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Effects of spring onset and summer duration on fish species distribution and biomass along the Northeast United States continental shelf

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Abstract Studies documenting distributional shifts of fishes typically rely on time series of annual sampling events with fixed seasonal timing and limited temporal range. Meanwhile, as temperatures along the Northeast continental shelf have increased, the seasonal cycle also shifted towards earlier spring warming and longer summers. Seasonal migrations of fish and macroinvertebrates on the continental shelf in the Northeast US are thought to be primarily controlled by temperature and as such likely follow the temperature phenology of the shelf. This study sought to determine whether apparent changes in fish biomass and distributions are linked to spring warming phenology and/or duration of summer, the effective growing season for most species. We hypothesized that the earlier spring thermal transition would occur earlier and would cause centers of biomass to be more poleward during the spring survey. We also expected lengthening summers, primarily a function of later fall cooling, to cause centers of biomass in the fall survey to be more poleward and for biomass on the shelf to be greater within and following longer growing seasons. We did not detect a strong effect of the timing of the spring thermal transition in sea surface temperature on the distribution or abundance for most of the 43 fish stocks that we examined. However, later fall cooling and longer summers had a strong effect on both abundance and biomass of many fish stocks. These findings suggest that more focus should be placed on the length of the growing season and population-level processes that result in distributional shifts and changes in abundance.

Keywords Distribution · Marine fish · Seasonal · Spring transition · Temperature

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Introduction

As climate change progresses, changes other than in mean temperature are important to understanding how climate change impacts marine ecosystems. In the northern hemisphere region, onset of spring thermal transition advanced by 2.08 days per decade on average over the last 50 years while the fall transition delayed by 1.73 days per decade (Burrows et al. 2011). Although the magnitude of warming is progressing faster on land, shifts in seasonal temperature

transitions have been greater in the ocean (Burrows et al. 2011). Additionally, seasonality, defined as the difference between the summer and winter temperatures, increased in coastal systems both globally (Baumann and Doherty 2013) and in the Northeast US (Friedland and Hare 2007).

Multiple changes in annual temperatures have been observed in the Northeast Atlantic including an increase in the annual range of sea surface temperature, faster rates of warming and cooling in the spring and autumn seasons (Friedland and Hare 2007), and altered timing of seasonal transitions (Thomas et al. in review; Friedland et al. 2015). In the Northeast United States continental shelf, summer duration, as a function of both earlier spring warming and later fall cooling, lengthened over the past 3 decades along the Northeast continental shelf (Thomas et al. in review). A 22-day advancement in the spring transition was also a notable feature of an "ocean heatwave" in 2012 that generated sudden and dramatic changes in multiple fisheries, particularly lobster (Mills et al. 2013).

In general, the ecological effects of changing seasonal temperature transitions are not well-documented in marine systems including even the well-studied Northeast US shelf. Previous work has focused on lower trophic levels because such data can be collected at high temporal resolution, a necessity for assessing changes occurring on the order of days. In particular, the timing of phytoplankton blooms can be measured via satellite. Ji et al. (2010) summarized recent work on phytoplankton and zooplankton phenologies globally. Most studies focus on spring phenology in the northern hemisphere.

Friedland et al. (2015) used color satellite and shipboard sampling data to look at spring phenology of phytoplankton and zooplankton blooms, respectively. They found regional differences in bloom dynamics, suggesting that more research may be necessary. Edwards and Richardson (2004) found that changes in the phenology of peak abundance in phytoplankton, zooplankton, and fish larvae varied throughout taxa and may lead to potential decoupling of predator–prey relationships, altering ecosystem dynamics. Monthly transect data from the Continuous Plankton Recorder (CPR) has also been used to study temporal variability in harmful algal blooms (HABs) in the northeast Atlantic Ocean and the North Sea (Edwards et al. 2006). The CPR survey and nearshore surveys have also been used to examine zooplankton phenology globally.

Phenologies of other organisms that support fisheries can potentially be assessed using data from commercial landings. For example, Northern shrimp (*Pandalus borealis*) hatch periods lengthened in the Gulf of Maine from 1980 to 2011 (Richards 2012). Richards (2012) concluded that in the near future, this would provide more opportunity for larvae to encounter good feeding conditions. In the long-term, sustained warming trends will generate unpredictable effects.

Little work has been done to examine the effects of phenology on marine fishes because time-consuming sampling methods limit the spatial and temporal resolution at which such surveys can occur. Most fish surveys have coarse temporal resolution (i.e., typically seasonal or annual). Some exceptions include surveys of diadromous fish migrations in and out of rivers (Juanes et al. 2004; Peer and Miller 2014), bioacoustic surveys (Rountree et al. 2006), and industry-based data, such data derived from commercial landings (Richards 2012). However, it is important to consider that industry data are strongly influenced by regulations (seasonal closures) and economic factors (seasonal markets). Previous studies have focused on annual distributions and did not address the complicating factor of variable phenology (Nye et al. 2009; Pinsky et al. 2013). However, Nye et al. (2009) proposed that as temperatures warmed, fishes might initiate an earlier migration that would appear as a poleward shift in distribution. A spatially and temporally fixed survey would observe the same distributions at different points during migration and inaccurately detect an apparent shift in annual distribution.

The goal of this study was to examine the effects of variable temperature seasonality on trends in fish distribution and to evaluate whether distribution effects were caused by earlier spring warming or longer summer duration. We hypothesized that as spring transition dates shift earlier and warm summer temperatures persist, fishes may respond to earlier warming in a number of ways. First, fishes could migrate onto the shelf earlier and this would be reflected in more poleward and inshore distributions of center mass during the spring survey, linearly related to the onset of spring warming. Alternatively, interannual variation in spring transition could be more important than the long term trend, and fishes may respond nonlinearly or only to extreme spring warming events. Lastly, fish stocks could exhibit a lagged

biomass response to earlier spring warming via population level processes. For example, a longer growing season may increase spawning stock biomass and generate greater recruitment in subsequent seasons.

Longer summer seasons, a function of both early spring warming and later fall cooling could also affect fish distributions in similar ways. A longer summer season may encourage fishes to stay northward later in the year and subsequently be detected further north during the fall survey. Similarly, fish may stay inshore later in the year, resulting in more inshore distributions during the fall survey. A longer growing season may also improve growth conditions, alter maturity schedules and improve reproductive success of some stocks, resulting in a lagged increase in stock biomass following longer growing seasons.

Methods

Fish data

Fisheries independent data were gathered from the Northeast Fisheries Science Center (NEFSC) spring (1968–2014) and fall (1967–2013) bottom trawl surveys. Though the fall survey began in 1963, the mid-Atlantic strata used in this study were not added to the survey until 1967. The surveys begin near Cape Hatteras and end in the Gulf of Maine. The spring survey has been scheduled for approximately the same 2-month period (March–April) for nearly 5 decades (Fig. 2a, b, c). The fall survey phenology varied more in the past but sampling has occurred during approximately the same 2-month window (September–October) over the last 3 decades (Fig. 2d, e, f). Sampling details are described in Azarovitz (1981). Strata used in this study are 01010-01300, 01360-01400, and 01610-01760, the same strata used in Nye et al. (2009). There were no issues of continuity in these strata except in 1988 when the fall survey did not sample the 01300 stratum located in the Gulf of Maine. For this study, strata were clustered into two regions, North and South, to coincide with previously defined fish stock distributions (Nye et al. 2009). The North region covers the Gulf of Maine and the South region extends from Georges Bank through Southern New England and the Mid-Atlantic Bight (Fig. 1 in Nye et al. 2009). Some fish stocks cover both regions; therefore, the
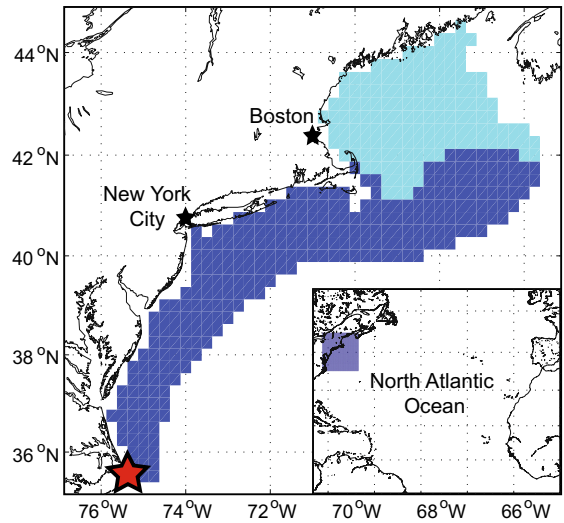
Fig. 1 OISST data 0.25° × 0.25° grid and regional divisions. The Gulf of Maine (*light blue*) is the 'northern' region and the dark blue region is the 'southern' region. North and south are combined for the whole shelf region. The *red star* indicates the southernmost extent of the fish trawl survey, Cape Hatteras, North Carolina, US Inset of the North Atlantic Ocean shows the northeast United States shelf region in blue

North and South regions were also combined into one shelf-wide region in this study. We selected 43 fish and invertebrate stocks for this study that were well-represented throughout the survey. Most species have one stock throughout the NE US shelf region. Six species have been identified as containing separate stocks in the North and South regions (Table 1).

Annual measures of center of biomass, maximum latitude, minimum latitude, biomass-weighted mean latitude, longitude, along-shelf distance, cross-shelf distance, and biomass-weighted mean depth of occurrence were calculated using the same methods as Nye et al. (2009). Biomass weighted latitude and longitude of sampling were converted to cross-shelf and along-shelf distances from the 200 m isobath and from Cape Hatteras, North Carolina. Center of biomass was defined as the great circle distance between each annual coordinate (biomass weighted latitude and longitude) and a fixed point near Cape Hatteras, North Carolina, USA (35° N and 75° W) calculated using the 'Imap' package in R. Minimum and maximum latitude were defined as the annual latitudinal extremes where each species was sampled. Annual metrics of mean stratified biomass were also calculated for each species by taking the stratified mean of the log-transformed tows.

Table 1 Fish and invertebrate species' common and scientific names, life history characteristics, and whether there are distinct stocks by Northern and Southern ecoregion (N, S)

Common name	Scientific name	Eco-region	Migratory? (Y/N)	Lifespan (years)	Age at maturity (years)
Acadian redfish	*Sebastes fasciatus*		Y	30–50	5.5, 8–9
Alewife	*Alosa pseudoharengus*		Y	8–10	4–5
American lobster	*Homarus americanus*		Y	100+	5–8
American plaice	*Hippoglossoides platessoides*		Y	30	11
American shad	*Alosa sapidissima*		Y	13	2–4
Atlantic halibut	*Hippoglossus hippoglossus*		Y	50	7–8 (M), 10–11 (F)
Atlantic herring	*Clupea harengus*		Y	15–18	3
Atlantic mackerel	*Scomber scombrus*		Y	20	2–3
Atlantic rock crab	*Cancer irroratus*		–	–	–
Atlantic wolffish	*Anarhichas lupus*		Y	22	5–6
Black Sea Bass	*Centropritstis striata*		Y	8 (F), 12 + (M)	
Blackbelly rosefish	*Helicolenus dactylopterus*		N	43	15–16 (M), 13 (F)
Atlantic cod	*Gadus morhua*	N, S	Y	20+	1.7–2.3
Cusk	*Brosme brosme*		N	15	5 (M), 7 (F)
Fourspot flounder	*Hippoglossina oblonga*		Y	–	–
Goosefish	*Lophius gastrophysus*		–	6 (M), 12 (F)	3–4
Haddock	*Melanogrammus aeglefinus*	N, S	Y	9–14	1–2
Jonah crab	*Cancer borealis*		N	6–7 (M), 8 (F)	–
Little skate	*Leucoraja erinacea*		Y	12	7–7.5
Longfin squid	*Loligo pealeii*		Y	<1	–
Longhorn sculpin	*Myxocephalus octodecemspinosus*		–	11	–
Northern shortfin squid	*Illex illecebrosus*		Y	115–215 days	40–60 days
Ocean pout	*Zoarces americanus*		N	16–18	2+
Pollock	*Pollachius virens*		Y	18	4–7
Red hake	*Urophycis chuss*	N, S	Y	14	1–2
Sea raven	*Hemitripterus americanus*		Y	9–11	4–5
Silver hake	*Merluccius bilinearis*	N, S	Y	6 (M), 12 (F)	2–3
Spiny dogfish	*Squalus acanthias*		Y	35 (M), 40 (F)	6 (M), 12 (F)
Spotted hake	*Urophycis regia*		Y	20+	1.5
Striped Bass	*Morone saxatilis*		Y	30	2–4
Summer flounder	*Paralichthys dentatus*		Y	3[a]	2
Thorny skate	*Amblyraja radiate*		Y	–	–
White hake	*Urophycis tenuis*		Y	20+	1.5
Windowpane	*Scopthalmus aquosus*		Y	7	3–4
Winter flounder	*Pseuodopleuronectes americanus*	N, S	Y	15+	3–3.5
Winter skate	*Leucoraja ocellata*		–	–	9.5–12.5
Yellowtail flounder	*Limanda ferruginea*	N, S	Y	12	1.5–2

[a] Although summer flounder live longer than 3 years, most individuals sampled are not older than 3 years due to overfishing (Packer et al. 1999)

Temperature data and metrics

Spring transition and summer duration metrics were derived from daily sea surface temperature (SST) data from the NOAA Optimum Interpolation Sea Surface Temperature (OISST) series (1982–2013) where SST on the scale of 0.25° spatial resolution is reconstructed by combining observations from satellites, ships, and buoys on a regular global grid (Reynolds et al. 2007). Daily SST values from this data product were gathered over the region of the Northeast continental shelf designated in Xu et al. (2015). A metric for spring warming phenology was calculated for each grid point as the first day of the year, after the seasonal minimum, on which a given temperature threshold was held or exceeded for 8 consecutive days. To determine an appropriate spring warming temperature, various thresholds beginning with 6 °C, were tested for the Gulf of Maine, Georges Bank, Southern New England, and the Mid-Atlantic Bight regions separately. Subsequent thresholds included 8, 10, and 14 °C. Principal components analysis (PCA) was used to determine which threshold explained the most variability in warming phenology since 1982 by region, where variables were the time series for each temperature threshold.

Summer duration was calculated for each grid location as the number of days between the first and last day of the year that summer SST exceeded a threshold, set as the temperature that was 0.5° cooler than the coldest maximum summer SST observed at the location in the 33-year record (Thomas et al. in prep). The gridded spring phenology and summer duration metrics were aggregated into average phenologies for all three aforementioned ecoregions corresponding to species distributions (Fig. 1).

Analyses

We performed a PCA on the distributional metrics (center of biomass, biomass-weighted mean depth, maximum latitude, minimum latitude, latitude, longitude, along-shelf distance, and cross-shelf distance) for each fish stock to determine which metrics were most variable for each species. In nearly all stocks, center of biomass (measured as distance from Cape Hatteras, NC) was the most influential metric of all eight indicators of distributional changes in the first PC, closely followed by along-shelf distance. Because

center of biomass is essentially a combination of along and cross-shelf distance, we focus on this metric to define stock distributions in subsequent analyses.

We tested the hypothesis that there would be a linear relationship between spring transition (summer duration) and spring (fall) center of biomass by fitting linear regressions for each stock. The explanatory variable was spring onset or summer duration and the response variable was stock distribution. Relationships between temperature seasonality metrics and distributions were also tested using Spearman rank correlations which make no assumptions about the distribution of data.

We descriptively looked at the effects of extremely early and late spring warming on fish species distribution and biomass. We defined extreme spring warming by using the 8 °C transition date over the whole northeast shelf region. Years in which the 8 °C mean day-of-year threshold was greater than one standard deviation (SD) away from the 1982–2014 mean were considered to be "extreme." We descriptively examined the relationship between extremely early/late warming, mean biomass, and distribution along the shelf. For each stock, the biomass-weighted mean latitude and longitude were plotted on a chart of the northeast continental shelf. The size of each point was a function of the annual mean stratified biomass. The color of each point indicated whether it was an extremely early (red), late (blue), or within the range of "normal" (gray) spring warming phenology that year.

Finally, cross-correlation analyses were used to test whether stock distributions and biomass might have lagged relationships with spring warming phenology or summer duration. These were performed using the 'ccf' function in R ('stats' package) which performs a series of autoregressive Pearson correlations for each lag, in this case up to a 5-year lag.

A Bonferroni correction was used to adjust the critical p value for multiple comparisons to $p = 0.001$ (0.05/43 species).

Results

Survey timing

Spring survey timing has been relatively consistent. Mean stratified day-of-year (DOY) of spring

sampling by ecoregion varied little since the beginning of the survey (Fig. 2a, b, c). Spring survey mean stratified DOY (+SD) was 110.65 (+10.16), 86.97 (+7.92), and 94.90 (+7.99) in the northern, southern, and shelf-wide regions, respectively. Spring sampling DOY was more variable prior to 1980. Since 1982 (the start of the OISST time series), the spring survey mean stratified DOY (+SD) was 109.50 (+8.45), 85.44 (+6.18), and 93.51 (+6.65) in the northern, southern, and shelf-wide regions. Fall survey time has been more variable (Fig. 2c, d, e) though it stabilized after 1990. Fall survey mean stratified DOY (+ SD) was 302.75 (+ 11.00), 277.28 (+9.49), and 285.75 (+9.67) for the northern, southern, and shelf-wide regions. Since 1982, fall survey mean stratified DOY was 297.85 (+8.43), 272.59 (+5.51), and 280.96 (+6.31) in the northern, southern, and shelf-wide regions. Mean DOY of the survey appears to be well correlated between all three regions in both seasons.

Spring transition and summer duration

Principal component analyses of spring transition temperature thresholds indicated that the lowest, most consistently observed temperature across all regions, 8 °C, accounted for the greatest proportion of the variance in the first principal component (Table S1). Although, 6 °C accounted for more variance in most regions, the Mid-Atlantic Bight region does not consistently cool to that temperature. Thus, we chose to use the 8 °C threshold to define spring transition date. The transition to 8 °C occurred earlier in the southern region and later in the northern region. In 1982, the southern region reached 8 °C about 25 days earlier but near the end of the time series, the difference was just 14 days. Average DOY spring onset (+SD) was 78.35 (+11.96), 54.96 (+7.94), and 61.87 (+8.35) in the northern, southern, and shelf-wide regions. Spring transition was highly variable throughout the time series. The northern and southern

Fig. 2 Day-of-year (DOY) of the spring (a, b, c) and fall (d, e, f) NOAA NEFSC survey phenology by ecoregions, North (a, d), South (b, e), and whole shelf (c, f). Solid lines indicate stratified mean DOY that the survey occurred. Shaded gray areas indicate the range between the first and last day of sampling within each region
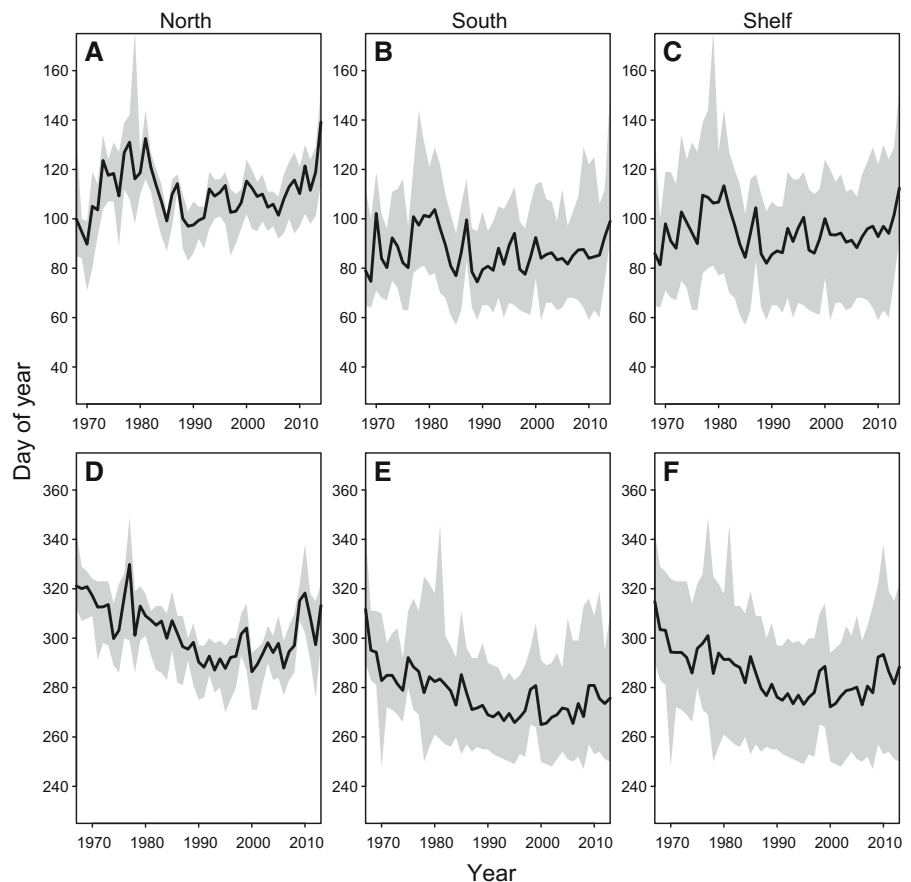
regions started with similar spring onset DOY (approximately 10 days apart) in 1982. The difference between north and south expanded and varied from 11.60 (1984) to 36.65 days (2005) over the next three decades. In 2012, spring transition advanced by about 20 days across the whole shelf while the difference between the northern and southern regions was about 25 days. In 2013 spring onset advanced nearly another 20 days in the northern region but only about 1 day in the southern region. This resulted in nearly the same onset DOY across the entire shelf, with only a 0.4 day difference between the north and south regions. Following the cold winter of 2014, spring onset delayed by 30 days in the north and 15 days in the south, generating a 22 day difference between the two regions.

The summer season consistently lengthened since 1995 (Fig. 3b). Before then, summer length was more variable with a slight trend towards lengthening. The difference in the length of summer between the northern and southern regions also decreased over time, indicating that the summer period expanded faster in the north than in the south. This was primarily a function of later fall cooling (Thomas et al., in review). From 1982 to 2014, summer duration was 56.21 ± 6.22, 64.62 ± 4.55, and 61.93 ± 5.02 days in the northern, southern, and shelf-wide regions, respectively.

Nine years were found to have spring transitions greater than one standard deviation away from the mean shelf-wide transition DOY (61.87 ± 8.35 days) (Fig. 4). Six years had unusually late spring warming (1982, 1988, 1990, 1994, 1996, and 1997) and 3 years had unusually early warming (1983, 2012, and 2013).

Fish stock response to variable spring transition and summer duration

Spring center of biomass was negatively associated ($p < 0.05$) with spring transition in seven stocks (black sea bass, northern cod, northern haddock, ocean pout, southern red hake, spotted hake, and Atlantic mackerel; Fig. 5a). Negative regressions and correlations mean that with earlier spring onset, centers of biomass were further north during the spring survey. Spearman correlations were not significant between spring centers of biomass and transition DOY for any stocks (Fig. 5c).
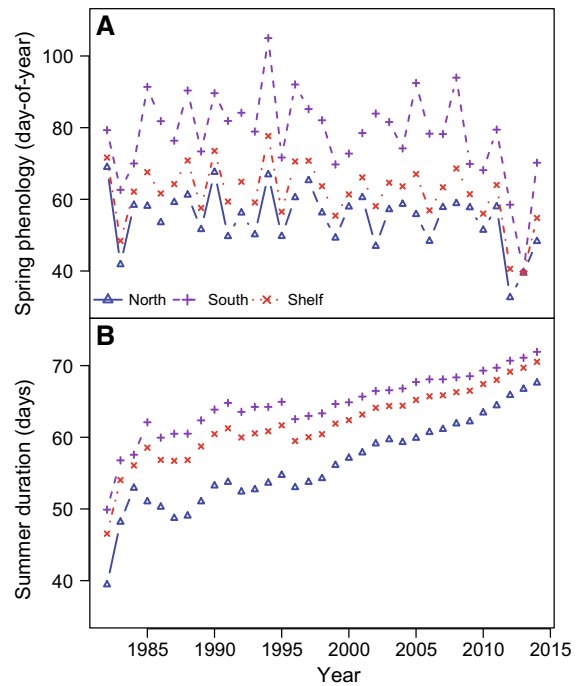
Fig. 3 a Spring warming phenology (regional mean DOY on which the 8 °C SST threshold was held of exceeded for 8 consecutive days) time series. Mean $\pm$ standard deviation of spring phenology in the northern, southern, and shelf-wide regions was 78.35 ± 11.96, 54.96 ± 7.94, and 61.87 ± 8.35 days, respectively. **b** Summer duration (days) for all three ecoregions. Mean $\pm$ standard deviation of summer duration (1982-2014) was 56.21 ± 6.22, 64.62 ± 4.55, and 61.93 ± 5.02 days in the northern, southern, and shelf-wide regions, respectively

Fall center of biomass was negatively associated ($p < 0.05$) with summer duration in four stocks (little skate, spiny dogfish, striped bass, thorny skate; Fig. 5b). Five stocks had significantly positive relationships at $p < 0.05$ (black sea bass, longhorn sculpin, spotted hake, summer flounder, and southern yellowtail flounder) and four stocks at $p < 0.001$ (blackbelly rosefish, American lobster, Atlantic herring, and Atlantic mackerel; Fig. 5b). Positive regressions and correlations indicate that with longer summers, centers of biomass were further north during the fall survey. Spearman correlations were significantly negative in four stocks (northern cod at $p < 0.05$; little skate, spiny dogfish, and thorny skate at $p < 0.001$; Fig. 5d) and significantly positive in nine stocks (black sea bass, blackbelly rosefish, summer flounder, southern yellowtail flounder, alewife, and Atlantic mackerel at $p < 0.05$; spotted hake,
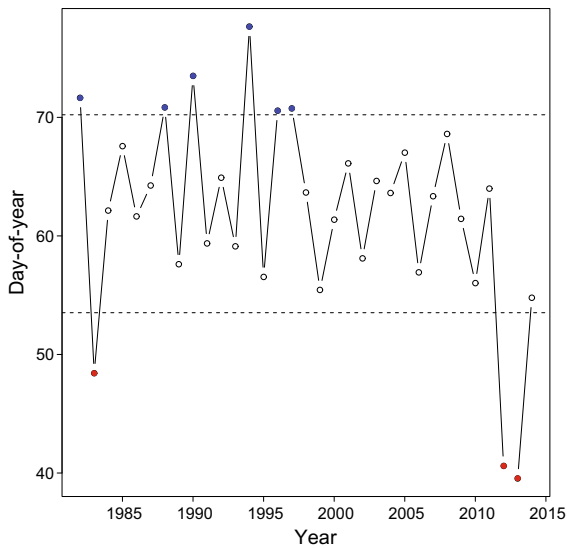
Fig. 4 Defining extreme spring warming using the 8 °C phenology from the whole shelf region. A 5-year running mean is denoted by the *solid line*. Years in which the whole shelf mean 8 °C day-of-year lies greater than one standard deviation (*dashed lines*) away from the mean (61.87 $\pm$ 8.35 days) are considered "extreme" phenologies. Late years were 1982, 1988, 1990, 1994, 1996, and 1997 (*blue*), early years were 1983, 2012, and 2013 (*red*)

American lobster, and Atlantic herring at $p < 0.001$; Fig. 5d).

Spring distributions as indicated by center of biomass were negatively correlated with spring transition at various lags in seven stocks (black sea bass, ocean pout, summer flounder, longfin squid, northern shortfin squid, American shad, and Atlantic mackerel at $p < 0.05$; Fig. 6a). Spring distributions were positively correlated with spring transition in four stocks (cusk, southern red hake, and southern winter flounder at $p < 0.05$; striped bass at $p < 0.001$; Fig. 6a). The survey-estimated biomass in the spring was negatively correlated with spring onset in eight stocks (Atlantic halibut, southern haddock, northern silver hake, northern yellowtail flounder, Jonah crab, and American shad at $p < 0.05$; northern haddock and little skate at $p < 0.001$; Fig. 6b), meaning that with earlier arrival of spring, mean stratified stock biomasses were greater in the spring survey. Three stocks exhibited positive lagged correlations between spring biomass and spring transition DOY (longhorn sculpin, sea raven, and longfin squid at $p < 0.05$; Fig. 6b).

The fall center of biomass was negatively correlated with summer duration at various lags in 10 stocks (Atlantic wolfish, northern cod, striped bass, thorny skate, windowpane, winter skate, and northern yellowtail flounder at $p < 0.05$; little skate, spiny dogfish, and northern winter flounder at $p < 0.001$; Fig. 6c) and positively correlated in 11 stocks (black sea bass, southern haddock, longhorn sculpin, summer flounder, southern yellowtail flounder, and alewife at $p < 0.05$; blackbelly rosefish, spotted hake, American lobster, Atlantic herring, and Atlantic mackerel at $p < 0.001$; Fig. 6c). The fall survey-estimated biomass was negatively correlated at various lags in 13 stocks (American plaice, longhorn sculpin, ocean pout, southern red hake, sea raven, white hake, windowpane, and Atlantic rock crab at $p < 0.05$; Atlantic wolffish, northern and southern Atlantic cod, cusk, and thorny skate at $p < 0.001$; Fig. 6d) and positively correlated in 19 stocks (Atlantic halibut, black sea bass, fourspot flounder, northern and southern haddock, little skate, spotted hake, striped bass, northern and southern winter flounder, and Jonah crab at $p < 0.05$; Acadian redfish, blackbelly rosefish, spiny dogfish, southern silver hake, summer flounder, American lobster, alewife, American shad, and Atlantic herring at $p < 0.001$; Fig. 6d).

In years with extremely early or late spring warming, stock distributions and biomasses indicated varied responses. Some stocks (e.g., American lobster, Atlantic herring, and Atlantic mackerel; Fig. 7a, c, d) indicated northward spring distributions during years with early warming and southward distributions during years with late warming. However, distributions in extreme years also overlapped with distributions from normal spring transition years. American lobster spring survey biomasses were also much larger in years with early warming than in years with late warming. A few other stocks, namely spiny dogfish (Fig. 7b), indicated the opposite. Spiny dogfish were distributed northward during years with late warming and southward in years with early warming. Many stocks did not indicate any clear response to extreme spring transition (southern silver hake and northern and southern red hake, Fig. 7f–h). And some stocks, like northern silver hake (Fig. 7e), suggested that fish might be responding to extreme transition DOY
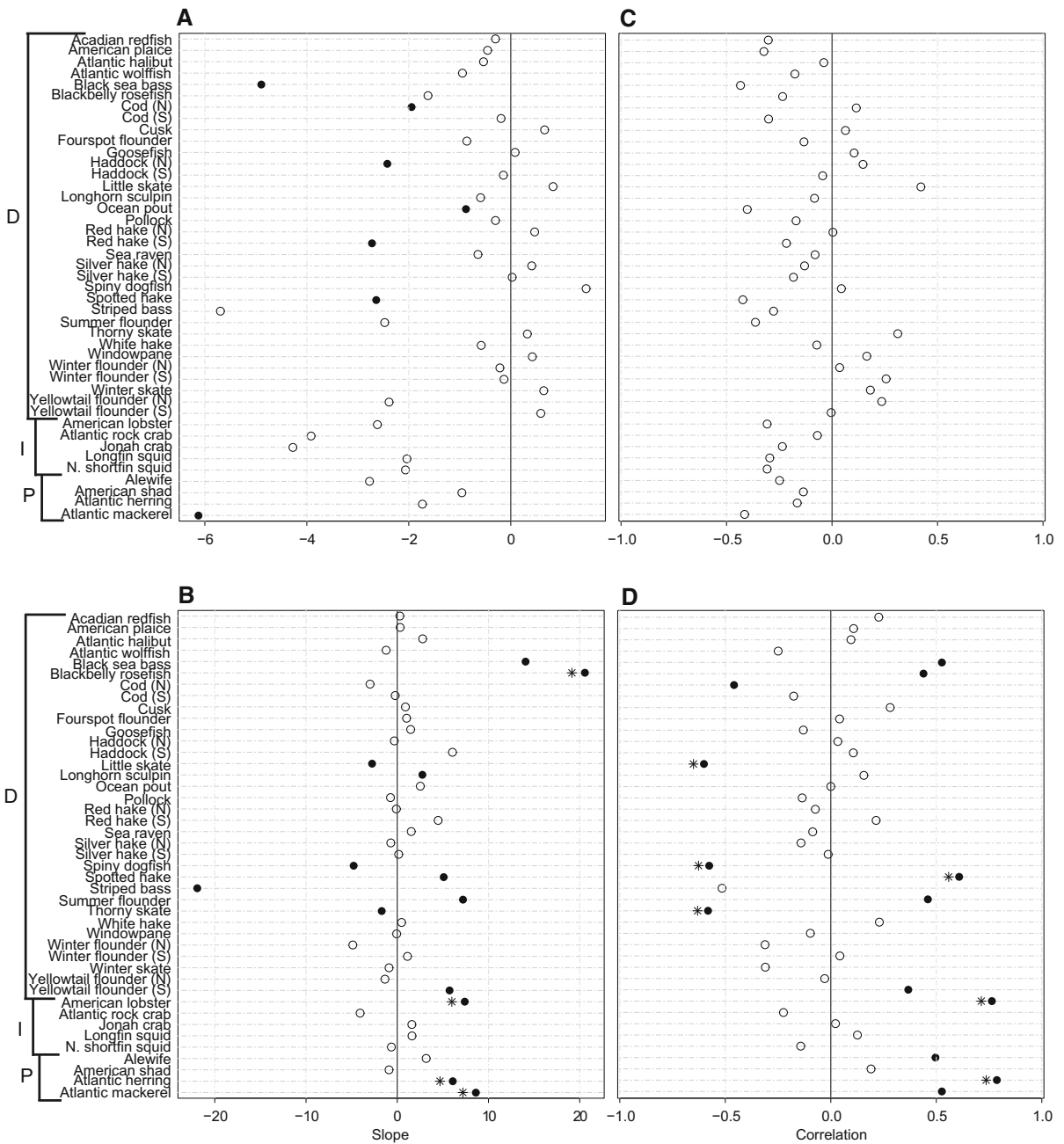
Fig. 5 Slopes from linear regressions of **a** spring phenology and spring center of biomass (distance from Cape Hatteras, North Carolina, US) and **b** summer duration and fall center of biomass. And spearman rank correlations between **c** spring phenology and spring center of biomass and **d** summer duration and fall center of biomass. *Open symbols* are not significant, *filled symbols* are significant ($p < 0.05$), and *filled symbols* with *asterisks* are significant ($p < 0.001$). Species are grouped as follows: demersal fish (D), invertebrates (I), and pelagic fish (P)

with slightly more northward distributions in early warming years, but the late warming years were scattered. Figures of extreme spring warming distributions for all stocks are in Fig. S1.

Discussion

Summer duration appeared to affect species distributions and biomasses more than spring onset. However,
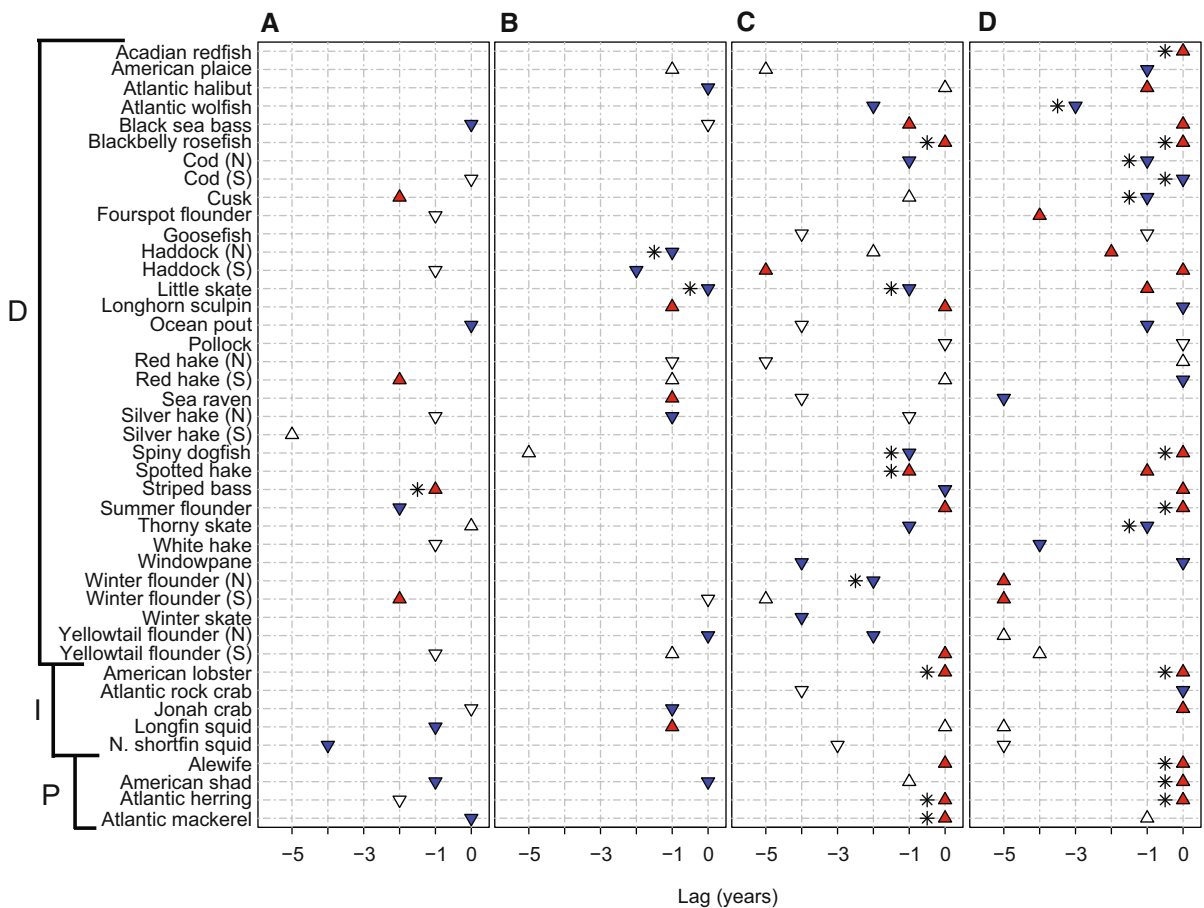
Fig. 6 Lags of maximum correlations. **a** Spring center of biomass lags spring phenology. **b** Mean log-transformed spring stock biomasses lag spring phenology. **c** Fall center of biomass lags summer duration. **d** Mean log-transformed fall stock biomasses lag summer duration. Direction of *triangle* (*up*, *down*) and *fill color* (*red*, *blue*) indicate direction of correlation (positive, negative). *Open symbols* are not significant, *filled symbols* are significant ($p < 0.05$), and *filled symbols* with *asterisks* are significant ($p < 0.001$). Species are grouped as follows: demersal fish (D), invertebrates (I), and pelagic fish (P). Stocks that are *missing symbols* had positive lags, which are illogical

inferences are limited by the data available for this study.

Spring transition

In contrast with our expectation that spring transition had steadily advanced over time, spring onset over the NE US shelf has been highly variable since 1982 and only shifted earlier by 14 days since 2011. A similar trend towards earlier warming in recent years was documented by Friedland et al. (2015). However, their assessment estimated a greater advance in spring warming, with spring onset estimated to occur 19 days earlier in the Gulf of Maine and Georges Bank and about 2 weeks earlier further south along the NE US

shelf (Friedland et al. 2015). We attribute the differences in our analysis to methodological differences in defining the spring transition metric. Friedland et al. (2015) used the annual mean SST from each region to define a transition temperature. They smoothed the daily OISST data using a 5-day moving average and defined the spring transition date as the first day of year on which the smoothed temperature exceeded the transition temperature. Our study defined spring transition by looking at the succession of warming temperatures after the seasonal minimum to define the DOY when specific temperatures were maintained for 8 days.

In general, we did not detect a strong response in fish distribution or biomass to the timing of the spring

Fig. 7 Annual mean center of biomass (coordinates) and survey-estimated biomass (in kg; size of points) in normal (*gray*) versus extremely early (*red*) and late (*blue*) spring warming years. **a** American lobster, **b** spiny dogfish, **c** Atlantic herring, **d** Atlantic mackerel, **e** northern silver hake, **f** southern silver hake, **g** northern red hake, **h** southern red hake
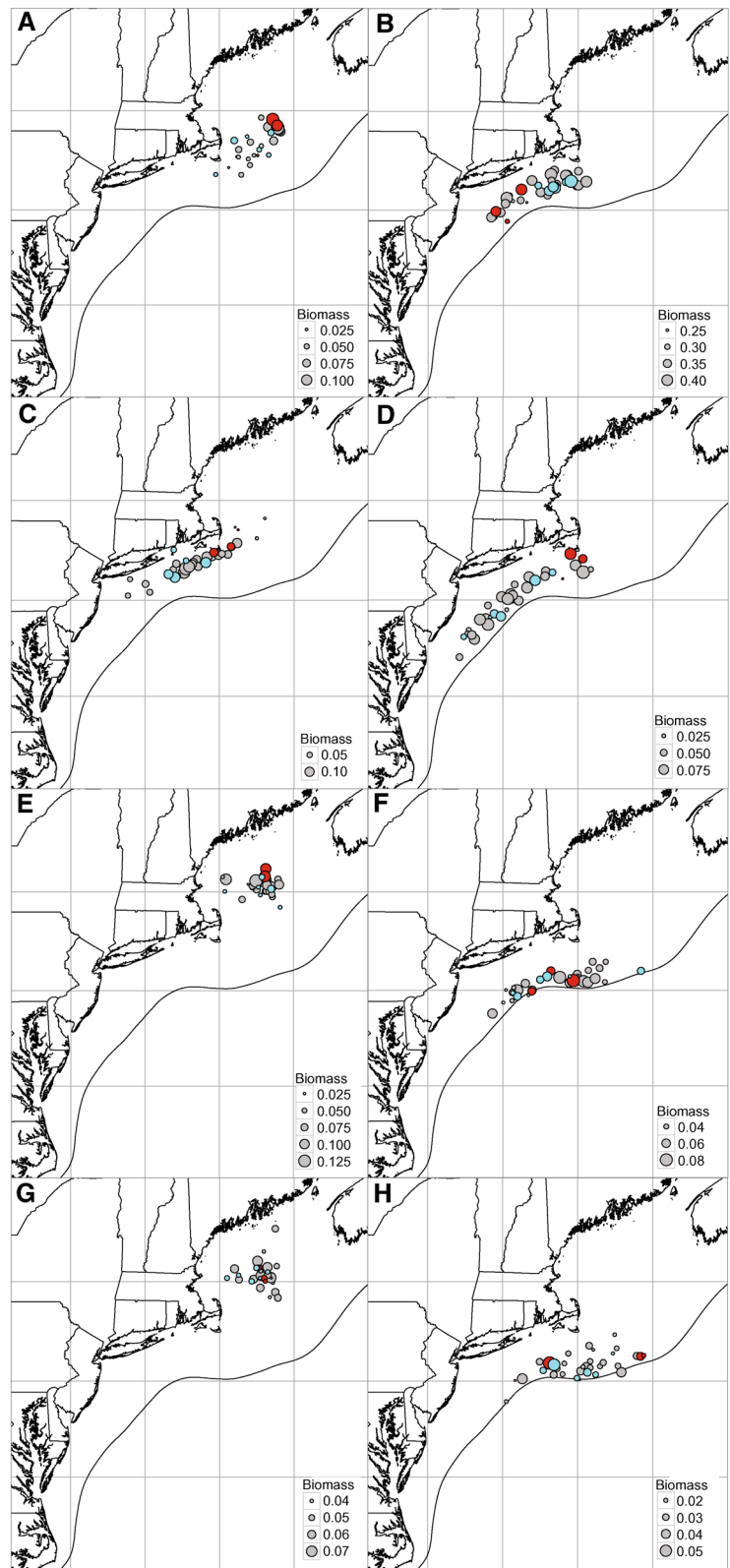
transition. Of the 43 fish stocks examined, only a few had statistically significant relationships with timing of spring warming—even when using a less conservative p value ($p = 0.05$). We suspected that the year 2012 contributed to poor regression fits because surface waters warmed so dramatically early that year as to make 2012 spring onset much earlier than all other years. However, there was little difference in our results when 2012 was removed from our analyses.

The strongest responses to extreme spring transition were apparent in the pelagic Atlantic mackerel and Mid-Atlantic stocks (e.g., summer flounder, fourspot flounder, and black sea bass). Murawski (1993) found that of 36 fish and squid species, Atlantic mackerel and Atlantic herring had the largest latitudinal responses to temperature. Their findings are consistent with the findings of this study showing mackerel and herring were among the most responsive stocks to both summer duration and spring transition.

Some responses may be explained by life history traits (Table 1). For example, Northern haddock biomass indicated a 1-year lagged negative response to spring onset ($p < 0.001$; Fig. 6b). Haddock reach reproductive maturity around 1–2 years of age (Cargnelli et al. 1999) and inhabit the Gulf of Maine, where changes in temperature seasonality are most dramatic (Thomas et al., in review). Recruitment in the northern haddock stock may be negatively impacted by earlier spring onset, thus generating a 1-year lagged biomass response to spring onset. Northern shortfin squid ($p < 0.05$; Fig. 6a) indicated a 4-year lagged relationship with spring transition. However, the short lifespan of shortfin squid (115–215 days; Table 1) indicates that this relationship might not be realistic.

Summer duration

In contrast to variable spring transition, summer has become progressively longer and it is this lengthening that seems to affect both distribution and abundance of fish and macroinvertebrates on the shelf more than spring onset. Summer duration, a combination of both spring advance and fall delay, lengthened at a consistent rate since the mid-1990s. The period of time in which surface waters were within a half degree Celsius of the 33-year peak summer temperature in each region lengthened by about 20 days over three decades.

Stock distributional responses to summer lengthening varied widely in our study. Some species (e.g., striped bass, spiny dogfish, little skate, and thorny skate) were found closer to Cape Hatteras in fall after longer summers while other stocks indicated more northward distributions (e.g., Atlantic herring, Atlantic mackerel, American lobster, and blackbelly rosefish), after longer summers. The latter agrees with our hypothesis that longer summers, also a function of later fall transition, would allow fish to stay north later into the period of the fall survey. Except for blackbelly rosefish, all the species that indicated relationships significant to $p < 0.001$ between fall COB and summer duration are migrant. Most spend time in the sampling region during spring and summer while only some stay into the fall. The fall COB for these species may be more responsive to summer duration because the fall transition is a cue to migrate offshore and now occurs later.

Lags were important to understanding the relationship between summer duration and stock biomasses. Our hypotheses that biomasses would increase (e.g., alewife, Atlantic herring, American shad, American lobster, and spiny dogfish) and distributions would be further north (e.g., Atlantic mackerel, alewife, Atlantic herring, and American lobster) with longer summers were supported only when we considered lags. Lagged biomass increases suggest that a longer growing season could be contributing to population level effects, a line of inquiry that merits further attention. A longer summer means warm-water fish (e.g., summer flounder and black sea bass) could conceivably persist in optimal growing temperatures for longer periods of time, and cold-water fish (e.g., Atlantic cod) now endure longer periods in which temperatures exceed those favorable for growth and survival. Positive correlations at zero lag suggest that either growth was affected within one year (Neuheimer et al. 2011) or that the population was simply sampled more during the fall because the stock remained in the survey area longer before migrating south or offshore that year. Among the significant correlations, some relationships contradicted our hypotheses, indicating that some stock biomasses decreased as summer duration increased (e.g., northern and southern cod, ocean pout, and American plaice). The biomass response in those species likely reflects negative impacts of temperature on growth,

survival, or recruitment as they are all at the southern edge of their range (Myers and Drinkwater 1989; Portner and Farrell 2008; Deutsch et al. 2015). In particular, past studies on cod have found warmer water leads to lower recruitment, survival, and growth (Fogarty et al. 2008; Pershing et al. 2015, 2016). Atlantic cod, Atlantic herring, silver hake, spiny dogfish, and summer flounder reach maturity between 1 and 2 years of age. Survey estimated biomass in these stocks may lag summer duration by one year because these fish have faster growth. Impacts of spring phenology are detectable the following year as increased/reduced biomass in the survey. Changes in season could potentially lead to predator–prey mismatch, similar to Edwards and Richardson (2004) that would in turn have population level effects.

Study limitations

This study contributes to the need for more marine phenological studies, particularly of fish. However, given the deficit of data appropriate for phenological work in marine systems, it is apparent that more creative data sources and approaches to take advantage of available data will be necessary.

Though this study found some links between temperature seasonality and spatial distributions and biomass of marine species along the NE US shelf, it was limited by the data available. Ideally, a study attempting to look at fish seasonality requires data with high temporal resolution to capture changes on the order of days. Marine biological data at this resolution is uncommon. Biological data suitable for marine phenological studies is typically limited to lower trophic levels, as these data can be collected through remote observations and automated sensors. We sought to extend phenological studies to upper trophic levels by taking advantage of a seasonal fish survey that has been relatively static over both space and time.

Beyond temporal resolution issues, the time series of daily sea surface temperatures spanned just 3 decades. Within that time, we detected a high degree of variability in the onset of spring transition and a shift towards earlier warming within the final 3 years. Terrestrial studies have access to both longer time series and higher temporal resolutions, making it possible to filter out short term variability. For

example, a 250-year index of flowering dates indicated high-frequency annual variability with low-frequency multi-decadal changes in first flowering (Amano et al. 2010). A longer time series for this study would likely provide better insight into changing phenology of fish stocks of the NE US shelf ecosystem. Although spring transition did not occur earlier over time since 1982, it may very well have become progressively earlier since the beginning of bottom trawl samples in the 1960s.

Additionally, the timing of the bottom trawl surveys—although less variable after 1982—still fluctuated on the order of several days. This variability is enough to potentially affect comparisons with spring transition which varied at a similar magnitude. In the late 1990s, survey DOY advanced by several days. At the same time, spring DOY also advanced. A fish responding to spring transition that year by moving north early would not be easily detectable because our analyses assumed a temporally static survey. It is possible that some species were responsive to spring transition but we were not able to detect correlation.

Conclusions

In reality, fish distributions probably respond to a combination of seasonal transitions and annual warming. Although, the onset of spring warming itself did not elicit a strong distributional response from most stocks in our study, we know from previous work that temperature is important to stock distributions globally (Murawski 1993; Perry et al. 2005; Nye et al. 2011; Mills et al. 2013; Mueter et al. 2013; Pinsky et al. 2013). Seasonal transitions appear to affect poleward distribution secondary to population-level processes like growth, survival and recruitment as reflected in biomass metrics. Both the spring and summer seasons cover critical periods in fish life cycles, thus affecting population biomass. Most stock assessments currently do not incorporate temperature effects, let alone how seasonality might impact growth, survival, recruitment and availability to the survey. While much research has been focused on how climate change will impact habitat, less has examined its effect on biomass and the interaction between abundance and distribution.

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