Meta-analysis of changing spatial distribution of Northwest Atlantic fish stocks in relation to temperature and stock structure

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Abstract

Ecosystem-based approaches to fisheries management require that we consider a broader set of considerations in how we manage our natural resources. This includes not only incorporating changing spatial distribution into assessments at the stock level, but also understanding changes in spatial characteristics of multiple species in relation to each other. We used several techniques to analyze trends in the mean centroid of abundance, mean depth, and population density for 36 fish stocks using the NMFS trawl survey data from 1968 to 2007. We identified several trends that are consistent with a response to the observed recent warming of Northwest Atlantic water temperatures. The center of abundance of numerous fish and invertebrate species has shifted to more northern latitudes in recent years. The range of some southern species has expanded while that of some northern species has become more restricted. Some species exhibit inshore/offshore shifts and have changed depth distribution. In contrast to these trends in distribution, some species such as winter skate and spiny dogfish appear to have shifted their distribution to more southerly waters. Depending on the stock, changes in distribution may be correlated with concomitant changes in temperature, abundance and/or size structure over time. We examine the management consequences of such movements in more detail for representative species.

Introduction

Temperature is a controlling factor that acts upon individual organisms and structures ecosystems. Physiological processes of poikilotherms such as fish are functions of temperature (Fry 1971). At the level of ecosystem, warming in the marine environment stratifies the water column and causes seasonal phytoplankton bloom (Mann and Lazier 1996). Recently, water temperatures both globally (Levitus et al. 2000; Knutson et al. 2007; Lozier et al. 2008) and on the continental shelf of the Northwest Atlantic have warmed (Friedland and Hare 2007). Whether or not this warming trend continues as it likely might (IPCC 2007), it is important to understand the distributional responses of individual species to changes in temperature.

Many recent studies have detected ecological impacts of climate change (Walther et al. 2002; Parmesan and Yohe 2003; Rosenzweig et al. 2008), but in many situations it remains difficult to disentangle the effects of climate change with that of other anthropogenic influences. This fact is especially true of exploited species that may exhibit responses consistent with both climate-induced and harvest-induced hypotheses. In reality, both processes act simultaneously on populations and ecosystems. Therefore, it is important not only to document temporal changes in species ecology, but also the relative importance of their causes, and the synergistic effects of multiple stressors.

Many have hypothesized that the first response of organisms to climate change is a shift in distribution in response to warming temperatures (Frank et al. 1990; Shuter and Post 1990; Perry et al. 2005). A distributional shift in marine organisms may be reflected in a change in the center of abundance of the stock, an expansion or contraction of the species range, or changes in depth (for marine species) and altitude (for terrestrial species). Reponses of marine fishes consistent with warming water temperatures would be a poleward shift in mean center of abundance and an increase in mean depth of occurrence. In the northwest Atlantic the ranges of "northern" species may be limited by warming waters, while "southern" species might expand their range.

The importance of temperature regime and climate on fish stocks, especially those that are economically important has been studied extensively on relatively short temporal and spatial scales in the Northwest Atlantic (Drinkwater et al. 2003; Hare and Able 2007) and several studies have hypothesized how long-term anthropogenic-induced climate change will affect fish stocks in the Northwest Atlantic based on these previous studies (Frank et al. 1990; Murawski 1993). Frank (1990) hypothesized that distributional changes would be most pronounced in Canadian fish stocks at the southern extent of their range based on historical reports of distributional changes due to warming in the 1950s (Taylor et al. 1957). Murawski (1993) showed that changes in mean and maximum latitude could be predicted by abundance and/or temperature for several species. He identified groups of species that had highly variable annual distribution and predicted that they would exhibit changes in distribution relative to temperature changes. He also identified sedentary species that showed a more narrow range of temperatures, which he predicted would exhibit less movement in a warming scenario. Since Murawski's (1993) work in the Northwest Atlantic, we have acquired 14 more years of data and experienced a consistently warm period in the last 10 years. The 10 warmest summers on record have been in the last eleven years (Smith and Reynolds 2007).

The purpose of this paper was to examine the relationship between spatial distribution of Northwest Atlantic fish to changes in temperature regime and abundance using a 40-year time series of data. We hypothesize that warming water temperatures would induce at least one of the following responses in the 36 fish stocks examined:

- 1) A poleward shift in the mean center of abundance
- 2) An increase in mean depth of occurrence

- 3) Range expansion or contraction
- No movement consistent with warming, but an increase in the temperature of occurrence

We also hypothesize that these responses would be mediated by the changes in abundance of each stocks, many of which have experienced dramatic changes in abundance in relation to fishing.

Methods

Several metrics were used to detect and summarize changes in spatial distribution of 36 fish stocks using the NEFSC spring trawl survey that has occurred on the Northwest Atlantic continental shelf since 1968 (Figure 1). The data collection and sample processing methods are described in Azarovitz (1981), but a brief description is given here. The survey employs a stratified random design with stations allocated proportionally to stratum area. A 12-mm mesh codend liner is used to retain smaller bodied and juvenile fish. All fish for each species were counted and weighed and a subsample measured for length composition.

We chose 36 stocks to investigate because these species were caught in every year of the spring survey and they were consistently caught in relatively high numbers. Those species that are currently assessed as separate stocks were analyzed separately in this analysis as well. Red hake and silver hake consist of a Northern (N) and Southern (S) stock, the northern stock primarily residing in the Gulf of Maine (GOM) and the southern stock ranging from Southern New England (SNE) and George's Bank (GB). Yellowtail flounder and winter flounder have similar stock structure to these hakes. However, stock assessments evaluate the GOM, GB and SNE stocks separately. We have combined the GB and SNE stocks in this analysis and analyzed the "southern" stock (S) separately from the GOM or "northern" (N) stock. Atlantic cod and haddock both have a GOM stock and a GB stock and were analyzed accordingly. The remaining species were analyzed at the species level.

For ease of illustration, the 5-year biomass-weighted center of abundance for each of 9 time periods were shown for each stock. However, for statistical analysis, mean latitude, longitude, temperature and depth of occurrence were calculated for each year for each stock with the general formula:

$$X_{j} = \frac{\sum_{i=1}^{n} w_{i} X_{ij}}{\sum w_{i}}$$

where *X* is the parameter of interest (latitude, longitude, temperature or depth), *j* is the survey year, w_i is the biomass (kg) for each station *i*. Only strata that were consistently sampled over the spring survey time series were used because in some years additional strata were added to increase spatial coverage. Specifically, strata south of Cape Hatteras and in the Western Scotian Shelf were omitted. To calculate mean annual relative abundance, biomass tow⁻¹ was summed for each strata and then biomass was weighted by the number of tows within a stratum and stratum area.

Because stocks along the Northeast coast are restricted by the geography of the coastline, simple north-south movement is not possible. Rather, most stocks inhabiting this area of the continental shelf must move in a northwesterly direction if they were to move "poleward" in response to warming water temperatures. Therefore, we calculated

the distance of the mean center of abundance from a fixed point to get a better idea of the magnitude of distance moved by each stock. To do this, we calculated the distance between each center of abundance from 35°N latitude and 76°W longitude, which roughly corresponds to Cape Hatteras, NC and the southernmost extent of the NEFSC trawl survey (Figure 1). We used the great circle distance formula to calculate the distance (*d*) from this point to the center of abundance in each year for each stock:

$$d = A\cos(\cos(90 - 35)) \bullet \cos((90 - mlat)) + \sin((90 - 35)) \bullet \sin((90 - mlat) * \cos((-75 - mlon)))$$

where *mlat* is the mean latitude at the center of abundance and *mlon* is the mean longitude at the center of abundance. All latitudes and longitudes are converted to radians. The value of *d*, hereafter called distance, was converted to kilometers by assuming the radius of the earth is 6367 km.

Mean annual bottom temperature (BT) at the time of each survey was estimated from bottom temperature measurement taken at each station during the spring survey. Additional measures of temperature on the continental shelf were estimated using the extended reconstructed sea surface temperature (ERSST version 3) dataset. This dataset is based on the SST compilation of the International Comprehensive Ocean-Atmospheric Data Set and uses interpolation procedures to reconstruct SST in regions with sparse data (Smith and Reynolds 2004). While the dataset extends back to 1854, we used values from 1968-2007 corresponding to the timing of the NEFSC trawl survey where the 95% confidence uncertainty of ERSST data is 0.1°C or less (Smith and Reynolds 2004). The spatial resolution of the data is 2° longitude by 2° latitude and we used only grids that overlapped spatially with our survey area to calculate mean annual ERSST, hereafter abbreviated SST. Mean SST and the severity of winter (FEB) characterized by the mean SST in February as described by Friedland and Hare (2007) were used as explanatory variables in statistical analysis.

We used two indices of longer term climatological conditions that affect the area of the NEFSC survey, the North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO). The mean winter NAO index was used because most of the variance in the NAO occurs in the winter months and is the only teleconnection pattern that is evident throughout the year in the northern hemisphere (Hurrell et al. 2003). The NAO index we used is calculated as the difference between surface pressure of the subtropical (Azores) high and the Subpolar (Iceland) low. While variability in the NAO has been associated with changes in precipitation, sea surface temperature, sea ice formation and thus, with ecosystem change (Drinkwater et al. 2003; Greene et al. 2003) and fish recruitment (O'Brien et al. 2000; Reid et al. 2001; Lindley et al. 2003), its effects are stronger at high latitudes of the northern hemisphere (Hurrell et al. 2003).

Therefore we also used the AMO, a 20-40-year cycle in the Atlantic thought to be driven by ocean thermohaline circulation (Sutton et al., 2008). The AMO is based on the detrended Kaplan SST dataset (5 x 5 degree latitude x longitude grids) from $0-70^{\circ}$ N. The linear effects of anthropogenic climate change are removed from this time series in order to represent the natural variation in sea surface temperatures that has been observed over the last 150 years and has been correlated with natural fluctuations that have occurred over the last millennium (Gray et al. 2004; Sutton and Hudson 2005). The AMO can camouflage or exacerbate the effects of human induced warming.

To statistically test for changes in spatial distribution measures over time we conducted linear regressions incorporating the appropriate autocorrelation structure for each stock. We did a separate linear regression for each stock and for each distributional measure, mean distance, mean depth, mean temperature, and area occupied, and maximum latitude. ArcGIS software was used to create smoothed maps in five-year time blocks of several representative species using the inverse distance weighting (IDW) method. For each species, raster size was maintained at a constant level and the smoothing power, p, was equal to 2. The spatial pattern of mean annual bottom temperature for each 5 year time block was depicted using IDW in ArcGIS, in the same manner that species distributions were smoothed.

Because there are many possible distributional responses of fishes to changes in both temperature regime and population abundance, we used canonical correlation analysis (CanCorr) to examine the linear relationship between multiple response variables and multiple explanatory variables in each species. CanCorr is a multivariate generalization of univariate correlation analysis which relates two sets of variables. A pair of canonical variates is generated from each set of original variables, where each canonical variate is a linear combination of the original variables. The explanatory variables included mean distance, mean depth, mean temperature, minimum latitude, maximum latitude, and area occupied. The explanatory variables included SST, AMO, NAO, BT, FEB and relative biomass (BIOMASS). BIOMASS was log transformed, log(x+1).

Results

There were clear northward shifts consistent with warming in many fish stocks of the Northwest Atlantic (Figure 2). While these figures show the five year averages in mean latitude and longitude of abundance, linear regression of annual centroids of abundance indicated a statistically significant northward shift in 12 of the 36 stocks (Table 1). Stocks with a statistically significant poleward movement include alewife, American shad, silver hake-S, Atlantic cod-GB, white hake, red hake-N, red hake-S, spotted hake, halibut, yellowtail flounder-S, blackbelly rosefish, longhorn sculpin. Stocks that indicate some poleward movement, but that were not statistically significant include fourspot flounder, summer flounder, goosefish, and ocean pout. The center of abundance for some species appeared to shift southward, which would be inconsistent with a response to warming. These species include three elasmobranchs (spiny dogfish, winter skate, little skate) and four stocks found primarily in the GOM (Atlantic cod-GOM, American plaice, yellowtail flounder-N, and winter flounder-N). Haddock-GB also showed a southward movement in its center of abundance.

The range expansion or contraction of these species is complicated by the fact that many species occur outside the area of the survey so changes in area occupied, maximum latitude and minimum latitude were all used as evidence of changes in range. An increase in the area occupied is indicative of a range expansion and was detected in eight stocks: winter skate, little skate, American shad, silver hake-N, red hake-N, spotted hake, summer flounder, and fourspot flounder (Table 1). Strong evidence of range expansion includes statistically significant increase in area occupied in addition to an increase in maximum latitude and a decrease in minimum latitude. Little skate, and spotted hake fit these criteria. The range expansions (area occupied) of largest magnitude occurred in winter skate and American shad. The minimum latitude of winter skate decreased, further illustrating its southward range expansion. American shad showed a northward range expansion as illustrated by the increase in its maximum latitude along with an increase in area occupied (Table 1). Several species indicated northward movement concomitant with range expansion as exhibited by a decrease in their minimum latitude such as red hake-S, halibut, Yellowtail flounder-S, and longhorn sculpin. Red hake-S experienced a dramatic poleward movement along with both an increase in maximum latitude and decrease in minimum latitude.

Fifteen species experienced range contraction, the most dramatic of which occurred in Atlantic cod-GB and longhorn sculpin where area occupied decreased at a rate of 13.21 and 8.45 km y⁻¹ respectively (Table 1). Strong evidence of range contraction includes statistically significant decreases in the area occupied, a decrease in maximum latitude, and an increase in minimum latitude. Acadian redfish, Atlantic wolfish, and cusk fit these criteria. Six fish exhibiting range contraction also exhibited northward movement and include silver hake-S, Atlantic cod-GB, white hake, red hake-S, plaice, yellowtail flounder-S, and longhorn sculpin. Pollock, sea raven, ocean pout, and goosefish also experienced range contraction as indicated by a decrease in area occupied.

Increases in mean depth of occurrence were detected for nine species, four of which also exhibited northward shifts; yellowtail flounder-S, Atlantic cod-GB, white hake and halibut (Figure 3, Table 1). The other four of those nine depth-shifting species (pollock, cusk, ocean pout and goosefish) are "deepwater" fishes, generally found in the

GOM that showed no significant poleward shift in distribution. American plaice shifted distribution from the western edge of GB to the GOM area which is reflected in the statistically significant increase in mean depth of occurrence. There were several species that were found at increasingly deeper stations, but that did not produce statistically significant linear increases in depth. Alewife, American shad, silver hake-S, red hake-N, red hake-S, and longhorn sculpin may have shifted to deeper water in more recent years, but this was not be detected by linear regression (Figure 3). Five species were found at increasingly shallow depths including Atlantic mackerel, silver hake-N, winter flounder-N, yellowtail flounder-N and little skate.

Only eight of the 36 stocks examined showed a change in mean temperature over time. The three stocks that exhibited an increase in mean temperature of occurrence showed no significant northward movement over time (Atlantic herring, Pollock, and cusk). However, pollock and cusk experienced range contraction and a change in depth. Five species experienced statistically significant decreases in mean temperature of occurrence, four of which exhibited a poleward shift in mean center of abundance (blackbelly rosefish, American shad, alewife and spotted hake). Spotted hake, one of the more southerly species examined, shifted its distribution north, expanded both its range, increased its maximum latitude, and its mean temperature of occurrence was lower presumably because of this strong northerly distributional shift and range expansion.

Sixteen of the 36 stocks displayed statistically significant changes consistent with warming. Another seven stocks showed weak signs of distributional changes. Only three stocks, Haddock-GOM, winter flounder-S, and windowpane, exhibited no statistically significant changes in any of the six spatial distribution metrics examined. A striking

aspect of these results is the difference in response between stocks located along the SNE and GB as compared to those that are restricted to the GOM even within the same species. To illustrate this, red hake was used as an example because this species occurs both in the GOM (red hake-N) and SNE-GB (red hake-S) region. The distribution of red hake-S has changed quite dramatically in comparison to the red hake-N stock as shown in 5-year time blocks (Figure 4). From the 1970s and into the late 1980s, there are many high density areas of red hake in both the northern and southern stocks. There were even high densities of fish located south of Long Island sound in the Mid-Atlantic Bight region. The statistical findings that the center of abundance of the southern red hake stock shifted while its range contracted are corroborated by these maps. These maps also support the finding that the northern red hake stock was found more frequently in the northern part of the GOM starting in the 1990s and exhibited a northward shift of much smaller magnitude than red hake. The distributional changes of red hake reflect the movements of species with similar stock structure, but also species that are traditionally found in SNE and the Mid-Atlantic bight as compared to those that are restricted to the GOM.

The movements of red hake mirror the spatial pattern in warming observed along the Northwest Atlantic coast as shown analogously in 5-year time blocks (Figure 5). The most obvious result of this warming trend is a lack of cold-water refuges starting in 1995. Note the lack of habitat between $0-4^{\circ}$ C from 1995-2007 especially as compared to the period from 1981-1990. The spatial patterns of temperature reflect the temporal trends in both ERSST and AMO, both of which have consistent positive anomalies in the last 10-12 years (Figure 6) Species range or area occupied in these fish stocks is strongly related to the abundance (Figure 7a). However, the relationship between area occupied and abundance varies among taxonomic groups. While there is a general increase in area occupied with an increase in the abundance of most groups (Figure 7a,b,d,e,f), the area occupied appears to be inversely related to abundance in deepwater fishes (Figure 7c).

CanCorr analysis indicated a significant linear relationship between species distributional measures (response variables) with explanatory factors for all species (Table 2). The first canonical variates were significant in all stocks (p<0.05) except for blackbelly rosefish (p=0.07). The first two canonical variates were significant in 24 of the 36 stocks (p<0.10) and cumulatively explained at least 77% of the variability. Biplots of the loadings (correlations between the variables and their respective canonical variates) are shown only for these stocks (Figure 8). We hypothesized that CanCorr would separate out those species that changed distribution in response to warming water temperatures from those that changed distribution due to changes in abundance. If a species changed distribution as a response to warming, distributional metrics such as distance, depth, and temperature of occurrence should have loadings similar to that of temperature variables (BT, NAO, SST, FEB, and AMO). Conversely, if a species changed distribution in response to changes in relative biomass (BIOMASS) distributional changes would most likely be a result of changes in area occupied and the loadings between these variables would be similar. The advantage of CanCorr is that correlations between multiple response and multiple explanatory variables can be examined, but in addition correlations within the response and explanatory variables also become clear.

Temperature variables (SST, BT, FEB, and NAO) were often grouped together as might be expected, but the AMO was not as highly correlated with these explanatory variables (Figure 8). Several species had similar loadings for distance as compared to SST, BT, FEB, and NAO and include fourspot flounder, mackerel, herring, and summer flounder. The similarities in loadings indicate that when temperatures were high the distance that these species moved poleward increased. In addition, several species had very similar loadings between distance and AMO. The loadings between these two variables were very similar in cod-GB, red hake-S, halibut, yellowtail flounder-S, and goosefish, but weakly grouped together in haddock-GOM. The stocks had loadings indicating poleward movement due to warming with BIOMASS loaded orthogonally.

BIOMASS was loaded in a very similar manner as area for 15 of the 24 stocks with significant 1st and 2nd canonical axis, which is as expected given the strong relationships we quantified between area occupied and abundance for the species in this study (Figure 7,8). The loadings between BIOMASS and area were almost identical for Atlantic cod-GB, but were more weakly associated in winter skate, pollock, and ocean pout. In many cases BIOMASS was opposite in sign to AMO, indicating that for these species abundance decreased as the AMO index increased over the time series. In these instances, it is easier to tease out the relationship between abundance, temperature, and distribution. For instance, in thorny skate, Atlantic cod-GB, red hake-S, halibut, yellowtail flounder-S, and goosefish, AMO and BIOMASS have opposite loadings as do distance and area. The results of the CanCorr in these stocks support our hypothesis that movement in the center of abundance is caused by warming and changes in biomass are reflected in area occupied. Another important result is that a decline in abundance of these species, all of which are at the southern extent of their range in this region, might be correlated with positive phases of the AMO.

Conversely, AMO was loaded similarly to BIOMASS for spiny dogfish, little skate, spotted hake, Atlantic herring, summer flounder, yellowtail flounder-N, fourspot flounder, and searaven (Figure 8). Many of these species are more "southerly" distributed species with the exception of yellowtail flounder-N, little skate, and sea raven, indicating that perhaps an increase in abundance of these species might be expected in warm phases of the AMO. In three cases, BIOMASS was loaded similarly to distance, the opposite of our expectation. In two of these cases, spotted hake and summer flounder, the AMO was also associated with BIOMASS, distance, and area. This suggests that spotted hake and summer flounder are increasing in abundance, shifting their distribution northward, and increasing their range in a warm AMO environment. In the third instance where BIOMASS and distance load similarly, American plaice has a negative response in several metrics as the AMO has increased. Again, BIOMASS, area, and distance are all closely associated, but the AMO is loaded in the opposite direction, suggesting that American plaice is a species whose abundance has decreased, range decreased, and movement into the GOM are negative consequences caused by a warming phase of the AMO.

The loading patterns of cusk and pollock are remarkably similar to each other (Figure 8). Depth and AMO loaded very positively with the second axis supporting our findings that these two species had changed their depth distribution in response to a warming temperature regime whereas loadings with distance are low. Depth is often loaded on the same axis, reflecting the fact that deeper water are found in the northern

part of the continental shelf. Those species that move southward often show a decrease in depth of occurrence (little skate and spiny dogfish). Temperature of occurrence was usually grouped with temperature explanatory variables (SST, BT, FEB, NAO), indicating that a change in temperature of occurrence is probably the least sensitive measure of distributional change.

Discussion

We demonstrate clear changes in spatial distribution of majority of the 36 fish stocks that we examined in the Northwest Atlantic, and statistically significant changes that are consistent with recent warming in 16 of these stocks. Although distributional changes consistent with warming have been reported for many terrestrial systems (Parmesan and Yohe 2003; Rosenzweig et al. 2008 for reviews), there are fewer such long-term studies in marine fishes (but see (Southward et al. 1995; Perry et al. 2005; Holbrook et al. Nov., 1997). Responses were most pronounced in species whose center of abundance was historically in SNE and MAB, as illustrated by the comparison between the southern and northern stocks of red hake. The center of abundance for most of the southern stocks, as illustrated by red hake moved to the northwest over the time series. Northern stocks, particularly those traditionally found in the GOM, including the northern red hake stock moved poleward only slightly. Thus, the bathymetry and geography of the survey area was important in detecting changes in spatial distribution. Stocks that were restricted to the GOM did not exhibit northward shifts in center of abundance, but many exhibited increases in mean depth and temperature of occurrence, as was the case in cusk and pollock.

Murawski (1993) hypothesized that more "migratory species" would be most sensitive to warming while "shallow-water sedentary" fishes would show less dramatic changes in distribution. However, we have shown that distributional changes were evident for species across many families, life histories, and habitat preference. Murawski termed yellowtail flounder, winter flounder, windowpane, and longhorn sculpin as "shallow-water sedentary", but even these species showed northwesterly movements. Summer flounder was identified as a "warm-water migratory" fish and was predicted to alter abundance readily in response to warming, but in this analysis did not show a strong northward movement in centroid of abundance. However, there was some evidence that the range of summer flounder expanded over time, that its abundance increased, and perhaps a slight poleward movement based on the CanCorr loadings. Murawski also identified a deep-water sedentary group that was in general restricted to the Gulf of Maine. While temperatures in the deep waters of the Gulf of Maine may not experience as large fluctuations in temperature, we did see range contraction in many of these species (white hake, Acadian redfish, Pollock, and American plaice). The presence of distributional changes even in species for which a response was not expected heightens concerns over how these species will respond if warming trends continue. Our analysis supports Murawski's contention that deepwater sedentary fish may not adjust their spatial distribution in response to warming and may experience greater changes in growth, reproduction, and recruitment than those fish that have shifted their distribution.

Gabriel (1992) identified remarkably consistent fish communities that persisted over time along the Northwest Atlantic coast. However, the boundaries of southern MidAtlantic Bight and Georges Bank species assemblages were the most variable and

seem to be modified by annual differences in temperature. Our analysis supports these finding and while we only analyzed 36 stocks we suspect a similar analysis of the finfish community would indicate a northward shift in the southern boundary of the MidAtlantic Bight and Georges Bank fish community.

CanCorr effectively separated out the effects of warming from fishing pressure for most of the stocks we examined. The overwhelming response of these stocks to warming was a poleward shift in centroid of abundance and the response to increases in biomass was a range expansion. CanCorr analysis also emphasized that distributional responses involve the complex interaction between abundance and environmental forcing. Consistent with hypothesized spatial shifts induced by warming (Hughes 2000; Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003), many southern species have shifted their range north, but also experienced more favorable conditions for growth and recruitment resulting in abundance increases and range expansion (Hare and Able 2007). More northerly species made slight shifts north, their range contracted, or were found at increasingly greater depths.

We suspect that the intense fishing pressure may intensify the effects of climate change (Hsieh et al. 2008), especially at the southern extent of the species range. Commercially important species such as red hake, Atlantic cod, yellowtail flounder, alewife and American shad have historically experienced intense fishing pressure and all of these stocks are at record low levels, particularly in the southern extent of their range. For example, in Chesapeake Bay, harvest of American shad has been prohibited since 1994, but shad population is still low in this region and unable to support viable fisheries. A similar lack of recovery is reported for alewife and yellowtail flounder-S. We

hypothesize that these species have failed to recover in the southern extent of their range in part because of warming along the continental shelf and that temperature and/or changes in distribution should be incorporated into stock assessments and management scenarios. By incorporating a broader set of considerations into stock assessments by using an index of warming such as the AMO index or similar, we might be able to better predict stock-recruitment relationships, explain the lack of recovery and provide better management advice.

We did not examine many of the more southerly species caught in the NEFSC survey, but the results of red hake, southern flounder, and fourspot flounder suggest that similar results would be apparent for species with similar distributions. Still, distributional shifts may be clouded by changes in abundance. We observed no distributional shifts in haddock-GOM and a southward movement in the GB haddock stock. The abundance of haddock has increased dramatically since its lowest abundance in the 1990s. Therefore, shifts in the center of abundance by this stock might be masked by its dramatic fluctuations in abundance. Similarly, we saw southward shifts in center of abundance with range expansion in winter skate, spiny dogfish, and to a lesser extent little skate. All three of these species experienced dramatic increases in abundance in the 1990s.

We found a tight relationship between abundance (number of individuals) and the area occupied by the species for most functional groups of fish that we examined. This relationship is well documented in the ecological literature (Brown 1984; MacCall 1990). These tight relationships are not surprising. However, deepwater fish had an opposite trend in the abundance-area relationship indicating perhaps some sampling difference in

these species as compared to the other species in the survey. The CanCorr analysis also supported our findings that changes in area occupied or range is most influenced by abundance and that shifts in the center of abundance are responses to changes in temperature regime.

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Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416: 389-395 Table 1: Summary of trends in time series of distributional responses. Northward and southward movement was indicated by a statistically significant (P<0.05) positive or negative slope respectively of mean latitude regressed on year after incorporation of temporal autocorrelation structure. Range contraction was indicated by a change in the latitudinal and longitudinal range and/or a decrease in the distance between 1st and 3rd guartiles. Increase in depth was indicated by a change in mean depth over time.

Species	North- South movement (km/y)	Maximum latitude (°lat/y)	Minimum latitude (°lat/y)	Range expansion- contraction (km/y)	Mean temperature (°C/y)	Change in Depth (m/y)
Spiny dogfish	-3.78					
Winter skate	-4.99		-0.096	10.41		
Little skate	-3.35	0.013	-0.018	2.94		-0.46
Thorny skate		-0.0086				
Atlantic herring			-0.037		0.023	
Alewife	4.90				-0.020	
American shad	5.80	0.059		10.75	-0.033	
Silver hake-Northern				0.78		-1.32
Silver hake-Southern	2.73			-4.67		
Atlantic cod-GB	2.10	-0.0077		-13.21		0.84
Atlantic cod- GOM	-0.87		0.077			
Haddock-GB	-1.19					
Haddock-GOM						
Pollock		-0.0063		-6.09	0.028	1.30
White hake	2.36			-6.09		1.03
Red hake-N	0.56			0.57		
Red hake-S	7.29		0.022	-4.37		
Spotted hake	3.77	0.032	-0.013	6.14	-0.034	
Cusk		-0.030	0.022	-3.48	0.028	0.76
Halibut	3.23		0.020			1.06
American plaice	-1.34	-0.0050		-3.30		0.40
Summer flounder			-0.017	6.76		
Fourspot flounder		0.043		4.56		
Yellowtail flounder-N	-1.73	-0.020		-0.79		-0.85
Yellowtail flounder-S	4.71		0.044	-6.30		0.55
Winter flounder-N	-5.91		-0.019			-1.22
Winter flounder-S						
Windowpane flounder						
Atlantic Mackerel					-0.059	-1.53
Acadian redfish		-0.0067	0.038	-4.60		
Blackbelly rosefish	9.84				-0.045	
Longhorn sculpin	1.90		0.065	-8.45		
Searaven			0.025	-4.71		
Atlantic wolfish		-0.031	0.019	-3.65		
Ocean pout			0.020	-4.19		0.29
Goosefish				-5.07		1.49

Figure 1: Survey area with strata used in this analysis. Geographic regions referred to in the text are labeled accordingly. The star indicates the fixed point used to calculate distance, d, in each year.



Figure 2: Five-year strata-weighted centroids of abundance for 36 fish stocks. (70s=1968-1970, 75s=1971-1975, 80s=1976-1980, 85s=1981-1985, 90s= 1986-1990, 00s=1991-2000, 05s=2000-2005, 2006=2006).



Figure 2 cont'd: Five-year strata-weighted centroids of abundance for 36 fish stocks. (70s=1968-1970, 75s=1971-1975, 80s=1976-1980, 85s=1981-1985, 90s=1986-1990, 00s=1991-2000, 05s=2000-2005, 2006=2006).



Figure 3: Annual mean depth of occurrence in spring for 36 northwest Atlantic fish stocks caught on spring NEFSC multispecies survey.



Figure 3 cont'd: Mean depth of occurrence in spring 36 northwest Atlantic fish species caught on NEFSC multispecies survey.



Figure 4: Smoothed maps of red hake spatial distribution (north and south stocks combined) in five year time blocks using IDW. Units of biomass are in kg tow⁻¹



Figure 5: Smoothed bottom temperature from measurements taken during the NEFSC spring trawl survey in five year time blocks using IDW.



Figure 6: Trends in ERSST and AMO during the time series of the spring NEFSC survey



Figure 7: Relationship between abundance and distribution (species areal range) from spring survey data for a) elasmobranchs (spiny dogfish, winter skate, little skate, thorny skate), b) gadids (silver hake, cod, haddock, pollock, white hake, red hake, spotted hake, and cusk), c) Deepwater fishes (Acadian redfish, Blackbelly rosefish, longhorn sculpin, sea raven, Atlantic wolfish, ocean pout, fawn goosefish) d) pelagics (herring, alewife, American shad, Atl. mackerel) e) flatfish and f) all species combined.



Figure 8: Loadings (correlations with canonical variates) for the first two canonical axes for the explanatory variables (open triangles) and response variables (closed circles) for 24 species.



Figure 8 cont'd: Loadings (correlations with canonical variates) for the first two canonical axes for the explanatory variables (open triangles) and response variables (closed circles) for 24 species.

