, preferring water greater than 5°C. Annual changes in the winter and early-spring distributions of Atlantic mackerel were investigated using satellite imagery, research trawl surveys, geographical information systems, and spatial and standard statistical analyses. During the past 40-plus years (1968–2008), the distribution of the stock has shifted about 250 km to the north and east. Also, a change has occurred in the depth distribution of the stock, from deeper off-shelf locations to shallower on-shelf ones. Areal and bathymetric changes in distribution are correlated with interannual temperature variability and gradual warming. These results have implications for U.S. commercial and recreational mackerel fisheries because, despite the current high abundance of the stock, the changes in distribution will probably make it more difficult to find and catch Atlantic mackerel in certain areas in the future.

The Northwest Atlantic stock of Atlantic mackerel *Scomber scombrus* is composed of two components (northern and southern) that annually migrate long distances on a seasonal basis (Sette 1950; Anderson and Paciorkowski 1980). These migrations are associated with spawning and feeding areas off the East Coast of the United States (the southern component) and in the Gulf of St. Lawrence region (the northern component) (Anderson and Paciorkowski 1980). Both components are thought to overwinter off the eastern United States (Sette 1950). Although there are distinct seasonal patterns in the distribution of Atlantic mackerel, these patterns have been variable historically, as evidenced by areal changes in the fishery during the last century (Sette and Needler 1934; Sette 1950). This interannual variability, especially during the winter, is linked to temperature patterns on the continental shelf (Sette 1950; Olla et al. 1976; Berrien 1982; Murray et al. 1983;

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Overholtz et al. 1991; Mountain and Murawski 1992; Murawski 1993).

Historically, Atlantic mackerel were generally found in the Middle Atlantic Bight (often as far south as Chesapeake Bay) during winter and confined to a narrow band of habitat along the shelf–slope break (Sette 1950; Berrien 1982; Collette and Klein-MacPhee 2002). This was due primarily to the thermal preferences of this species; water temperatures on the continental shelf were generally too cold. In winter, the water column in this region is often vertically well mixed, with temperatures less than 5°C (Olla et al. 1976; Han and Niedrauer 1981; Mountain and Holzwarth 1989). At these low temperatures, much of the shelf and Georges Bank probably represented a thermal barrier for Atlantic mackerel. Historically, water temperatures cooler than 7°C were considered to be too cold for Atlantic mackerel, as evidenced by surface temperatures and catches in the fishery during 1926–1935 (Sette 1950). A more contemporary study indicated that Atlantic mackerel are intolerant of temperatures less than 5–6°C (Olla et al. 1976).

During the 1960s and early to mid 1970s, Atlantic mackerel supplied an early-spring recreational fishery along the nearshore region of the Middle Atlantic Bight; however, this fishery began to decline in the late 1970s and early 1980s (Overholtz et al. 1991). Recreational landings of Atlantic mackerel in the Middle Atlantic Bight further declined from the 1990s to 2007. Beginning in 2005, the U.S. commercial fishery began to experience difficulty in locating large schools of Atlantic mackerel during the winter fishery (NEFSC 2006). In contrast, the Canadian fishery has continued to thrive and Atlantic mackerel seem to be readily available to coastal commercial vessels (DFO 2008). Recently, Atlantic mackerel have frequented the shallower waters of the Northeast Continental Shelf during winter, possibly owing to a general warming pattern in the region (Mountain and Murawski 1992; NEFSC 2006; Friedland and Hare 2007; Radlinski 2009).

Interannual variability in the cooling of the Northwest Atlantic Continental Shelf during winter is primarily caused by local atmospheric forcing (Thompson et al. 1988; Junge and Haine 2001; Mountain et al. 1996). In winter, changes in sea surface temperatures (SSTs) are related to the heat exchanged between the cooler atmosphere and the warmer surface waters, with the range and duration of cooling events being important (Junge and Haine 2001). Atmospheric forcing events in the region, such as intense winter storms and prolonged arctic high-pressure systems, are related to large-scale climatic patterns such as the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO). Variation in these large-scale drivers causes change in the position of the jet stream and consequently induces variability into temperature, precipitation, and storm activity over the eastern United States (Archer and Calderia 2008). A gradual northward repositioning of the jet stream over North America and increases in SSTs on the Northeast Continental Shelf have been documented (Friedland and Hare 2007; Archer and Calderia 2008). These longer-term changes are probably related to the AMO and the gradual warming forced by increasing CO_2 emissions.

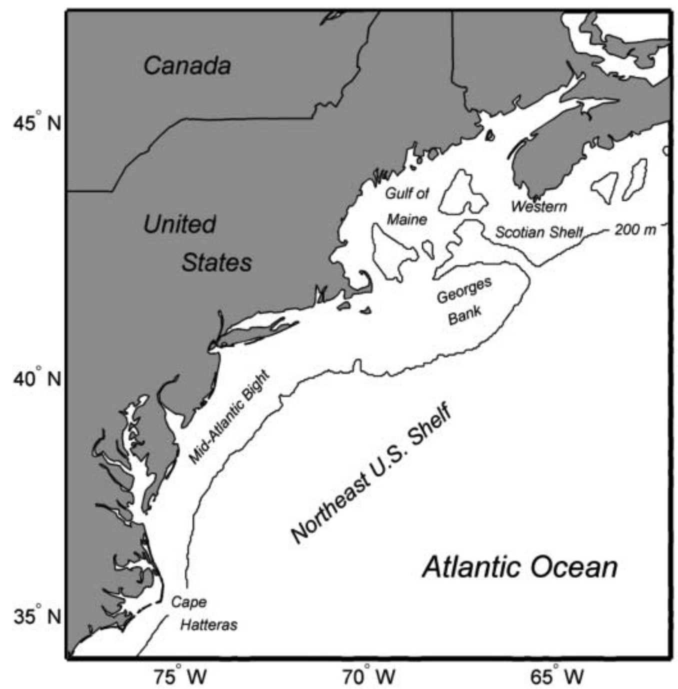

FIGURE 1. Map of the area in which the effects of climate change on Atlantic halibut were studied.

The purposes of this paper were to investigate the changes in the distribution of Atlantic mackerel in the region during the late winter and early spring of 1968–2007 and to determine the relationship between that distribution and the interannual variability associated with atmospheric forcing and the general warming of the Northeast Continental Shelf. Some impacts of the changes in the distribution of Atlantic mackerel on the U.S. recreational and commercial fisheries for this species were also evaluated.

METHODS

Trawl Survey

Northeast Fisheries Science Center (NEFSC) "spring" bottom trawl survey data were analyzed to determine the annual distribution of Atlantic mackerel during 1968–2008 on the Northeast Continental Shelf from Cape Hatteras to the Gulf of Maine (Figure 1). This survey covers the period from late winter to early spring (March–April) during each year, with much of the sampling activity being focused on the late-winter period (March) because of geographic coverage. The survey is based on a stratified random design, with strata defined primarily on the basis of water depth. Offshore strata (depth range, 25–200 m) from the NEFSC spring survey were used in the analysis. Approximately 350 stations are sampled per year, with station allocation based on the area of each survey stratum. Survey operations are conducted 24 h/d with a bottom trawl rigged with rollers and a 12.5-mm stretch-mesh liner in the cod end (the height of the opening is 2 m and the wing spread is 11 m); catch is identified to species, counted, and weighed (see Azarovitz 1981 for more detail).

Average along and across Shelf Location

The annual average latitude and longitude of the catch were calculated from the station locations of positive catches each spring. Biomass- and numbers-weighted averages were not calculated because the Atlantic mackerel is a pelagic species and its availability to a small research bottom trawl may not be related to its absolute abundance at any particular site. Calculating an average latitude and longitude can be problematic because the Northeast U.S. Continental Shelf runs from southwest to northeast (see Figure 1). Simple calculations of the average latitude and longitude of mackerel catch often resulted in locations off the shelf where no sampling was performed. To avoid this problem, we developed a curvilinear grid based on along-shelf and cross-shelf locations. The 200-m isobath was extracted from 2-min bathymetry data for the region obtained from the National Geospatial Data Center (http://www.ngdc.noaa.gov/mgg/coastal/coastal.html). The 200-m isobath, excluding the northern flank of Georges Bank and the basins in the Gulf of Maine, was smoothed using a 50-span locally weighted scatterplot smoothing (LOWESS) filter. The distance along this isobath from Cape Hatteras was used as the along-shelf distance. At 2-km intervals along the smoothed 200-m isobath, the local perpendicular was found and onshore (−) and offshore (+) across-shelf distances from the isobath were calculated. All points along the perpendicular were assigned the along-shelf location where the perpendicular traversed the 200-m isobath. The along- and cross-shelf locations of all stations were then determined using a nearest-neighbor interpolation based on the latitude and longitude locations of points on the along- and cross-shelf grid. Without this correction, plotting the along- and across-shelf centers of distribution of the Atlantic mackerel stock relative to the shelf bathymetry would not have been as useful. Average along- and across-shelf locations in each year were calculated as the averages of all stations where Atlantic mackerel were caught. As noted earlier, stations were not weighted by catch number or biomass.

Area Occupied

Several spatial analyses were undertaken using the spring trawl survey data to calculate metrics and quantify changes in distribution. Selected survey catch data with about a 10-year interval from the 1960s to 2007 (i.e., 1968, 1978, 1988, 1998, and 2007) were used to produce kernel density–border curves that are useful for quantifying changes in distribution and the concentration points of Atlantic mackerel over time. The 80% kernel density confidence region around each survey distribution was used to delineate where the majority of the mackerel catches were located in each year. In addition, a density curve was added on the border of each latitude–longitude map to highlight the points of concentration (Bailey and Gatrell 1996).

To quantify the area occupied by Atlantic mackerel each spring, the localized convex hull method (Getz and Wilmers 2004) was used to define a polygon around annual survey mackerel catches. This approach can deal with landscapes with distinct but irregular boundaries, such as the shelf edge and the coast. The latitudes and longitudes of positive stations were converted to Universal Transverse Mercator coordinates using the mfwdtran function of the MatLab Mapping Toolbox. The 100% isopleth area for each year was then calculated using the nearest-neighbor convex hull function in the adehabitat package of R.

Pelagic Habitat

Sea surface temperature.—Marine satellite imagery for the eastern USA and Canada was used to investigate changes in sea surface temperature in selected years and to identify different patterns in shelf cooling during winter. Images from consecutive months (December–February) were examined to evaluate the progression of cooling during 2005 and 2007. These years were chosen because they represent two different patterns with respect to warm- and coldwater conditions on the Northeast Continental Shelf. Imagery was obtained from the Rutgers University Coastal Ocean Observation Laboratory Web site (http://marine.rutgers.edu/mrs/data.html).

Hydrographic data.—Temperature and salinity were measured at all spring survey stations. Prior to 1990, temperature was measured by means of expendable bathythermographs and salinity was measured from water samples. From 1990 onwards, temperature and salinity have been collected using conductivity, temperature, and depth instruments. Bottom temperature and salinity measurements were summarized by kriging using a spherical model and software available in Arcmap (Maguire et al. 2005). From the temperature data in each spring survey, the average annual bottom temperature was calculated from Cape Hatteras to western Scotian Shelf. We quantified the relationship between temperature and the annual location of the Atlantic mackerel stock through correlation analysis. Since environmental data are often autocorrelated and this can affect statistical inference, we used the method suggested in Pyper and Peterman (1998) to adjust for this problem.

Quotient Analysis

A quotient approach was used to calculate the range of preferred temperature and salinity to determine whether the ranges were narrow or broad and to aid in calculating the area of preferred habitat of Atlantic mackerel (van der Lingen et al. 2001). Stations were grouped in 1.0°C bottom temperature classes and 0.5 bottom salinity classes. The proportion (p) of stations (S) in each environmental class (pS_E) was determined by dividing the number of stations within the class by the total number of stations. The proportion of stations positive for Atlantic mackerel (M) in each environmental class (pM_E) was determined by dividing the number of stations in the class with mackerel by the total number of stations with mackerel. The quotient value for the environmental class (Q_E) was then calculated as pM_E/pS_E. Quotient values greater than 1 indicate a greater number of positive mackerel stations in a class than expected based on sampling effort, and quotient values less than 1 indicate fewer positive mackerel stations than expected. The significance of Q_E, relative to the null-hypothesis value of 1, was determined using a bootstrapping technique similar to that in Bernal et al. (2007). The area of preferred habitat was then calculated for the northern Middle Atlantic Bight region (a key area historically for Atlantic mackerel) using the algorithm of Mountain (2003) and the preferred temperature and salinity ranges derived from the quotient analysis.

Relationship between Distribution and Habitat

Initial comparisons involved the examination of SST images, survey catch distribution, and bottom temperatures. Contrasting years were chosen to include cold and warm winters. Although these comparisons were qualitative, they were used to establish general patterns between Atlantic mackerel distribution and environmental variability. To establish a more formal relationship for these variables, correlation analyses were undertaken to examine the temporal trends in Atlantic mackerel distribution, area occupied, bottom temperature, and habitat volume.

Relationship to Larger-Scale Environmental Variability and Spawning Stock Biomass

Canonical correlation analysis was used to examine the relationship between various environmental variables and measures of Atlantic mackerel distribution. Canonical correlation is a multivariate procedure for assessing the relationship between two sets of variables. Seven independent variables were evaluated: AMO, North American CO_2 emissions, NAO, average winter SST, average summer SST, winter bottom temperature in the Middle Atlantic Bight, and Atlantic mackerel spawning stock biomass (Table 1; Figure 2). The extended-reconstruction SST data sets used in the analysis were obtained for the Northeast Continental Shelf region (Figure 2). Spawning stock biomass was included because the area occupied and the distribution of a fish stock often change with changes in population abundance. The dependent variables were the seven measures of Atlantic mackerel distribution (see Table 1).

Relationship to the Fishery

The distribution data for Atlantic mackerel were analyzed in relation to trends in U.S. commercial fishery landings. Spring survey distributions in 2005, 2006, and 2007, which represent cold, warm, and average years of temperature, respectively, were compared with the landings in these years to determine whether there was an environmental basis for the success or failure of the U.S. commercial fishery. Temporal trends in recreational landings from several mid-Atlantic and New England states were examined to see whether they have changed over time and whether they are associated with changes in environmental factors.

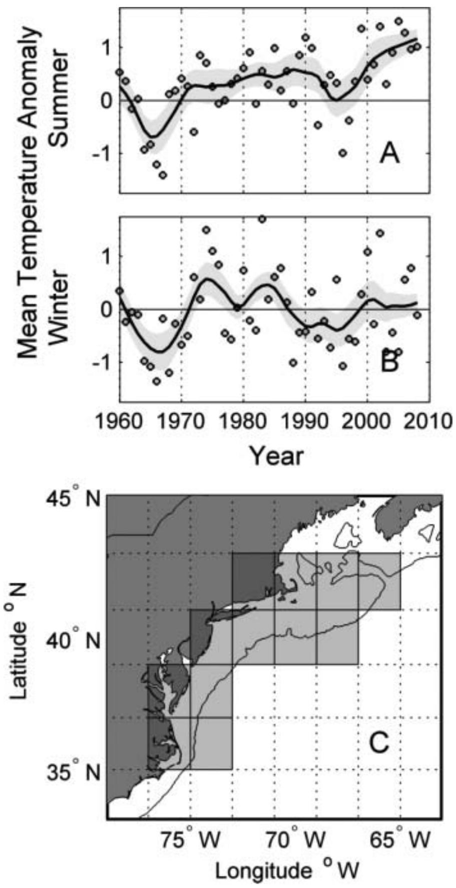

FIGURE 2. Panels **(A)** and **(B)** show mean summer and winter sea surface temperature anomalies for the Northeast U.S. Continental Shelf from 1960 to 2008 (Smith et al. 2008). The black lines represent 10-point LOWESS smoothings of the data and the gray shadings 10-point LOWESS smoothings of the standard deviation. Panel **(C)** shows the region for which the data were extracted from the extended-reconstruction sea surface temperature data set.

RESULTS

Temperature and Distribution

Mean summer SST has increased in the Northeast U.S. Continental Shelf ecosystem since the 1960s, and recent mean summer temperatures were some of the warmest in the 40 years of the spring trawl survey (Figure 2A). This is consistent with a basinwide warming trend and a recent multidecadal positive pattern in AMO. Winter temperatures, however, are near the long-term mean and have not increased since the 1960s. This has resulted in an increase in the seasonal range of temperatures on the Northeast U.S. Continental Shelf (see Friedland and Hare 2007).

Comparing Atlantic mackerel distribution and bottom temperature during a cold year (1968) and a warm year (2001) illustrates the importance of temperature to distribution. In 1968,

TABLE 1. Variables used in the canonical correlation analysis.

Variable	Symbol	Data source
Independent variables		
Atlantic Multidecadal Oscillation (anomaly)	AMO	http://www.cdc.noaa.gov/timeseries/AMO/
North American CO_2 emissions (1000's metric tons [mt])	CO_2	http://www.esrl.noaa.gov/gmd/ccgg/trends/
Middle Atlantic Bight temperature (°C)	MAB_T	http://www.nefsc.noaa.gov/epd/ocean/mainpage/
North Atlantic Oscillation (anomaly)	NAO	http://www.cgd.ucar.edu/cas/jhurrell/data/naodjfmindex.asc
Mean winter[a] sea surface temperature (anomaly)	wSST	http://dss.ucar.edu/datasets/ds277.0/docs/v3bersst.readme
Mean summer[b] sea surface temperature (anomaly)	sSST	http://dss.ucar.edu/datasets/ds277.0/docs/v3bersst.readme
Spawning stock biomass (mt)	SSB	http://www.nefsc.noaa.gov/publications/crd/crd0609/b.pdf
Dependent variables		
Area occupied (km^2)	Area	Calculated from positive tows of Atlantic mackerel using the localized convex hull method in a given year
Along-shelf location (km)	Along	Average along-shelf position of positive tows in a given year
Cross-shelf location (km)	Cross	Average cross-shelf position of positive tows in a given year
Mean depth occupied (m)	Depth	Average depth of capture for positive tows in a given year
Mean temperature occupied (°C)	Temp	Average bottom temperature for positive tows in a given year
Latitude (°N)	Lat	Average latitude for positive tows in a given year
Longitude (°W)	Long	Average longitude for positive tows in a given year

[a]December–March.
[b]June–September.

Atlantic mackerel were found offshore and far to the south off Cape Hatteras, whereas in 2001 they occurred much further north on the shelf and well out on Georges Bank (Figures 2B, 3A, B).

Comparisons of Atlantic mackerel distribution during two recent years with very different temperatures highlight the role of temperature in determining distribution. Satellite imagery from December 2004 shows that the Middle Atlantic Bight and Georges Bank had already experienced pronounced cooling (Figure 4A). Satellite images during January and February 2005 show that the shelf continued to cool, with SSTs below 5°C by February (Figures 4B, C). Bottom temperatures from the spring survey in March 2005 were mostly 4°C or lower (Figure 5A). Atlantic mackerel were distributed much further south and occupied a band of favorable temperatures (6°C or higher) offshore and east of the Delmarva (Delaware–Maryland–Virginia) peninsula and New Jersey (Figure 5A).

During December 2006 and the early part of January 2007, the Middle Atlantic Bight remained relatively warm, with SSTs of about 10°C; Georges Bank was similarly warm (Figure 6A, B). However, after the onset of a persistent arctic high over the region starting in mid-January, shelf temperatures rapidly declined and by February 2007 inshore SSTs were 5°C or less and offshore surface water temperatures had also declined (Figure 6C). Throughout the remainder of the winter season, however, this intense cooling period had only a limited impact on shelf bottom temperatures. During the 2007 spring survey, Atlantic mackerel were caught well to the north, on the shelf, and on Georges Bank at temperatures higher than 5°C (Figure 5B).

Analysis of annual along- and cross-shelf centers of distribution shows the northeastward movement of the Atlantic mackerel stock from the late 1960s through the first decade of the 21st century (Figure 7A). Although there was considerable interannual variability in the distribution of mackerel over this time period, the stock has progressively moved from the offshore mid-Atlantic region to the southern New England shelf and most recently (2007 and 2008) to Georges Bank. If the data from the late 1960s are indicative of the southernmost limit in the overwintering distribution, the change in the northern and eastern extent of the winter distribution of the stock is relatively large (Figure 7B). Decadal centers of distribution show a progressive shift from the 1960s, with repositionings of about 250 km northeastward and 50 km westward in the overwintering distribution of the stock (Figure 7B). Atlantic mackerel are now on the continental shelf more often in winter and much farther north and east of their previous winter positions.

Time series of average locations on the shelf indicate an increase in the average latitude of the Atlantic mackerel stock during 1968–2007 (Figure 8A, B). The average longitude of Atlantic mackerel exhibited no major long-term trend owing to interannual variability in the time series. Average latitude and longitude were positively correlated ($P < 0.01$) with mean winter bottom temperature (Figure 9A, B). At the annual scale, Atlantic mackerel tend to be further north and east during warm winters (Figure 8A, B). Major changes have also occurred in the mean depth and mean temperature occupied by the mackerel stock (Figure 10A, B). Mean depths have changed from more than 100 m to approximately 75 m. Mean capture temperatures

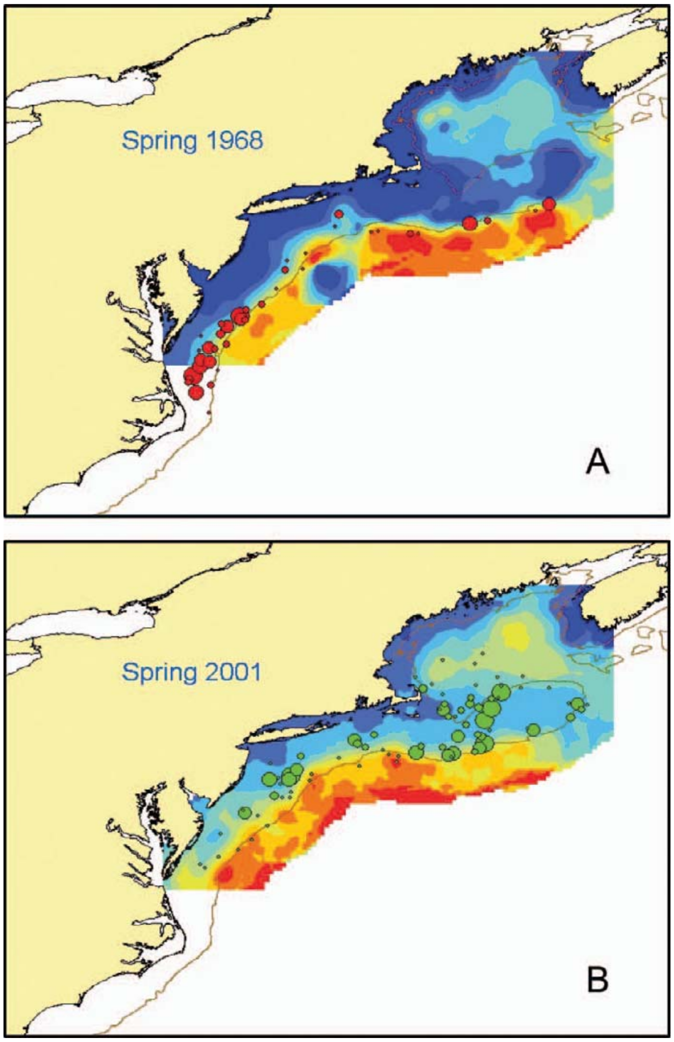

FIGURE 3. Distributions of Atlantic mackerel and bottom temperatures from Northeast Fisheries Science Center spring bottom trawl surveys during **(A)** cold (1968) and **(B)** warm (2001) periods. Fish catches are represented by dots, with the dot size being proportional to that of the catch. Isotherms range from 4°C (dark blue) to 12°C (red).

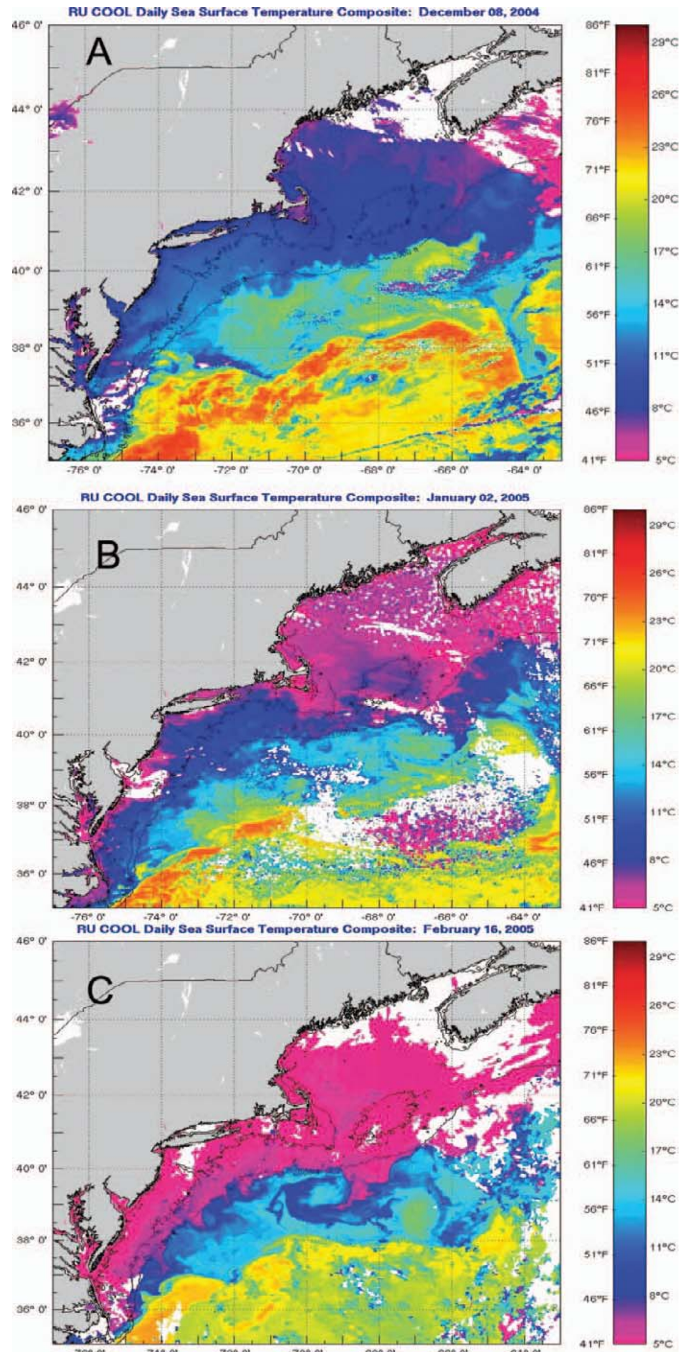

FIGURE 4. Sea surface temperatures in the study area on **(A)** December 8, 2004, **(B)** January 2, 2005, and **(C)** February 16, 2005. (Source: Rutgers University Coastal Ocean Observation Laboratory.)

have decreased from about 9°C to 6°C as Atlantic mackerel have moved onto the continental shelf.

Area Occupied and Preferred Habitat

Based on kernel density and border curve plots, the spatial distribution of Atlantic mackerel changed considerably during 1968–2007. The geography and nautical position of the mackerel stock has shifted from the southern Middle Atlantic Bight to southern New England and, most recently, to Georges Bank. Atlantic mackerel are now regularly found further to the east and north of their previous overwintering positions. The extent of the distribution has also changed since the late 1960s, with the stock now occupying a larger area than previously (Figure 11). The overwintering distribution of Atlantic mackerel is now centered at roughly 40–41°N and 68–73°W, while historically the center was at 37–40°N and 73–76°W.

Atlantic mackerel exhibited clear preferences for the temperature and salinity of the habitats they occupied. Temperatures between 5°C and 13°C and salinities between 32.5‰ and 34.5‰ had quotient values significantly higher than 1 (Figure 12A, B). Temperature preference formed a flat-topped curve with

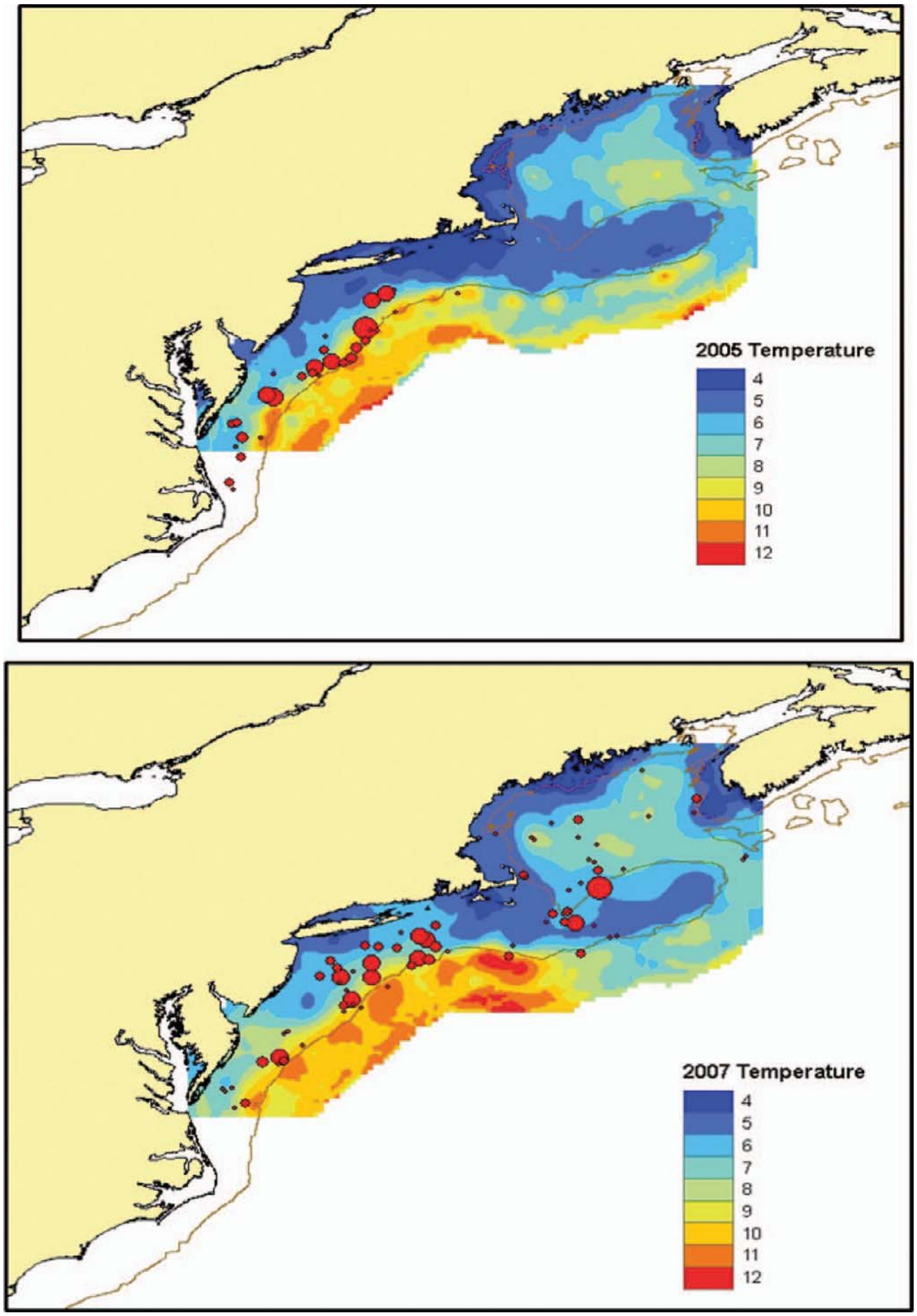

FIGURE 5. Distributions of Atlantic mackerel and bottom temperature from Northeast Fisheries Science Center spring bottom trawl survey in 2005 (top panel) and 2007 (bottom panel). See Figure 3 for additional details.

quotient values that were almost equal between 5°C and 13°C (Figure 12A). Salinity preference, however, was decidedly peaked, with quotients increasing to 33‰ and then decreasing (Figure 12B).

The area occupied by the Atlantic mackerel stock has increased over time (Figure 13A). The area of preferred habitat shows no trend over time and exhibits substantial interannual variability (Figure 13B). Nonetheless, the area occupied by the Atlantic mackerel stock is positively correlated with the availability of preferred habitat; when more preferred habitat is available, mackerel occupy a broader geographic area (Figure 13C).

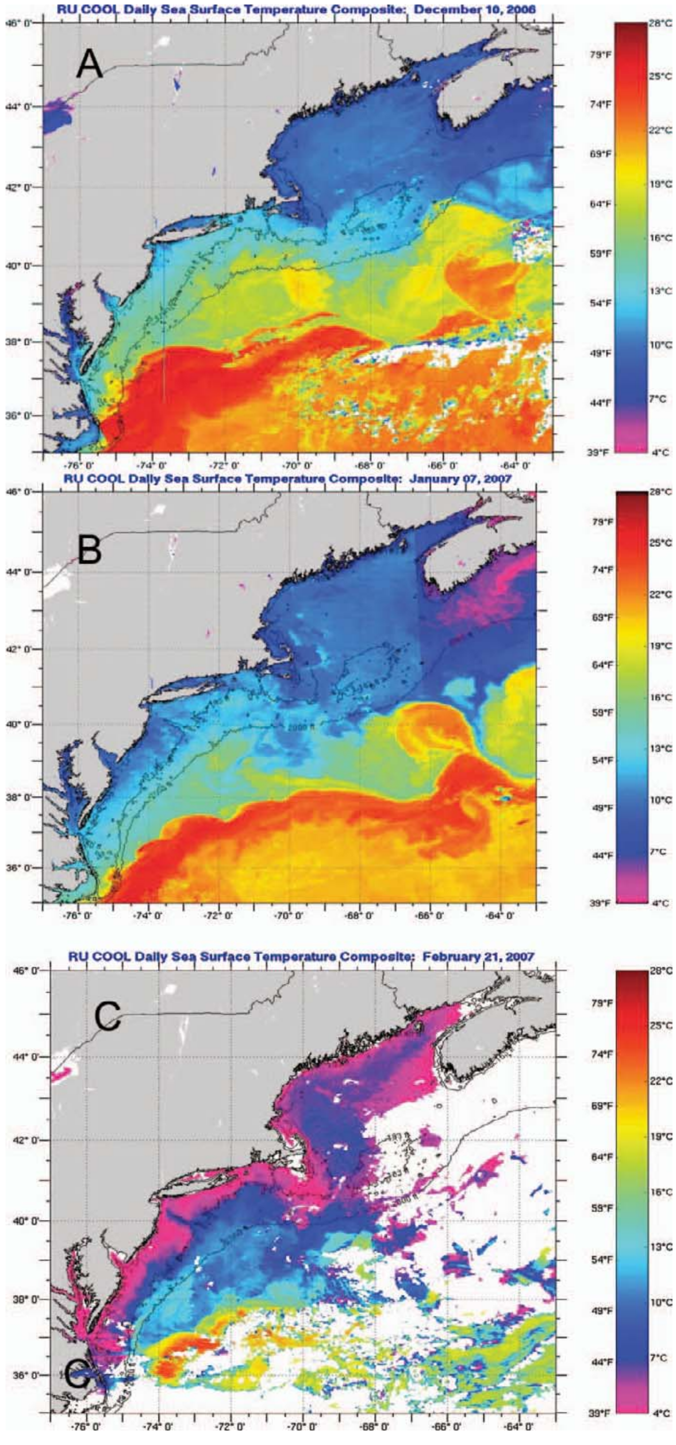

FIGURE 6. Sea surface temperatures in the study area on **(A)** December 10, 2006, **(B)** January 7, 2007, and **(C)** February 21, 2007. (Source: Rutgers University Coastal Ocean Observation Laboratory.)

Links to Larger-Scale Climate Variability

The canonical correlation analysis indicated that the distribution of Atlantic mackerel is related both to long-term trends in environmental forcing and to its interannual variability. Three canonical variates were significant (Table 2), but the percent variance explained decreased dramatically after the second canonical variate. The first two variates explained approximately 47% of the variance in the seven independent variables (AMO, NAO, CO_2, MAB_T, SSB, wSST, and sSST) and approximately 74% of the variance in five dependent variables (Area, Depth, Temp, Lat, Long). For the independent variables, canonical variate 1 was negatively related to AMO, CO_2, and SSB and positively related to MAB_T (Figure 14). Canonical variate 2 was negatively related to NAO, MAB_T, and wSST. For the dependent variables, canonical variate 1 was positively related to Depth and Temp and negatively related to Area, Lat, and Long. Canonical variate 2 was negatively related to Area, Lat, and Long.

Evaluating the overall patterns in the canonical correlation analysis, Area, Lat, and Long were similar, all being negatively correlated with canonical variates 1 and 2. The pattern exhibited by these variables was most closely related to those of NAO (and, to a lesser extent, SSB, AMO, and CO_2) with canonical variate 1 and wSST and MAB_T with canonical variate 2 (Figure 14). During positive NAO periods and warmer winter temperatures, Atlantic mackerel were found further north and east and over a greater area. Depth was negatively related to Area, Lat, and Long; as these variables increased, depth decreased. This indicates that the depth occupied by Atlantic mackerel responds not only to the interannual variability in NAO, wSST, and MAB_T but also to the long-term trends in AMO, SSB, and CO_2. Temp was separate from other dependent variables and most closely associated with patterns in AMO, SSB, and CO_2—the variables aligned with canonical variate 1. Interestingly, as AMO increased (temperatures became warmer), Atlantic mackerel were found in increasingly cooler waters. This temperature response may be related to movement into shallow waters (Depth), but Temp does not show relationships with NAO or wSST (Table 3).

Relationship to the Fishery

The trends in both commercial and recreational landings of Atlantic mackerel are not related to fishery regulations or management actions; there were no size limits, bag limits, or constraining quotas in effect during this period. Recent annual landings by the U.S. commercial fishery seem to reflect the changing distribution of the stock. Landings during the winters of 2005 and 2007 (41,000 and 25,000 metric tons, respectively), were considerably lower than in 2006 (57,000 metric tons). This was probably related to the temperature on the shelf and the distribution of the fish relative to the preferred catch sites off of New Jersey and Rhode Island. During the winters of 2005 and 2007 Atlantic mackerel were offshore and south (Figure 5), while in 2006 the stock overwintered further north along the coast of New Jersey and just south of Rhode Island. Temperatures were relatively cool along the northeastern shore during 2005 and 2007 but were significantly warmer in 2006 (Figures 2B, 5). Recreational landings of Atlantic mackerel have declined in the mid-Atlantic and southern New England regions while remaining relatively steady in the New England region during 1990–2008 (Figure 15).

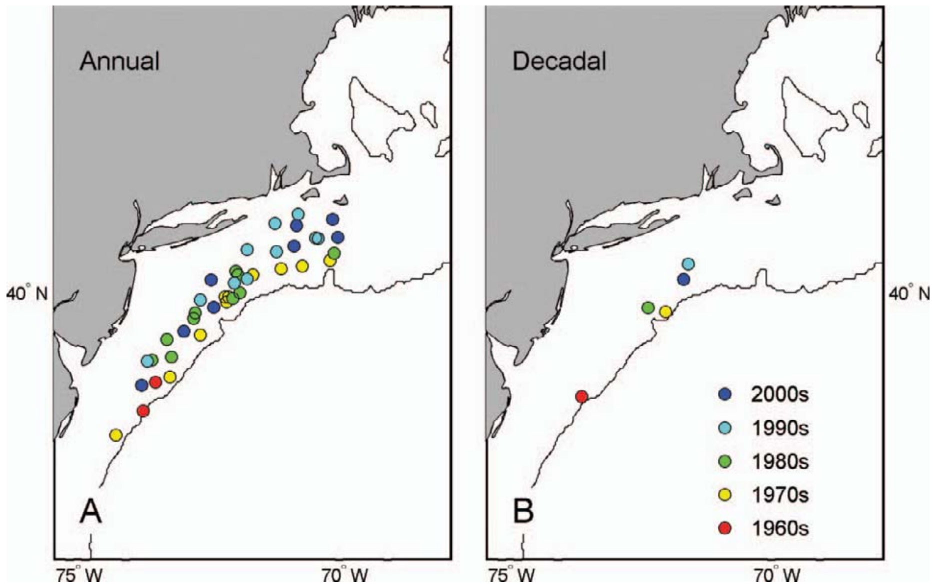

FIGURE 7. **(A)** Annual and **(B)** decadal along- and across-shelf centers of distribution of Atlantic mackerel during 1968–2007.

DISCUSSION

Climate change is already impacting many of the natural resources in the New England and mid-Atlantic regions (Frumhoff et al. 2007). Both subtle and noticeable changes in forests, agriculture, and fisheries are occurring in the region and future impacts could be substantial if the predicted warming trends ultimately occur (Frumhoff et al. 2007). Climate-driven changes in the marine environment are inevitable, and many such changes have already been noted, including declines in the biomass of commercial species, changes in fish distributions, and modifications in physical and biological oceanographic processes (Mountain and Murawski 1992; Murawski 1993; Weinberg 2005; Friedland and Hare 2007). Since Atlantic mackerel are very responsive to changes in temperature, it is natural to assume that the distribution and biology of the stock would be affected by a long-term warming trend. Other things being equal, a warmer environment is probably conducive to the growth, reproduction, and recruitment of Atlantic mackerel. Therefore, in the Northwest Atlantic both an increase in biomass and an extension in range might be expected for this species. The latter will probably occur on Georges Bank, the Scotian Shelf, and off the coast of Newfoundland. These habitat areas were previously unavailable because winter temperatures were generally too low. A change in the distribution of Atlantic mackerel may also impact other species, as these mackerel are active predators on larval fish (Garrison et al. 2000).

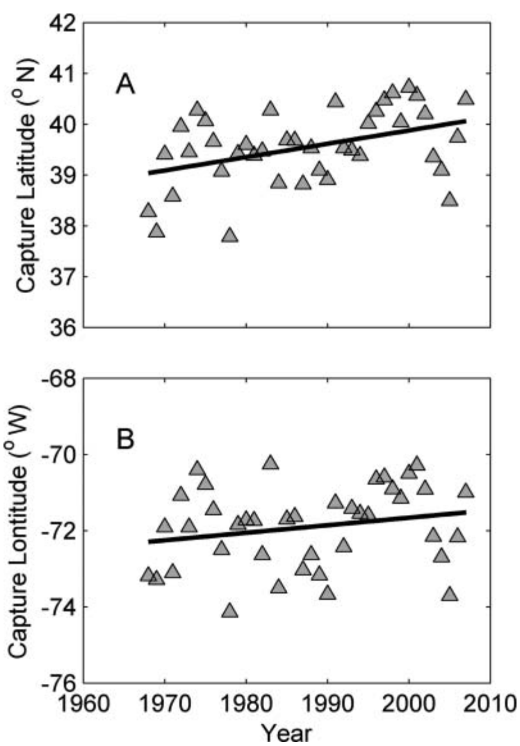

FIGURE 8. Trends in **(A)** the average latitude and **(B)** the average longitude of spring captures of Atlantic mackerel in the study area, 1968–2007. Data are shown as triangles and linear regression is marked by the solid lines.

Climate and weather patterns in New England are rapidly changing, as evidenced by long-term air and nearshore and at-sea temperature records as well as an increases in regional SSTs (Nixon et al. 2004; Friedland and Hare 2007; Maine Department of Marine Resources 2008). These changes are causing warmer summer conditions, resulting in a general warming of the ecosystem and a major change in the processes that are responsible for the cooling of the continental shelf each year. Increased global warming with a continued northerly repositioning of the jet stream during the winter will probably exacerbate this trend (Archer and Calderia 2008). The Middle Atlantic Bight experiences one of the largest annual temperature cycles

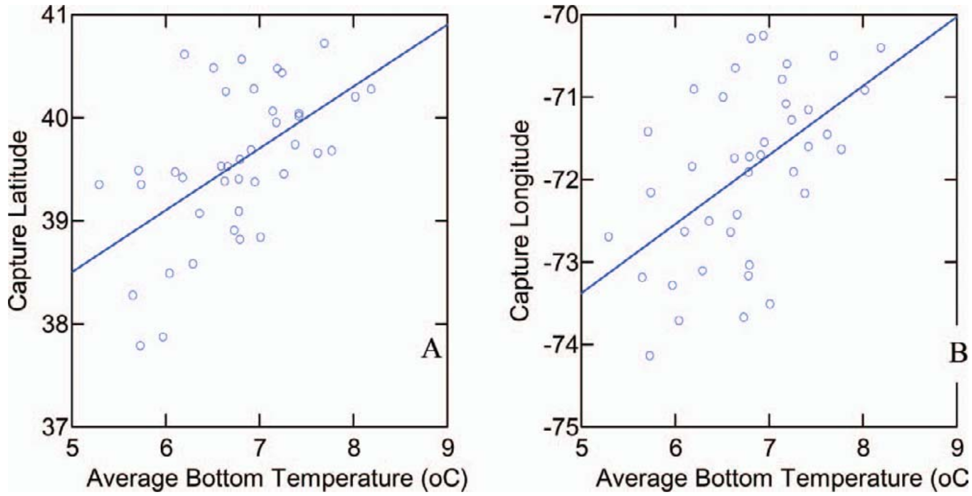

FIGURE 9. Relationships between mean bottom temperature and **(A)** the mean latitude and **(B)** the mean longitude of Atlantic mackerel distributions in spring. Both relationships were significant ($P < 0.01$). Data are shown as open circles and linear regression is marked by the solid lines.

in the Atlantic Ocean, with surface temperatures differing by more than 20°C between the summer peak and the winter low (Murawski 1993), and the annual range in SST is now expected to further increase (Friedland and Hare 2007). Since shelf cooling is a cumulative process over the winter, any retardation of the cooling process will generally produce higher temperatures on the continental shelf during winter. The distribution of Atlantic mackerel is responsive to the shelf cooling cycle, but the process is probably influenced by the geographic position of the stock in autumn as well as the timing and duration of meteorological events and the topography of the shelf. Murawski (1993) found that Atlantic mackerel were among the most sensitive species to shelf warming in the region. With each 1°C increase in average water temperature, the stock moves 0.5–0.8 degrees of latitude to the north (Murawski 1993).

Two different factors affect the distribution of Atlantic mackerel: the interannual variability in shelf temperatures and general warming (as indicated by AMO and CO_2). In cold years Atlantic mackerel are closer to Cape Hatteras, while in warmer years they are further north. With increases in preferred habitats related to long-term warming, Atlantic mackerel have shifted closer to shore and into cooler waters. Thus, the results suggesting that the distribution is related to AMO and CO_2 emissions (variables with long-term trends) as well as to bottom temperature and

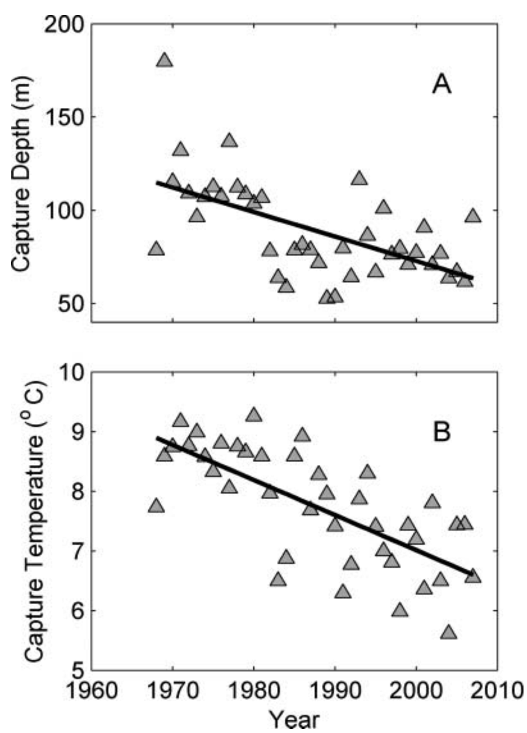

FIGURE 10. Trends in **(A)** mean depth and **(B)** mean temperature for spring captures of Atlantic mackerel in the study area, 1968–2007. Data are shown as triangles and linear regression is marked by the solid lines.

TABLE 2. Summary statistics of canonical correlation analysis for canonical variates 1–5.

	Canonical variate				
Statistic	1	2	3	4	5
Wilks' lambda	0.06	0.16	0.38	0.74	0.93
F	2.89	2.69	2.08	1.13	0.69
P	<0.001	<0.001	0.02	0.36	0.57
Canonical correlation	0.78	0.77	0.70	0.45	0.26
Approximate variance explained					
In independent variables	27%	20%	11%	9%	11%
In dependent variables	41%	33%	19%	2%	5%

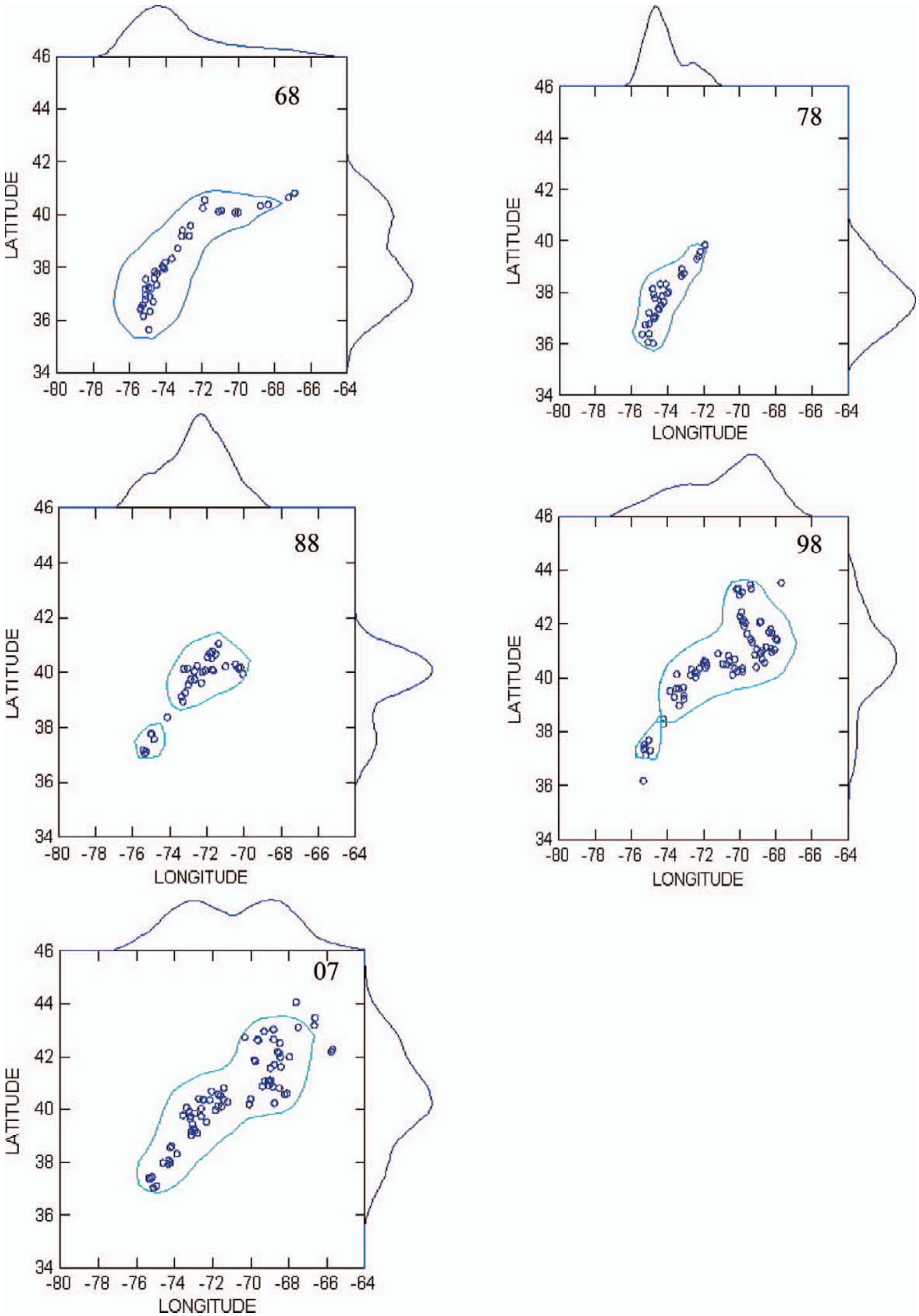

FIGURE 11. Kernel density plots with border histograms of survey positions of Atlantic mackerel catches during 1968, 1978, 1988, 1998, and 2007.

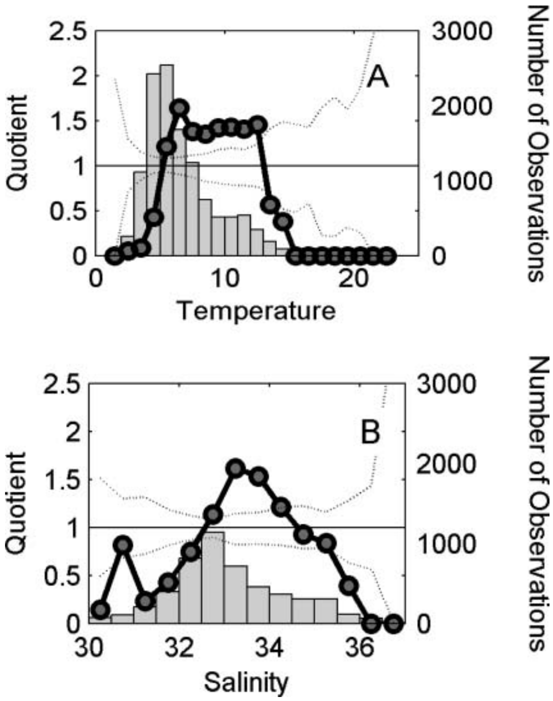

FIGURE 12. Quotient analyses for capture bottom temperature and salinity for Atlantic mackerel survey catches. Bars represent station effort; circles show quotient values; and dotted lines represent confidence intervals of H_o quotient = 1.

NAO (variables with more interannual variability) are concordant. Cross-shelf position is related to a change in temperature selectivity, with Atlantic mackerel being found in cooler waters in recent years. This is not because the species' temperature preference has changed but because much more habitat is now available at temperatures within the preferred range.

The relationships between the distribution of Atlantic mackerel and shorter- and longer-scale variability need to be further resolved. Recent analyses have indicated poleward distributional shifts in a number of species on the Northeast U.S. Continental Shelf (Nye et al. 2009). Additionally, work by Hare et al. (2010) documents shifts in the distribution and increases in the biomass of Atlantic croaker *Micropogonias undulatus*

TABLE 3. Correlation matrix for the variables included in the canonical correlation analysis (Table 1); $P < 0.05^{*}$, $P < 0.01^{**}$, $P < 0.001^{***}$.

Independent variable	Dependent variable				
	Area	Depth	Temp	Lat	Long
AMO	0.33∗	−0.33∗	−0.64∗∗∗	0.20	0.09
NAO	0.22	−0.61∗∗∗	−0.11	0.23	0.06
CO_2	0.59∗∗∗	−0.38∗	−0.56∗∗∗	0.50∗∗	0.38∗
MAB_T	0.15	0.01	0.43∗∗	0.26	0.23
SSB	0.20	−0.13	−0.35∗	0.12	0.10
sSST	0.31	−0.06	0.16	0.44∗∗	0.50∗∗
wSST	0.14	−0.26	−0.02	0.01	−0.03

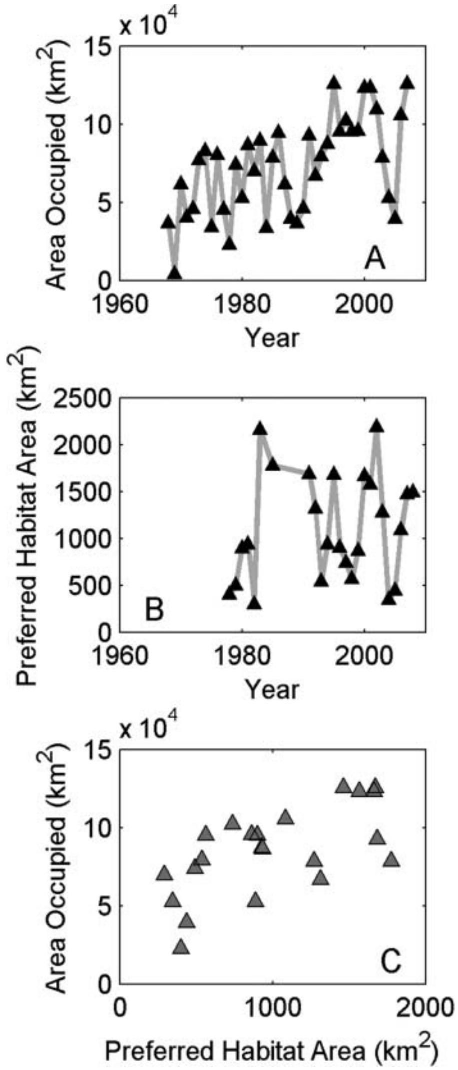

FIGURE 13. Panels **(A)** and **(B)** show the trends in the area occupied by Atlantic mackerel and their preferred habitat area over the period 1968–2007; panel **(C)** shows the relationship between these two factors.

associated with warming. These two studies, along with the current work on Atlantic mackerel, indicate that the changes in distribution are related to both interannual variability in temperature and a general warming trend. The mechanism by which the general warming trend affects seasonal migrations needs to be investigated in more detail. Friedland and Hare (2007) found that the range in seasonal temperature is increasing in the Northeast U.S. Continental Shelf ecosystem. Summers are becoming warmer, while winters are remaining the same or becoming somewhat cooler (Figure 2). An important issue is the impact of this increased seasonal temperature range on migrating species. Does greater northward migration in the spring result in less southward migration in the fall? Are annual migrations cumulative, resulting in a greater shift in distribution than predicted by winter temperatures alone? Answering these questions will be

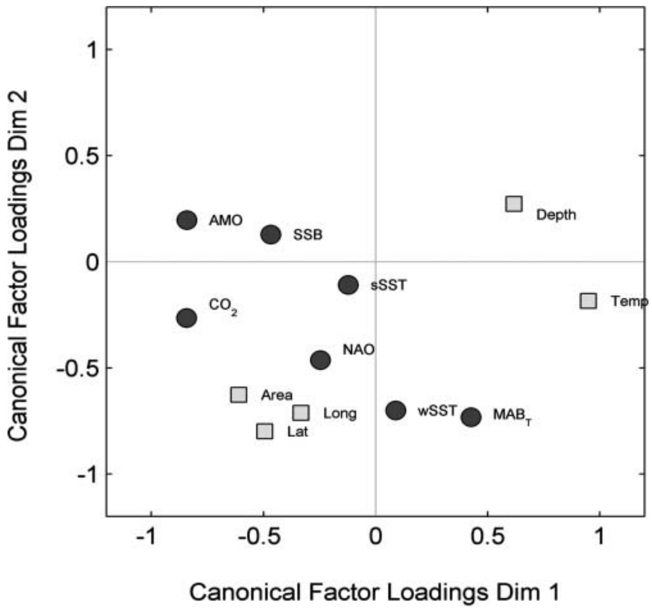

FIGURE 14. Results of canonical correlation analysis of environmental and location variables (see Table 1) for Atlantic mackerel.

important to understanding the response of migratory species to climate change.

Our findings also suggest that both the commercial and recreational Atlantic mackerel fisheries in the United States will probably be faced with more variable resource conditions in the future in terms of the winter distribution of the stock. Because the shelf is warming, more thermally favorable habitat will be available to Atlantic mackerel in the future, increasing the areal distribution of the stock. This could pose a challenge to the commercial fishery in locating these fish without a great deal of offshore searching. The recreational fishery along the mid-Atlantic coast will also probably continue to decline as the availability of fish shifts to the north. As the continental shelf continues to become warmer, these fishery changes will occur irrespective of the current abundance of the Northwest Atlantic mackerel stock (Overholtz et al. 1991).

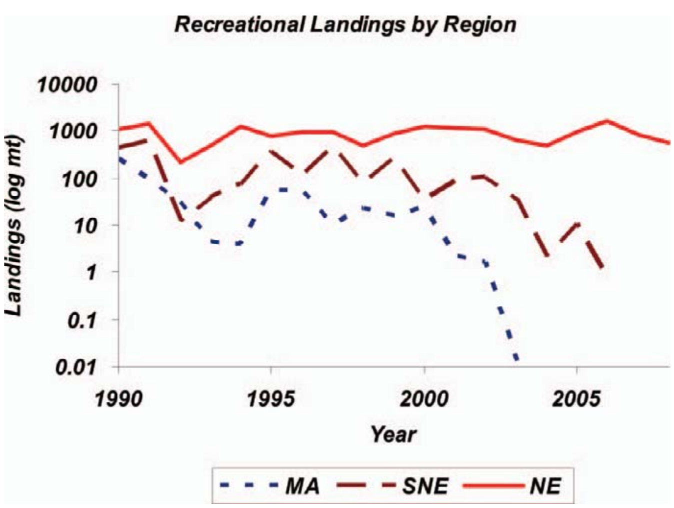

FIGURE 15. Recreational landings ($\log_e$ transformed metric tons [mt]) of Atlantic mackerel by region during 1990–2008; MA = mid-Atlantic, SNE = Southern New England, and NE = New England.

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