Marine assemblages respond rapidly to winter climate variability

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Abstract

Even species within the same assemblage have varied responses to climate change, and there is a poor understanding for why some taxa are more sensitive to climate than others. In addition, multiple mechanisms can drive species’ responses, and responses may be specific to certain life stages or times of year. To test how marine species respond to climate variability, we analyzed 73 diverse taxa off the southeast US coast in 26 years of scientific trawl survey data and determined how changes in distribution and biomass relate to temperature. We found that winter temperatures were particularly useful for explaining interannual variation in species’ distribution and biomass, although the direction and magnitude of the response varied among species from strongly negative, to little response, to strongly positive. Across species, the response to winter temperature varied greatly, with much of this variation being explained by thermal preference. A separate analysis of annual commercial fishery landings revealed that winter temperatures may also impact several important fisheries in the southeast United States. Based on the life stages of the species surveyed, winter temperature appears to act through overwinter mortality of juveniles or as a cue for migration timing. We predict that this assemblage will be responsive to projected increases in temperature and that winter temperature may be broadly important for species relationships with climate on a global scale.

Keywords: climate change, distribution, fisheries, range shifts, temperature, winter

Introduction

The global redistribution of species is a prominent impact of climate change (Parmesan & Yohe, 2003; Chen et al., 2011; Sunday et al., 2012). Within species assemblages, spatial shifts of individual taxa have been associated with local climate velocities, but these distribution responses can vary widely among taxa (Comte & Grenouillet, 2013; Pinsky et al., 2013; VanDerWal et al., 2013; Sunday et al., 2015). Complex responses within assemblages are expected because co-occurring species vary in thermal preference and habitat requirements. However, we are only beginning to understand the sources of interspecific variation in climate responses (Poloczanska et al., 2013; Sunday et al., 2015). Potential drivers of species’ responses to climate include directed movement of mobile taxa (Murawski, 1993; Lehikoinen et al., 2013; Hill et al., 2016), dispersal of offspring into new habitat (Figueira & Booth, 2010; Hare et al., 2012), and differential population growth rates at range boundaries (Hare et al., 2010; Pershing et al., 2015). Understanding these mechanisms is not straightforward because organisms are likely to be most sensitive to climate only at certain times of year or during specific periods of the life cycle (Poloczanska et al., 2013; Sunday et al., 2015).

Determining how assemblages respond to interannual climate variability can provide insights into mechanisms behind long-term changes and can indicate how rapidly communities might respond to future climate change (Ladwig et al., 2016; Ozkundakci et al., 2016). There is still a poor understanding for how climate variability impacts entire assemblages, which consist of many species with variable dispersal abilities. For example, highly mobile species may be able to rapidly respond to annual variation in temperature (Kohut et al., 2013; Hill et al., 2016). For other species, larval dispersal and juvenile mortality can affect the distribution of a single year class, which may persist through the adult stage (Rindorf & Lewy, 2006; Hare & Able, 2007; Wuenschel et al., 2012; Cooper & Nichol, 2016). Because long-term trends in the distribution of marine species have been linked to thermal preference (Sunday et al., 2012; Pinsky et al., 2013), we expect that the thermal preference of a species may be a useful predictor for how it will respond to climate variability in a region (Simpson et al., 2011).
Here we use scientific survey and commercial fishery data to show that interannual variation in the distribution and biomass of species within the coastal marine assemblage of the Southeast United States Shelf is related to variation in temperature. Our results suggest that winter temperatures are an important factor determining the geographic distribution of species on the US southeast coast. We show that species do not respond uniformly to winter temperatures, but that the direction and magnitude of species’ responses are predictable based on thermal preference. Therefore, thermal preference can provide a framework for predicting how future climate change may impact assemblages. Based on the life stages of taxa captured in the survey, we are able to infer potential mechanisms that drive species responses to climate variability, many of which may contribute to long-term distribution shifts.

Materials and methods

Study area

The Southeast US Shelf is bound by Cape Hatteras, North Carolina, to the north and Cape Canaveral, Florida to the south (Fig. 1). Both of these coastal features represent major oceanographic and biogeographic breaks. North of Cape Hatteras, coastal water temperatures decline sharply (Shearman & Lentz, 2010) and larval transport across the Cape is disrupted by the divergence of the Gulf Stream (Grothues et al., 2002; Pappalardo et al., 2015). South of Cape Canaveral, the range in annual temperatures is relatively low (Shearman & Lentz, 2010) and fish communities to the north and south of this break are distinct (Shertzer et al., 2009). The Southeast US Shelf is often described as an area of overlap between temperate and tropical fauna, and tropical species are common on the outer continental shelf where winter temperatures are mild (Parker & Dixon, 1998; Shertzer et al., 2009; Whitfield et al., 2014). Nearshore water temperatures of the Southeast US Shelf are mostly influenced by atmospheric processes; during winter, a strong cross-shelf gradient exists, and temperatures become more moderate in deeper waters due to the influence of the Gulf Stream (Atkinson et al., 1983; Miles & He, 2010). There has been no long-term trend (~120 years) in sea surface temperature in the coastal southeast, which contrasts sharply with the continental shelf of the northeast United States (Shearman & Lentz, 2010).

Temperature data

We calculated annual winter and spring temperature anomalies using both atmospheric and water temperatures at five locations in the southeast United States (Fig. 1). However, we found that temperature anomalies from the North Carolina atmospheric data effectively represented interannual temperature variation throughout the southeast United States, and so we only used the North Carolina atmospheric data for comparison to biological data (Fig. 2; Appendix S1; Table S2). The North Carolina atmospheric data record was also more complete than the other sources. Atmospheric temperatures have been used previously to represent coastal water temperatures in this region (Hare & Able, 2007; Hare et al., 2012), and we found a strong correlation between water and atmospheric temperatures throughout the coastal southeast United States in winter and spring (Fig. 2; Appendix S1; Table S1). Satellite-derived sea surface temperature data were examined as an alternative (Reynolds et al., 2007), but we did not use these data because they had an unrealistic decline in winter temperatures over the past 25 years that was not present with buoy data.

Annual anomalies were calculated using mean daily temperature values, excluding days with <15 hourly measurements. Missing daily values were interpolated using generalized additive models (GAMs) where daily temperature was a response predicted by day of year as a smoothed term and year as a categorical predictor. Years with more than 15% of daily values missing for a given season and location were excluded. We used December 1 through March 20 for winter
temperature anomalies because this represented the coldest 110 days of the year in North Carolina. We chose a spring date range of March 21 through May 10, which begins two weeks before the average initiation of the spring trawl survey and ends when 90% of the survey is typically complete (Fig. S1). Two annual spring anomalies were missing for the North Carolina atmospheric data, and these values were estimated from regressions with North Carolina water temperatures (Table S1).

Trawl survey

The Southeast Area Monitoring and Assessment Program in the South Atlantic (SEAMAP-SA) has been conducting spring, summer, and fall bottom trawl surveys on the nearshore Southeast US Shelf annually since 1989. The survey samples between Cape Hatteras, North Carolina, and Cape Canaveral, Florida (Fig. 1). Only a single depth stratum has been sampled consistently, which occurs between the 4- and 10-m isobaths and is split into 24 strata that follow the coastline. The deeper strata (10–19 m depth) lacked spatial and temporal coverage and so were not included in our analysis. We only examined taxa that were sorted to the species level. Further information regarding the SEAMAP-SA survey is available online (http://www.seamap.org/CoastalSurvey.html).

All analyses of survey data (both distribution and biomass) were based on annual biomass estimates within strata, and each season was analyzed independently. We calculated biomass for each species in each stratum by dividing total captured biomass by area sampled per stratum and then multiplying this by stratum area. Stratum areas were calculated by multiplying length of coastline by a standardized value for stratum width equal to the net-sampling width of the SEAMAP-SA dual trawls. Some year-season combinations were excluded from analysis due to low sampling effort (all of 1989) or incomplete sampling of strata (fall 1990 and spring 2013). Only species that were collected at least an average of 10 times per year within seasons were considered for analysis (Table S7).

Annual mean center of latitudinal biomass (centroid) was estimated for each species within each season by calculating the stratum-biomass weighted average latitude. Our analysis of distribution was restricted to latitude, because the strata for this survey are predominantly arranged in a north–south direction. Annual biomass for each species was calculated within seasons by summing stratum biomass estimates. We expected that species responses to interannual variation in winter temperatures would be most pronounced in the northern region of the Southeast US Shelf where seasonal variation is greatest (Shearman & Lentz, 2010). Therefore, biomass was estimated using strata that are located north of 32°N latitude (n = 14), which corresponds to North and South Carolina. South of 32°N, average winter water temperatures increase rapidly with declining latitude, while isotherms north of 32°N generally follow the coastline (Atkinson et al., 1983; Wuneschel et al., 2012). Annual biomass values were transformed by adding one and taking the natural logarithm of the sum to normalize residual distributions, then standardized by subtracting the mean and dividing by the standard deviation to aid in comparing parameters across taxa (Gotelli & Ellison, 2013).

We used linear regression to describe long-term trends in distribution and biomass between 1990 and 2015 (Nye et al., 2009; Pinsky et al., 2013). A two-way contingency test was used for each season to determine whether taxa with significant (P < 0.05) long-term distribution shifts were more likely to be associated with significant long-term trends in total biomass.

Response of assemblages to interannual temperature variation

We determined whether winter and spring temperature anomalies explained annual variation in centroid location and total biomass for both the spring and summer assemblages. The fall assemblage was not included with these analyses.
because catches in this season are comprised largely of young-of-the-year for many species (ASMFC, 2000). Also, we did not relate summer temperatures to species data because regional temperature anomalies within the southeast United States did not covary (Table S2) and because atmospheric and water temperatures were not as strongly coupled (Table S1) during this season. To focus on interannual variation rather than long-term trends, we detrended annual time series of latitudinal centroids and of standardized biomass for each species and season using one of three regression models: a null model containing only an intercept term, a model containing an intercept and slope term, or a model containing intercept, slope, and quadratic terms (Fig. 3a, d). For a given species and season, the residuals of the model with the lowest AICc (AIC adjusted for smaller sample size; Burnham & Anderson, 2002) were used as the annual distribution or biomass anomalies. We then used linear regressions to test whether the annual anomalies of distribution and biomass were related to annual temperature anomalies in winter (Fig. 3b, e) and spring (Fig. 3c, f).

Next, we examined whether the magnitude and direction of species responses to interannual temperature variability were related to species’ thermal preference. Thermal preferences were estimated by combining data from the southeast United States (SEAMAP-SA) with other surveys conducted in the Gulf of Mexico, the northeast United States, and the Scotian Shelf (Table S5). Data from these surveys had been previously organized and quality controlled for species distribution analysis (Pinsky et al., 2013). For each species, two GAMs were fit to the combined survey data. The first GAM modeled the probability of species presence in a haul based on bottom temperature and had binomial errors. The second GAM was fit only to hauls where a given species was present and modeled log catch-per-unit-effort based on bottom temperature and survey region, which was included as a factor variable. This approach worked well for our goal to create a simple metric of species temperature preference. For each species, the product of the two GAM predictions was used to create temperature-biomass curves. The median value under the curve was used as an indicator of thermal preference.

We then examined whether thermal preference helped explain assemblage-level responses to interannual temperature variation. The distribution and biomass responses of all taxa to temperature variability (i.e., slope values from regressions, see Fig. 3b, c, e, f) were related to thermal preference of each species for the spring and summer assemblages. Annual winter and spring temperature anomalies in North Carolina were weakly correlated [slope(se) = 0.35(0.165), $F_{1,27} = 4.37$, $P = 0.05$, $r^2 = 0.11$; Fig. S3], and we therefore examined species responses to winter and spring temperatures separately. We compared the strength of results from these two seasons to
determine whether winter or spring temperatures had a greater impact on the assemblages.

In addition, we modeled annual centroid and biomass anomalies with linear mixed-effects models in a model choice framework. We examined four response variables: spring distribution centroid anomalies, spring biomass anomalies, summer distribution centroid anomalies, and summer biomass anomalies. For each response variable, the two full models included annual temperature anomaly (either winter or spring) and species’ temperature preference as main effects, as well as an interaction term between these two main effects. To help account for nonindependence in the data (multiple years of observations for each species), we included species as a random effect on the slope of the species-specific relationship with winter or spring temperature. Intercept terms did not improve model fits and so were excluded (this was expected because response variables were anomalies with means of zero). Diagnostic plots verified that residuals were approximately normally distributed and homoscedastic across fitted values.

We then compared the full models to each other and to simpler models that dropped the interaction term, that dropped the interaction term and the temperature preference term, or that only had a single mean value (the null model). For each group of models, we selected the model with the lowest AIC (Burnham & Anderson, 2002) to determine whether winter or spring temperatures better explained annual variation of species distribution and biomass and also to determine whether the interaction term should be included. Selecting an interaction term indicated that thermal preference helped explain species-level responses to interannual temperature variability. Finally, pairwise Wald chi-square tests were used to confirm model selection based on AIC values (Bolker et al., 2009); we found complete agreement between these two model selection techniques. All modeling was conducted with R version 3.3.1 (R Core Team, 2016) using the mgcv package for GAMs (Wood, 2011), and the lme4 package for mixed-effects models (Bates et al., 2015) with the car package to estimate P values for fixed effects (Fox & Weisberg, 2011).

**Commercial catch**

To compare our results from the scientific surveys with an independent data set, we also examined trends in commercial fishery landings. We extracted commercial landings data for 23 species in the southeast United States (North Carolina to Georgia) from the National Marine Fisheries Service’s Annual Commercial Landing Statistics web site (http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html). Florida was excluded because a majority of its eastern coastline is south of the area of interest. Only species that were analyzed in the survey data were included in the analysis of catch data. For eight species, one or more years were removed from the beginning or end of a catch time series if there was an obvious and rapid change in the fishery (Table S4), such as the drop in Atlantic menhaden landings in 2005 following the closure of the last processing plant in the southeast (SEDAR 40, 2015). Catch data were analyzed with the same methods that were used for the biomass analysis from the survey data, which included log-transforming and standardizing annual catch weight, and regressing the detrended values against winter and spring temperature anomalies.

**Results**

**Long-term distribution trends**

Consistent with the relative stability of recent temperatures in the southeast United States, there was no evidence for long-term trends in latitudinal distribution at the assemblage level (i.e., all taxa combined). The mean of all species slopes of centroid over time was not significantly different from zero in any season (t-tests within seasons: all $P > 0.17$; mean(se) slope for spring $= 0.006 (0.005)$, summer $= 0.007 (0.005)$, fall $= -0.002 (0.005)$). However, 32 taxa shifted significantly to the north or south in one or more seasons (Appendix S2). There was no significant association between shifts in distribution and biomass trends for the spring ($\chi^2 = 3.76, P = 0.052$), summer ($\chi^2 = 0.08, P = 0.78$), or fall ($\chi^2 = 0.03, P = 0.86$) assemblages.

**Effects of interannual temperature variation on distribution and biomass**

Species within the spring assemblage varied widely in annual distribution and biomass responses to winter temperatures. For 17 of the 61 species (28%) examined, winter temperatures explained a significant ($P < 0.05$, not corrected for multiple tests) amount of interannual variation in spring distribution. A majority of the significant slopes were positive, meaning these species were distributed farther north following mild winters (Fig. 4a). Of particular interest was that species-specific distribution responses to winter temperatures were related to the thermal preference of each species [slope (se) $= 0.015 (0.005)$, $F_{1,59} = 8.87, P = 0.004$, $r^2 = 0.11$]. Species with a thermal preference greater than $-22^\circ C$ were generally distributed farther north after warm winters, while species with lower thermal preferences displayed little response (Fig. 4a).

This pattern was stronger when we examined species’ biomass responses. In the northern region of the Southeast US Shelf, there was a positive relationship between a species’ thermal preference and its spring biomass response to winter temperatures [Fig. 4b; slope(se) $= 0.032 (0.005)$, $F_{1,59} = 43.69, P < 0.001$, $r^2 = 0.42$]. Of 61 species examined, 18 (30%) individual responses were significant. Therefore, after warm winters, the spring assemblage in the northern region of the Southeast US Shelf had relatively greater abundances of species with higher thermal preferences ($> 20^\circ C$) and reduced abundances of species with lower thermal preferences ($< 16^\circ C$).
The influence of winter temperatures carried over into the summer assemblage, but this effect was only observed with biomass and the effect was weaker. Across 64 taxa, species with lower thermal preferences had a greater tendency to have lower summer biomass following warmer winters, while warmer-water taxa showed no general response to winter temperature [Fig. 5; slope(SE) = 0.016(0.006), F1,62 = 6.70, P = 0.01, r2 = 0.08]. The distribution responses of species to winter temperatures were not related to thermal preference within the summer assemblage (F1,62 = 0.36, P = 0.55). Mixed-effects models for annual distribution and biomass anomalies suggested conclusions similar to those reached from separate linear regressions (Tables 1 and 2). While a model with only winter temperature could explain some of the interannual variation across all species, models that allowed the direction and magnitude of response to depend on each species’ temperature preference (i.e., models that included a winter temperature × thermal preference interaction) were preferred (Table 1). This effect was particularly strong for spring biomass (ΔAIC 30.3) and spring distribution (ΔAIC 4.9), was weaker for summer biomass (ΔAIC 2.6), and did not appear for summer distribution (preferred model only included spring temperature).

Generally, responses of species to spring temperature anomalies resulted in fewer significant relationships compared to relationships with winter temperatures (Table S6). In addition, our mixed-effects models strongly suggested that winter temperatures were a more important influence than spring temperatures on species distribution and biomass, even for the spring assemblage (ΔAIC values >28) and for biomass in the summer assemblage (ΔAIC = 19.6). Spring temperatures, however, were more important for summer distributions (Table 1). Overall, winter temperatures appear to be more important than spring temperatures for predicting the distribution and biomass patterns of this assemblage.

**Effects of interannual temperature variation on commercial landings**

Interannual variation in seven of 23 southeast US fisheries (30%) was significantly related to winter temperatures. These fisheries included some economically valuable species such as white and pink shrimp, for which landings were positively related to winter temperatures, and Atlantic croaker, summer flounder, and bluefish, for which landings were negatively related to winter temperatures. Variation in catch of Atlantic menhaden was the only fishery related to variation in spring temperatures. Commercial fishery landings’ responses to winter or spring temperatures were not...
significantly related to thermal preference [winter slope (se) = 0.011(0.01), F\textsubscript{1,21} = 1.27, P = 0.27; spring slope (se) = 0.001(0.01), F\textsubscript{1,21} = 0.04, P = 0.85].

Discussion

Winter has long been recognized as a critical season for marine taxa (Hurst, 2007). Winter climate can affect spatial mortality patterns and phenology, which can have cascading effects on assemblages throughout the year (Wingate & Secor, 2008; Ladwig et al., 2016). To date, research has primarily focused on a small number of species and been conducted in temperate zones or areas of high latitude, although recent studies suggest that the importance of winter climate may extend into lower latitudes (Parker & Dixon, 1998; Hare & Able, 2007; Tolan & Fisher, 2009; Figueira & Booth, 2010; Alheit et al., 2012). To our knowledge, the present study represents the first time winter temperatures have been examined for a wide array of marine taxa across broad spatial and temporal scales. We found that the effects of winter temperature were apparent in both the spring and summer assemblages, which suggests that winter temperatures can impact annual recruitment and migration patterns. We note that summer temperatures were not related to winter or spring temperatures (Appendix S1), so the response of the summer assemblage to temperatures during the previous winter was not confounded by years that may have been generally warm or cold in all seasons.

The distribution and biomass response to winter temperature varied substantially among species, ranging from strongly negative, to no response, to strongly positive. A key finding of our analysis was that this variation in response to winter temperatures was linked to thermal preference. This pattern was strongest for the spring assemblage. Following mild winters, species preferring warmer waters showed a greater tendency to be more abundant in the northern region of the Southeast US Shelf, resulting in a more north-shifted center of biomass. Conversely, cold-water species were less abundant following mild winters, although they showed no general distribution response. The lack of distribution responses among cold-water species may occur because many of these species are not as widespread throughout the Southeast US Shelf as warm-water taxa, which limited our ability to detect distribution responses among them.

During the spring, thermal preference explained a small but significant amount of variation in assemblage-scale responses to winter temperatures. The biomass of cold-water species within the summer assemblage generally decreased after warmer winters, which was consistent with the patterns observed in spring. There may be several explanations for why the summer responses were not as strongly related to thermal preference as in the spring assemblage. First, the species included in each assemblage differed, and the summer assemblage contained more warm-water species. When we restricted the summer assemblage to only contain species also represented in spring (n = 52), the relationship between species responses to winter temperatures and thermal preference markedly improved [Fig. S4; slope(se) = 0.027(0.007), F\textsubscript{1,50} = 15.64, P < 0.001, r\textsuperscript{2} = 0.22]. Second, while the spring survey caught mainly age-1 and older individuals for most species, the summer survey also captured young-of-the-year fish (ASMFC, 2000), which may not be as strongly affected by conditions during the previous winter. Finally, for some species, winter temperatures may most strongly influence the phenology of annual migrations, which may primarily occur in spring.

Distribution patterns of marine species are influenced by multiple factors, and we have focused only on seasonal temperatures and species thermal preferences. The unexplained variability in our regressions probably

![Graph](https://example.com/graph.png)

Fig. 5 Biomass responses of 64 species within the summer assemblage to winter temperature anomalies, as related to temperature preference. Positive values indicate species with higher summer biomass following warm winters. Solid points represent species with significant (P < 0.05) relationships between biomass and winter temperatures at an annual scale. Dashed lines are 95% confidence intervals around the regression (P = 0.01, r\textsuperscript{2} = 0.08). Graphic for bluefish Pomatomus saltatrix represents the species indicated by the circled point. [Colour figure can be viewed at wileyonlinelibrary.com].
Table 1  Mixed-effects models fit to annual species distribution (centroid) and biomass anomalies during spring and summer where $W_{temp} =$ winter temperature anomaly, $S_{temp} =$ spring temperature anomaly, $T_{pref} =$ species thermal preference, $\times =$ interaction between two variables, $\Delta AIC_c =$ difference in AICc between a model and the model with lowest score, and $w_i =$ AICc weight. The best model fit for each response variable is in bold. Individual species relationships with $W_{temp}$ or $S_{temp}$ were modeled as random effects.

| Model predictors             | Random effects | $\Delta AIC_c$ | $w_i$ |
|------------------------------|----------------|---------------|-------|
| Spring centroid anomalies    | $W_{temp}$, $T_{pref}$, $W_{temp} \times T_{pref}$ | $W_{temp}$|species| 0  | 0.89 |
| $W_{temp}$, $T_{pref}$      | $W_{temp}$|species| 6.8 | 0.03 |
| $S_{temp}$, $T_{pref}$, $S_{temp} \times T_{pref}$ | $S_{temp}$|species| 30.2 | <0.01 |
| $S_{temp}$, $T_{pref}$      | $S_{temp}$|species| 30.4 | <0.01 |
| $S_{temp}$                   | $S_{temp}$|species| 28.7 | <0.01 |
| Null-intercept only          | None          | 39.0          | <0.01 |
| Spring biomass anomalies     | $W_{temp}$, $T_{pref}$, $W_{temp} \times T_{pref}$ | $W_{temp}$|species| 0  | 0.99 |
| $W_{temp}$, $T_{pref}$      | $W_{temp}$|species| 31.8 | <0.01 |
| $W_{temp}$                   | $W_{temp}$|species| 30.3 | <0.01 |
| $S_{temp}$, $T_{pref}$, $S_{temp} \times T_{pref}$ | $S_{temp}$|species| 47.9 | <0.01 |
| $S_{temp}$, $T_{pref}$      | $S_{temp}$|species| 68.4 | <0.01 |
| $S_{temp}$                   | $S_{temp}$|species| 68.5 | <0.01 |
| Null-intercept only          | None          | 113.8         | <0.01 |
| Summer centroid anomalies    | $W_{temp}$, $T_{pref}$, $W_{temp} \times T_{pref}$ | $W_{temp}$|species| 7  | 0.02 |
| $W_{temp}$, $T_{pref}$      | $W_{temp}$|species| 5.3  | 0.04 |
| $W_{temp}$                   | $W_{temp}$|species| 3.3  | 0.10 |
| $S_{temp}$, $T_{pref}$, $S_{temp} \times T_{pref}$ | $S_{temp}$|species| 3.3  | 0.10 |
| $S_{temp}$, $T_{pref}$      | $S_{temp}$|species| 1.9  | 0.20 |
| $S_{temp}$                   | $S_{temp}$|species| 0    | 0.51 |
| Null-intercept only          | None          | 4.5           | 0.05  |
| Summer biomass anomalies     | $W_{temp}$, $T_{pref}$, $W_{temp} \times T_{pref}$ | $W_{temp}$|species| 0  | 0.72 |
| $W_{temp}$, $T_{pref}$      | $W_{temp}$|species| 4.5  | 0.08 |
| $W_{temp}$                   | $W_{temp}$|species| 2.6  | 0.20 |
| $S_{temp}$, $T_{pref}$, $S_{temp} \times T_{pref}$ | $S_{temp}$|species| 19.6 | <0.01 |
| $S_{temp}$, $T_{pref}$      | $S_{temp}$|species| 25.5 | <0.01 |
| $S_{temp}$                   | $S_{temp}$|species| 23.5 | <0.01 |
| Null-intercept only          | None          | 22            | <0.01 |

Table 2  Coefficient and significance values for predictors in four mixed-effects models that were chosen based on AIC criteria. Terms are described in Table 1.

| Model predictors | Effect          | SD  | $\chi^2$ | $P$       |
|------------------|-----------------|-----|---------|-----------|
| Spring centroid anomalies | $W_{temp}$      | -0.2770 | 0.117 | 16.19 | <0.001 |
|                   | $T_{pref}$      | -0.0004 | 0.001 | 0.18 | 0.670 |
|                   | $W_{temp} \times T_{pref}$ | 0.0150 | 0.005 | 9.47 | 0.002 |
| Spring biomass anomalies       | $W_{temp}$      | -0.6020 | 0.114 | 66.20 | <0.001 |
|                   | $T_{pref}$      | -0.0070 | 0.001 | 0.49 | 0.480 |
|                   | $W_{temp} \times T_{pref}$ | 0.0320 | 0.005 | 45.04 | <0.001 |
| Summer centroid anomalies      | $S_{temp}$      | -0.0490 | 0.019 | 6.50 | 0.010 |
| Summer biomass anomalies        | $W_{temp}$      | -0.4460 | 0.152 | 6.09 | 0.014 |
|                   | $T_{pref}$      | 0.0002 | 0.001 | 0.08 | 0.779 |
|                   | $W_{temp} \times T_{pref}$ | 0.0160 | 0.006 | 6.87 | 0.009 |

primarily as age-1 fish, particularly during the spring. The distribution patterns of these species may be influenced by recruitment dynamics during the previous year, which are notoriously stochastic (Rindorf & Lewy, 2006; Hare & Able, 2007; Wenschel et al., 2012; Cooper & Nichol, 2016). Considering the size of these other sources of variability, it is perhaps surprising that we can detect any influence of winter temperatures on species and on the assemblage.

Mechanisms behind species responses to winter temperatures

The mechanisms behind the observed responses to winter temperature variability depend in part on the species and life stage captured by the SEAMAP trawl survey. Many of the taxa included in our analysis are comprised mostly of age-1 individuals, particularly for the teleost fishes and penaeid shrimp (ASMFC, 2000). Therefore, for many nonmigratory species, variability in distribution and biomass during spring and summer is likely to reflect spatial patterns of overwinter mortality for young-of-the-year. This life stage is particularly vulnerable during winter (Hurst, 2007). For example, juvenile survival of Atlantic croaker (Micropogonias undulatus) is strongly related to winter temperatures off the northeast US coast, and mild winters result in strong year classes that can persist for many years (Hare & Able, 2007). Our analysis suggests that a number of species are similarly affected by winter severity in this region.
including silver seatrout (Cynoscion nothus) and star drum (Stellifer lanceolatus). These species are near their northern range limit, and year class strength appears to be related to winter severity.

White shrimp (Liopsetenaus setiferus) and pink shrimp (Farfantepenaus duorarum) were among the most sensitive taxa to winter temperatures in our analyses. These taxa represent resident species near their northern range limit, and their population growth rates are sensitive to winter conditions (Hettler, 1992; DeLancey et al., 2005). These species complete their life cycle within one year, and they have relatively limited capacity to avoid low temperatures during winter. To our knowledge, white and pink shrimp are the only commercial fisheries, of the twenty-three we examined, where a connection between winter temperatures and catch has been previously recognized and is included in a fishery management plan (Hettler, 1992; DeLancey et al., 2005). Winter temperatures are monitored, and closures may be enacted to protect the spawning stock of these species during spring (NMFS, 2013).

Winter temperatures may also influence more mobile species by affecting the phenology or extent of seasonal migrations. For example, young-of-the-year bluefish (Pomatomus saltatrix) overwinter on the Southeast US Shelf. Following winter, some of the age-1 fish remain in the region, while others migrate north and out of the study region (Morley et al., 2013). More severe winters lead to an energetic deficit in age-1 bluefish (Morley et al., 2007). Therefore, the increased summer biomass on the Southeast US Shelf following colder winters may represent a greater proportion of age-1 fish that have low-energy reserves and choose to remain in the region rather than migrating north. These age-1 fish typically comprise the majority of the commercial catch (SAW assessment report, 2015), which may explain why fishery landings were also significantly related to winter temperatures for this species.

Implications for climate change

The Southeast US Shelf is one of the few coastal regions of North America where long-term water temperatures have been relatively stable over the last century (Shearman & Lentz, 2010; Burrows et al., 2011). Therefore, the lack of a long-term latitudinal trend in the distribution of the coastal assemblage might be expected (Pinsky et al., 2013). However, a 2–3°C increase in winter bottom temperatures is projected for this region by the end of the century, unless major reductions in carbon emissions occur (Grieve et al., 2016). Examining interannual variation in community responses to climate variables can provide a basis for making projections of assemblage responses to future climate scenarios (Sims et al., 2001; Pershing et al., 2015; Ladwig et al., 2016; Ozkundaci et al., 2016). Our results provide insight into the mechanisms that may be driving changes in species distribution and regional biomass, which is important because mechanisms behind changes in species distribution are often poorly understood and because nonclimatic factors such as fishing pressure can obscure how species respond to climate (Bell et al., 2015; Brown et al., 2016). The southeast US coastal assemblage responded to interannual climate variability in a manner predicted by theory that associates geographic range of species with thermal tolerance (Sunday et al., 2012). Given the sensitivity of this assemblage at an annual timescale, we expect that it will also be responsive to future long-term increases in temperature.

On the Southeast US Shelf, winter temperatures may be of particular importance as a biogeographic barrier for many tropical species. While this region appears to be suitable thermal habitat for many tropical species during summer, sporadic cold winter temperatures may prevent these species from becoming fully established. For example, periodic cold winters prevent tropical invasive species from becoming permanently established within southeast US estuaries (Canning-Clode et al., 2011). Further, in deeper habitats of this region, winter appears to define depth distributions of taxa within the diverse reef fish assemblage (Parker & Dixon, 1998; Whittfield et al., 2014). These observations are consistent with a review by Myers (1998), which found that species associations with climate are more predictable near the edge of geographic ranges.

Based on our findings, we expect that increased winter temperatures will affect the Southeast US Shelf in a number of important ways. First, we expect that species with more southern affinities will experience increased juvenile survival during winter, which will lead to greater abundance of species like white shrimp and star drum north of Florida. This would impact overall community structure, as southern species will likely compete for the same niche space as taxa that are currently common. For example, on the northern Gulf of Mexico coast, many of the more northern taxa were lost entirely after ~3°C of warming, which led to the introduction of many tropical species (Fodrie et al., 2010). Second, the depth distribution of many warm-water species on the continental shelf may expand toward the coast, as winter isotherms shift into shallower habitats (Whittfield et al., 2014; Grieve et al., 2016). Parker & Dixon (1998) resampled a location offshore of North Carolina after a 15-year period of increasing winter temperatures and found higher abundances of tropical species. Third, the seasonal presence of more mobile species appears likely to change as winter temperatures affect phenology. Phenological changes can have dramatic effects on
ecological communities and on fisheries (Mills et al., 2013).

In a time of rapidly changing climate, detecting and anticipating changes in recruitment, population growth, phenology, and ultimately the distribution of marine species is of vital importance for successful resource management (Pinsky & Mantua, 2014). In the southeast United States, taxa such as penaeid shrimp that are commonly caught in the SEAMAP-SA survey may be useful indicators for bioclimatic variability, which is a management research priority in this region (http://secoora.org/fisheriesclimateriskworkshopsum). More broadly, examining the response of species to climate variability can be an effective tool to identify particularly vulnerable species.

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References

Alheit J, Pohmann T, Casini M et al. (2012) Climate variability drives anchovies and sardines into the North and Baltic Seas. Progress in Oceanography, 96, 128–139.

ASMFC (2000) SEAMAP-SA 10-year travel report: results of traveling efforts in the coastal habitat of the South Atlantic Bight, FY 1990–1999. Special Report No. 71 of the Atlantic States Marine Fisheries Commission. South Carolina Department of Natural Resources, Charleston, SC.

Atkinson LP, Lee TN, Blanton JO, Chandler WS (1983) Climatology of the southeastern United States continental shelf waters. Journal of Geophysical Research, 88, 4705–4718.

Bates D, Maechler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67, 1–48.

Bell RJ, Richardson DE, Hare JA, Lynch PD, Fratantoni PS (2013) Disentangling the effects of climate, abundance, and size on the distribution of marine fish: an example based on four stocks from the northeast US shelf. ICES Journal of Marine Science, 70, 1311–1322.

Bolker BM, Brooks ME, Clark CJ et al. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution, 24, 127–135.

Brown CJ, O’Connor MI, Poloczanska ES et al. (2016) Ecological and methodological drivers of species’ distribution and phenology responses to climate change. Global Change Biology, 22, 1548–1560.

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer, New York.

Burrows MT, Schoeman DS, Buckley LB et al. (2011) The pace of shifting climate in marine and terrestrial ecosystems. Science, 334, 652–655.

Canning-Clode J, Fowler AE, Byers JE, Carlton JT, Ruiz GM (2011) ‘Caribbean Creep’ chills out: climate change and marine invasive species. PLoS ONE, 6, e29657.

Chen I, Hill JK, Ohlemuller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science, 333, 1024–1026.

Comte L, Gomollaret G (2013) Do stream fish track climate change? Assessing distribution shifts in recent decades. Ecology, 96, 1236–1246.

Cooper DW, Nichol DG (2016) Juvenile northern rock sole (Leipsodesota polyzona) spatial distribution and abundance patterns in the eastern Bering Sea: spatially dependent production linked to temperature. ICES Journal of Marine Science, 73, 1138–1146.

DeLancey LB, Jenkins JE, Maddox MB et al. (2005) Field observations on white shrimp, Litopenaus setiferus, during spring spawning season in South Carolina, USA, 1980–2003. Journal of Crustacean Biology, 25, 212–218.

Figueira WP, Booth DJ (2010) Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. Global Change Biology, 16, 506–516.

Fedrice FJ, Heck KL, Powers SP et al. (2010) Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico. Global Change Biology, 16, 48–59.

Fox J, Weisberg S (2011) An (R) Companion to Applied Regression, 2nd edn. Sage, Thousand Oaks CA. Available at: http://soscerv.sosci.mcmaster.ca/jfox/Books/Companion (accessed 25 September 2016).

Gotelli NJ, Ellison AM (2013) A Primer of Ecological Statistics, 2nd edn. Sinauer Associates, Inc. Sunderland, MA, USA.

Grieve BD, Curchetser EN, Ryackowski RR (2016) Range expansion of the invasive lionfish in the Northwest Atlantic with climate change. Marine Ecology Progress Series, 546, 225–237.

Grohues TM, Cowen RK, Pietrzala JI, Bignami P, Weatherly GL, Flagg CN (2002) Flux of larval fish around Cape Hatteras. Limnology and Oceanography, 47, 165–175.

Hare JA, Able KW (2007) Mechanistic links between climate and fisheries along the east coast of the United States: explaining population outbreaks of Atlantic croaker (Micropogonias undulatus). Fisheries Oceanography, 16, 31–45.

Hare JA, Alexander MA, Fogarty MJ, Williams EH, Scott JD (2010) Forecasting the dynamics of a coastal fishery species using a coupled climate-population model. Ecological Applications, 20, 452–464.

Hare JA, Waenschel MJ, Kimball ME (2012) Projecting range limits with coupled thermal-tolerance-climate change models: an example based on gray snapper (Lutjanus griseus) along the U.S. east coast. PLoS ONE, 7, 1–13.

Hettler WF (1992) Correlation of winter temperature and landings of pink shrimp Penaeus aztecus in North Carolina. Fishery Bulletin, 90, 405–406.

Hill NJ, Tobin AJ, Reside AE, Pepperell JC, Bridge TCL (2016) Dynamic habitat suitability modeling reveals rapid poleward distribution shift in a mobile apex predator. Global Change Biology, 22, 1086–1096.

Hurst TP (2007) Causes and consequences of winter mortality in fishes. Journal of Fish Biology, 71, 315–345.

Kohut J, Palamara L, Curchetser IS, Didomenico G, Manderson J, Oliver MJ (2013) Toward dynamic marine spatial planning tools: an example with butterfish assessment in the Mid-Atlantic Bight. In: MTS/IEEE OCEANS Conference, 1–4. Institute of Electrical and Electronics Engineers, Curran Associates, Inc. Bergen, Norway, June 2013.

Ladwig LM, Ratajczak ZR, Ocheltree TW et al. (2016) Beyond arctic and alpine: the influence of winter climate on temperate ecosystems. Ecology, 97, 372–382.

Lehkoinen A, Jaatinen K, Vahatalo AV et al. (2013) Rapid climate driven shifts in wintering distributions of three common waterbird species. Global Change Biology, 19, 2071–2081.

Miles TN, He R (2010) Spatial and temporal variability of Chl-a and SST on the South Carolina shelf: relationship to water mass and air-sea forcing. Continental Shelf Research, 30, 1915–1926.

Murawski SA (1993) Climate change and marine fish distributions: forecasting from historical records. Marine and Freshwater Research, 43, 885–916.

Morley JW, Buckley JA, Lankford TE (2007) Winter energy storage dynamics and cohort structure of year-of-the-year bluefish Pomatomus saltatrix off North Carolina. Marine Ecology Progress Series, 334, 273–286.

Morley JW, Buckley JA, Lankford TE (2013) Relative contribution of spring- and summer-spawned bluefish cohorts to the adult population: effects of size-selective winter mortality, overwinter growth, and sampling bias. Canadian Journal of Fisheries and Aquatic Sciences, 70, 233–244.

Murawski SA (1993) Climate change and marine fish distributions: forecasting from historical analogy. Transactions of the American Fisheries Society, 122, 647–658.

Myers RA (1998) When do environmental-recruitment correlations work? Reviews in Fish Biology and Fisheries, 8, 285–305.

NMFS (2013) Shrimp fishery off the southern Atlantic states. Amendment 9. Federal Register, v. 78, No. 114, National Marine Fisheries Service. Available at: http://sams.net/resource/library/shrimp (accessed 10 April 2016).

Nye JA, Link JS, Hare JA, Overholtz WJ (2009) Changing spatial distribution of fish stocks in relation to climate and population size on the northeast United States continental shelf. Marine Ecology Progress Series, 393, 111–129.

Ozkundakci D, Goell AS, Hintze T, Tauscher H, Adrian R (2016) Winter severity determines functional trait composition of phytoplankton in seasonally ice-covered lakes. Global Change Biology, 22, 284–298.

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Pappalardo P, Pringle JM, Wares JP, Byers JE (2015) The location, strength, and mechanisms behind marine biogeographic boundaries of the east coast of North America. *Ecography*, 38, 722–731.

Parker RO, Dixon RL (1998) Changes in a North Carolina reef fish community after 15 years of intense fishing-global warming implications. *Transactions of the American Fisheries Society*, 127, 908–920.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.

Pershing AJ, Alexander MA, Hernandez CM et al. (2015) Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science*, 350, 809–812.

Pinsky ML, Mantua NJ (2014) Emerging adaptation approaches for climate-ready fisheries management. *Oceanography*, 27, 146–159.

Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine taxa track local climate velocities. *Science*, 341, 1239–1242.

Poloczanska ES, Brown CJ, Sydeman WJ et al. (2013) Global imprint of climate change on marine life. *Nature Climate Change*, 3, 919–925.

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/ (accessed 15 July 2016).

Reynolds RW, Smith TM, Liu C et al. (2007) Daily high-resolution-blended analyses for sea surface temperature. *Journal of Climate*, 20, 5473–5496.

Rindorf A, Lewy P (2006) Warm, windy winter drive cod north and homing of spawners keeps them there. *Journal of Applied Ecology*, 43, 445–453.

SAW Assessment Report (2015) Bluefish benchmark stock assessment for 2015. 60th Northeast Regional Stock Assessment Workshop. Northeast Fisheries Science Center. pp. 335–354.

SEDAR 48 (2015) Stock Assessment Report: Atlantic Menhaden. Southeast Data, Assessment, and Review. North Charleston, South Carolina.

Shearman RK, Lentz SJ (2010) Long-term sea surface temperature variability along the U.S. east coast. *Journal of Physical Oceanography*, 40, 1004–1017.

Shertzer KW, Williams EH, Taylor JC (2009) Spatial structure and temporal patterns in a large marine ecosystem: exploited reef fishes of the southeast United States. *Fisheries Research*, 100, 126–133.

Sims DW, Gennier MJ, Southward AJ, Hawkins SJ (2001) Timing of squid migration reflects north Atlantic climate variability. *Proceedings of the Royal Society of London B*, 268, 2607–2611.

Stockhausen WT, Fogarty MJ (2007) Removing observational noise from fisheries-independent time series data using ARIMA models. *Fishery Bulletin*, 107, 88–101.

Sunday JM, Bates AE, Duty NK (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, 2, 686–690.

Sunday JM, Pecl GT, Frusher S et al. (2015) Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, 18, 944–953.

Tolan JM, Fisher M (2009) Biological response to changes in climate patterns: population increases of gray snapper (*Lutjanus griseus*) in Texas bays and estuaries. *Fishery Bulletin*, 107, 36–44.

VanDerWal J, Murphy HT, Kutt AS et al. (2013) Focus of poleward shifts in species' distribution underestimates the fingerprint of climate change. *Nature Climate Change*, 3, 239–243.

Whitfield PE, Munoz RC, Buckel CA, Degan BP, Freshwater DW, Hare JA (2014) Native fish community structure and Indo-Pacific lionfish (*Pterois volitans*) densities along a depth-temperature gradient in Onslow Bay, North Carolina, USA. *Marine Ecology Progress Series*, 509, 241–254.

Wingate RL, Secor DH (2008) Effects of winter temperature and flow on a summer-fall nursery fish assemblage in the Chesapeake Bay, Maryland. *Transactions of the American Fisheries Society*, 137, 1147–1156.

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society B*, 73, 3–36.

Wuenschel MJ, Hare JA, Kimball ME, Able KW (2012) Evaluating juvenile thermal tolerance as a constraint on adult range of gray snapper (*Lutjanus griseus*): a combined laboratory, field and modeling approach. *Journal of Experimental Marine Biology and Ecology*, 436–437, 19–27.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Spatial and temporal variation of SAB temperatures.
Appendix S2 Long-term trends in species distribution.
Table S1 Summary of regression models comparing water vs. atmospheric temperature anomalies during three seasons at three locations within the Southeast U.S. Shelf region.
Table S2 Summary of regression models comparing Cape Lookout, North Carolina atmospheric temperature anomalies with values from other regions, including water and atmospheric values, in the Southeast U.S. Shelf region within seasons.
Table S3 Summary of regression models comparing winter and spring temperature anomalies, for both atmospheric and water temperatures, in four regions of the Southeast U.S. Shelf.
Table S4 Justification for removing select years from time series of commercial fisheries landings in the southeast U.S.
Table S5 Description of bottom trawl surveys used to estimate thermal preference for species within the Southeast U.S.
Table S6 Summary of regression models relating species responses to either winter or spring annual temperature anomalies against temperature preference.
Table S7 Taxa included in spring, summer, and fall assemblages and commercial catch analyses.
Figure S1 The average timing for the SEAMAP-SA annual bottom trawl survey during the spring (left) and summer (right) seasons.
Figure S2 Annual summer (Jun. 24–Aug. 3) temperature anomalies for atmospheric (dashed) and water (solid) temperatures in four regions within the Southeast U.S.
Figure S3 Regression of spring vs. winter atmospheric temperature anomalies for Cape Lookout, North Carolina.
Figure S4 Biomass responses of 52 species within the summer assemblage to winter temperature anomalies, related to temperature preference.