LIMITED RESPONSES OF BENTHIC MARINE COMMUNITIES TO LOCAL

TEMPERATURE CHANGES

By

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ABSTRACT OF THE THESIS

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As global climate change and variability drive changes in regional and local temperatures, species' distributions are shifting, leading to changes in ecological communities. One approach to the problem of anticipating community change has been to characterize communities by a collective thermal preference, or community temperature index (CTI), and then to compare changes in CTI with changes in temperature. However, this method has been tested in only a few ecosystems, and it carries untested assumptions about the responsiveness of communities to changes in their local thermal environments. We used CTI to analyze changes in benthic marine communities along the continental shelf of the Northeast United States. We found that, while community composition was associated with bottom temperature, communities responded much more strongly to interannual variation than to long-term trends in temperature, and a mixed-effects model found that for every 1 ºC increase in bottom temperature, CTI increased by 0.38 ºC. We also showed that nonlinear species' responses to temperature scale up to nonlinear community responses to temperature change. Future research into community change with increasing global temperatures should take into account these nonlinear responses, as well as examine the relative importance of interannual fluctuations and decadal trends.

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**<u>Introduction</u>**

Anthropogenic climate change is altering nearly every natural environment across the

planet (Parmesan & Yohe, 2003; Cheung *et al.,* 2013; IPCC, 2014). Unprecedented

trends and fluctuations in the climate are contributing to complicated and unanticipated

changes in biotic and abiotic environments (Walther *et al.,* 2002; Hoegh-Guldberg &

Bruno, 2010; Urban *et al.,* 2012; IPCC, 2014). Recent research has shown that many

species are responding to climate change by shifting their distributions and by altering the

timing and extent of migrations (Parmesan *et al.,* 1999; Davis & Shaw, 2001; Parmesan

& Yohe 2003; Kleisner *et al.,* 2016). These distribution shifts have often followed the

same trajectories as the species' preferred climates (Parmesan *et al.*, 1999; Dulvy *et al.*,

2008; Bertrand *et al.*, 2011; Pinsky *et al.*, 2013).


However, these same studies have documented substantial heterogeneity in the direction

and magnitude of each species' response to climate change, even among species within

the same ecosystem (Dulvy *et al.*, 2008; Moritz *et al.*, 2008; Sunday *et al.*, 2012, Kleisner

*et al.,* 2016). Unequal responses by coincident species may be due to differences in their

thermal performance curves: two species of ectotherms experiencing the same

temperature change at different points in their thermal performance curves may undergo

disparate changes in metabolism, affecting their respective energetic demands and ability

to catch prey or evade predation (Pörtner, 2001; Pörtner & Knust, 2007), or triggering the

timing of migration or reproduction (Dunn & Winkler, 1999; Parmesan, 2006). An

increase in temperature may be detrimental if it is above a cold-adapted species' thermal

optimum, but beneficial if it moves the environment closer to the optimal temperature for

a cohabitating warm-adapted species (Menendez *et al.*, 2006; Moritz *et al.*, 2008; Bertrand *et al.*, 2011; Kordas *et al.*, 2011).

For this study, we focus on temperature, which has been a useful, first-order approximation of environmental suitability (Sunday *et al.*, 2012; Pinsky *et al.*, 2013). However, differences in individual species' responses to climate change may result from diverse physical and biological niche requirements, such as habitat structure, nutrient levels, and light, or from predators, prey, and symbionts that may enhance or counteract the effects of temperature (Lenoir *et al.*, 2010; Svenning *et al.*, 2014). In addition, human activities such as harvest, pollution, or habitat destruction can amplify or mediate the effects of climate change on already climate-stressed species and communities (Anderson *et al.*, 2008; Lucey & Nye, 2010; Planque *et al.*, 2010). Increased temperature variation, in addition to long-term temperature change, also plays a significant role in determining species' and communities' responses to change (Paaijmans *et al.*, 2013; Vasseur *et al.*, 2014).

As climate change drives increases in mean temperature in many coastal regions (IPCC, 2014), we expect that communities will also change as in-migrating or growing populations of warm-adapted species outcompete or replace out-migrating or declining cold-adapted species. Species turnover from cold-adapted to warm-adapted species causes a change in the community's mean thermal preference, also known as community temperature index (CTI). CTI has been used in a variety of recent studies as a metric for evaluating how well communities are suited to their thermal environments and for

comparing community changes in marine and terrestrial ecosystems on regional and global scales (Devictor *et al.*, 2008; Zografu *et al.*, 2014; Stuart-Smith *et al.*, 2015; Cheung *et al.*, 2013 as "Mean Temperature of the Catch"). While we may broadly expect communities and CTIs to change in response to climate change, we have a poor understanding of the shape of those responses and the rates at which they will change, particularly at the smaller spatial scales most relevant to community formation and species interactions (Menge & Olson, 1990; Levin, 1995; Leibold *et al.*, 2004).

Previous studies have measured community response to temperature change at regional and global scales by directly comparing the values and trends in both CTI and temperature. This comparison is based on the assumption that species turnover and community change should occur linearly with temperature change. More specifically, the (often unstated) null hypothesis is that there should be a one-to-one relationship between change in temperature and change in CTI. However, species' thermal performance curves are typically dome shaped, non-monotonic functions of temperature (Huey & Stevenson, 1979) and the shape of this dome is both asymmetric and varies among species. Changes in environmental temperature may thus lead to nonlinear responses in performance and abundance of each species (Deutsch *et al.*, 2008). Since communities are often comprised of multiple species with overlapping and often asymmetrical thermal performance curves of different heights and widths, we cannot necessarily assume that CTI and temperature change will be linearly correlated. In addition, marine communities tend to be "thermally biased," or dominated by species that have higher or lower thermal preferences than their local environments (Stuart-Smith *et al.*, 2015), which may lead to

communities lagging environmental changes until threshold-crossing temperature change drives a rapid community-wide shift. This combination of asymmetrical thermal performance curves and community thermal biases suggests that CTI may change nonlinearly in response to temperature change (Fig. 1). With the increasing use of CTI for measuring community response to climate change, a quantitative analysis of the effects of these nonlinearities is needed.

The Northeast U.S. continental shelf is home to a Large Marine Ecosystem (LME) that has experienced substantial warming over the last three decades, with the Gulf of Maine warming faster than nearly any other ocean environment in the world (Friedland & Hare, 2007; Belkin, 2009; Shearman & Lentz, 2009; Pershing *et al.*, 2015). This has led to a general shift in isotherms and in the species assemblage to the northeast (Pinsky *et al.*, 2013). Previous studies have also found that climate changes have led to changes in the distribution of several large species assemblages within the LME (Kleisner *et al.,* 2016), as well as to changes in species composition in four large sub-regions within (Lucey & Nye, 2010). While these large-scale and long-term climate and ecological changes are evident across the region, species interactions and communities are formed as much finer spatial scales, and it is not clear whether the same responses to climate change can be seen at these local scale of species interactions.

In this manuscript, we investigated (1) how benthic marine communities along the Northeast U.S. continental shelf have changed over the last 25 years, as quantified by changes in CTI, (2) how these marine communities would have changed if they were

only responding to temperature, and (3) whether temperature is an important factor driving these communities to change over both long and short time-scales. To answer these questions, we evaluated temperature and community change in 146 fine-scale spring and fall assemblages, compared them to interannual variations and long-term trends in the environment, and analyzed whether marine communities in this region are changing at the same rates and with the same sign as their local thermal environments.

**Materials and Methods**

*Survey method and study extent*

We used species and temperature data from the Northeast Fisheries Science Center

(NEFSC) biannual (spring: March-May; fall: September-November) stratified random

bottom trawl surveys of the Northeast U.S. continental shelf (Azarovitz, 1981). The

survey area was divided into 198 strata of varying sizes, with stratum extent determined

in part by depth contour.

The time of year at which the fall surveys were conducted changed over time from the

1960s to the 1980s, potentially creating artificial trends in observed temperatures and

communities (Fig. S1). To avoid this possibility, we used data from 1963-1989 only as a

training set for calculating species' thermal distribution curves, and restricted our analysis

of temperature and community change to the period from 1990-2014. While the fall

surveys earlier in the training set sampled cooler temperatures than did surveys later in

the time-series, these temperatures were similar to those seen throughout the spring time

series, suggesting that training on the first half of the dataset did not skew our calculated

thermal preferences. Most strata were surveyed every season of every year, though not all

strata had complete bottom temperature data.

*Species thermal distributions*

Using modeled biomass distribution across temperature as a measurement of realized

thermal niche (Rutterford *et al.*, 2015), we derived thermal distribution characteristics for

each of the 92 most common species in the survey (found in 100 or more tows in the

1963-1989 training dataset). For each species, we fit a two-stage Generalized Additive Model (GAM) (Hastie & Tibshirani, 1990) based on presence/absence and biomass in the training dataset. This two-stage approach is an effective technique for addressing zero-inflation (Barry & Welsh, 2002, Jensen *et al.*, 2005), a common feature of two-level biomass estimates in this data set (Pinsky *et al.* 2013) and, more generally, of species abundances in trawl or dredge surveys. Generalized Additive Models were fit using the mgcv package (Wood, 2011) in R (R Core Team, 2015), which allows the flexibility of the models (i.e., the number of knots) to be optimized using generalized cross validation.

The first stage of each GAM estimated the probability of presence with binomial errors and a logit link function. The second stage estimated log(biomass) with Gaussian errors and an identity link function, only for tows where a species was present. Explanatory factors in each model included the bottom temperature recorded *in situ* and the species' mean biomass for the year in all spring and fall tows of the testing dataset (including zeroes).

To calculate the full thermal distribution curve for each species, we multiplied the probability of presence from stage one by the exponent of the estimated log biomass from stage two for all temperatures from 0 to 28 °C. Because the use of the exponent of the log transformation creates a biased estimate of the untransformed expectation, we corrected estimated biomass from stage two by multiplying by Duan's smearing estimate (Duan, 1983). The species temperature index (STI), or species' mean temperature, was then calculated by finding the biomass-weighted mean of the modeled thermal distribution for

each species (Devictor *et al.*, 2008). The GAM allowed us to calculate the full thermal

distribution for each species, which was needed both for calculating STI and for our null

model. Given that many species' geographic ranges extend outside the survey, their

thermal distributions may similarly extend below or above the temperatures sampled

(Devictor *et al.*, 2008). We accounted for this as much as possible by generating species'

thermal distributions from both colder spring and warmer fall surveys, which

encompassed a range of bottom temperatures from 0 – 28.3ºC.

*Community temperature index (CTI) calculation*

For our working purposes, we defined a "community" as all species present in all tows in

a survey stratum in the same season and year. Survey strata ranged in area from 178 to

13,956 square kilometers (see map in Fig. S2) and represented both the level at which

tow locations were randomized and the smallest geographical areas that were consistently

sampled across the entire time series.

We measured community change through short- and long-term variations in CTI. CTI

was calculated in each stratum, season and year from 1990 – 2014 by multiplying each

species' STI by its relative biomass in the community (species biomass divided by the

total biomass of all species in the community), and summing across all species:

$$CTI = \sum_{i=1}^{n} \left[ \frac{b_i}{\sum_{i=1}^{n} b_i} \times STI_i \right]$$

where $b_i$ was the biomass of species *i* (*i* from 1 to *n* total species in the community).

*Null model for CTI change*

Given that the shapes of species' thermal distributions may cause communities to respond to temperature in a nonlinear fashion, we created a null model of the "idealized" community for each temperature in the dataset. For each temperature from 0-30 ℃, we created an idealized community containing all species whose thermal distributions included that temperature, with each species' biomass in the community represented by their GAM-predicted biomass at that temperature. Using the above formula, we then calculated a null CTI of the ideal community (assuming temperature is the only factor shaping community composition) for each environmental temperature between 0 ℃ and 30 ℃ (in 0.01 ℃ increments) (see example Fig.1). Once null CTI was calculated, we matched observed bottom temperatures in the testing dataset with null model CTI values to generate null time series for each stratum and season.

*Bottom temperature and CTI*

Of the 198 strata sampled in the trawl survey, 73 had recorded community and bottom temperature values in at least 20 of the 25 years of each spring and fall time series in the testing dataset from 1990-2014. We tested these 73 strata in both spring and fall, for a total of 146 time series. For each season and year, we aggregated all trawls across each stratum and calculated mean bottom temperature and mean CTI for the stratum. In years when bottom temperature was not available for a stratum, we omitted CTI for those same years for consistency in time series analysis.

To evaluate how well CTI followed bottom temperature, we analyzed the relationship between the two on both long-term and interannual time scales in the testing dataset (1990-2014). In order to directly compare how well communities matched their environment, we conducted several analyses:

(1) To evaluate static patterns, we calculated time-series mean bottom temperature and CTI values for each stratum and season, and compared them with a linear model.

(2) To evaluate overall correlation, we fit linear mixed-effects models to the biannual bottom temperature and observed CTI data, with CTI as the response variable, bottom temperature as the fixed effect, and season nested within stratum as random effects. We then evaluated statistical significance by fitting a null model without bottom temperature and comparing the two models with a likelihood ratio test, as implemented in the lmer package in R (Bates *et al.,* 2015).

(3) To investigate the relationship between long-term trends in bottom temperature and CTI, we fit linear models to each stratum time series of bottom temperature, null CTI, and observed CTI from 1990-2014. We then compared the slopes of these bottom temperature and CTI trends in each survey stratum to evaluate the extent to which long-term bottom temperature trends or long-term null CTI trends explained long-term observed CTI trends. Because the slopes involved observational error in both variables, we evaluated slope-slope fit using Model II Major Axis regression using the lmodel2 package in R (Legendre, 2014).

(4) Based on the hypothesis that climate variability affects community response to long-term change (Paaijmans *et al.*, 2013; Vasseur *et al.*, 2014), we also evaluated whether temperature variability, depth or latitude helped explain the relationship between bottom

temperature trends and CTI trends by including them as interactions in multiple linear regression models.

(5) To test for interannual correlations, we detrended the annual values of bottom temperature, null CTI and observed CTI in each stratum, and then calculated the Pearson product-moment correlation between each variable. We fit a linear mixed effects model with detrended CTI as the response variable, detrended bottom temperature or detrended null CTI as a fixed effect, and season nested within stratum as random effects, again comparing to a null model without bottom temperature or null CTI to evaluate statistical significance. We also tested for lags between temperature fluctuations and CTI change by conducting cross-correlation analysis of the detrended time series for each stratum in each season.

## Results

*Species thermal distributions*

We calculated thermal distribution curves and STI values for 92 fish and invertebrate species found on the Northeast U.S. continental shelf (Table S1). Species temperature index (STI) values ranged from 2.4 ºC to 27.7 ºC, with a median thermal range of 14.3 ºC (standard deviation across species = 7.8 ºC). Most species' thermal distributions were dome-shaped and asymmetrical, and a few were multimodal (the latter likely the result of different habitat temperatures in spring and fall).

*Null model for CTI*

The influence of species' asymmetrical, nonlinear thermal distributions was evident in the relationship between bottom temperature and null model CTI (solid line, Fig. 2). In colder temperatures, null model CTI was higher than bottom temperature, and in warmer temperatures, null model CTI was lower than bottom temperature. With increasing temperature from 0-15 °C, null model CTI increased in a relatively linear fashion, though the slope of null model community change was less than 1. Above 15 ºC, the slope of null model CTI change increased to near 1, continuing until 22.5 ºC, above which the slope of null model CTI dropped off sharply.

Similar to the null model predictions, time-averaged observed CTI in the testing dataset was correlated with bottom temperature, though the relationship was not one-to-one (linear model slope = $0.757 \pm 0.031$, $r^2 = 0.802$, $P < 0.001$) (black points, Fig. 2). Also similar to the null model, communities in colder environments (< 15 ºC) in both spring

and fall had CTI values that tended to be slightly higher than local bottom temperature, while in warmer environments ($\geq$ 20 ºC), CTI tended to be slightly lower than bottom temperature. On average, time series mean observed CTI values exceeded the predictions of the null model by 1.58 ºC (t-test: 95% CI: 1.29-1.87 ºC, $P < 0.0001$).

*Correlation of bottom temperature and CTI*

In a mixed-effects model fit to CTI and bottom temperature, we found that for every 1 ºC increase in bottom temperature, CTI increased by 0.38 ºC (95 % CI: 0.35-0.42, $P < 0.0001$). Comparing observations to our null model predictions, observed CTI increased only 0.48ºC for each 1 ºC increase in null model-predicted CTI (95% CI: 0.44 – 0.53, $P < 0.0001$).

*Long-term trends in bottom temperature and CTI*

Over the period 1990-2014, mean bottom temperature across the region increased by 0.34 $\pm$ 0.003 ºC/decade in the fall ($P < 0.0001$) and 0.24 $\pm$ 0.003 ºC/decade in the spring ($P < 0.0001$), but showed substantial spatial variation (Fig. 3a,b). In the same time period, CTI in individual strata changed greatly, but across all strata showed small but significant net change in the fall (mean -0.050 $\pm$ 0.005 ºC/decade, $P = 0.008$) and no significant net change in the spring (mean -0.001 $\pm$ 0.004 ºC/decade, $P = 0.526$). Long-term trends in CTI were also highly variable across the region (Fig. 3c,d). Comparing spring and fall trends, there was no indication that temperature or CTI in individual strata tended to change in the same direction between seasons (bottom temperature: $r^2 = 0.006$, $P = 0.259$; CTI $r^2 = 0.001$, $P = 0.41$)

There was some indication that long-term bottom temperatures and CTI trends had similar signs and magnitudes in the same strata, though there was little discernable geographic pattern and the overall relationship was very weak (both seasons combined: $r^2$ = 0.037, $P$ = 0.01). Of the two seasons, CTI trends were somewhat more closely correlated to temperature trends in the fall than in the spring (spring: $r^2$ = 0.021, $P$ = 0.123; fall: $r^2$ = 0.054, $P$ = 0.028) (Fig. 4, Fig. S2). The null model provided little additional explanatory power: as with bottom temperature, observed CTI was weakly but significantly correlated to null-model predicted CTI ($r^2$ = 0.038, $P$ = 0.013, Fig. S3). Interaction terms with latitude ($P$ = 0.186), depth ($P$ = 0.370), and standard deviation of bottom temperature ($P$ = 0.892) did not help further explain the relationship between long-term bottom temperature trends and CTI trends.

*Interannual changes in bottom temperature and CTI*

Individual strata experienced interannual temperature ranges as narrow as 1.6 to as wide as 14.8 ℃ over an entire same-season time series (detrended, average range across strata = 5.6 ℃). Communities experienced fluctuations in CTI of similar magnitudes, with interannual ranges from 1.4 to 12.5 ℃ (detrended, mean = 5.7 ℃). We found a weak negative relationship between the survey stratum area and standard deviations of bottom temperature ($r^2$ = 0.038, $P$ = 0.03) and of CTI ($r^2$ = 0.077, $P$ = 0.003).

Within a small majority of individual strata (57%), annual values of bottom temperature and observed CTI were moderately to strongly correlated ($r \geq 0.3$) (Pearson's correlation,

*r* mean across strata = 0.33, Fig. S4a), suggesting that interannual variations in bottom

temperatures were sometimes reflected in local CTI. Of the 146 time series correlations,

however, only 21 (14%) had $P < 0.05$, reflecting the limited strength of correlations at an

individual stratum level (Fig. S4b). Pearson correlation between null model and observed

CTI values revealed a similarly moderate effect size (r mean = 0.31, Fig. S4c,d)

Detrending the data suggested that much of the overall relationship between bottom

temperature and CTI change is due to community response to interannual temperature

changes: a mixed effects model fit to the detrended dataset supported the conclusion that

annual anomalies in CTI and temperature were significantly related, with CTI increasing

by 0.34 °C (95% confidence interval 0.31–0.37) for each 1 °C increase in bottom

temperature ($P < 0.0001$). Cross-correlation analysis of detrended time series suggested

that the majority of communities were most correlated with temperature or null model-

predicted CTI at time lag zero (Fig. S5).

**Discussion**

Interannual and long-term changes in CTI demonstrate that marine communities across the Northeast U.S. continental shelf have changed substantially over the last 25 years, with some evidence that they are following changes in environmental temperature. However, while CTI is moderately correlated with temperature on an interannual basis, long-term trends in CTI are less strongly connected.

*Community implications of nonlinear thermal distribution curves*

As with prior studies of community change, we used species' weighted mean temperature (STI) to calculate CTI. However, species' thermal distributions were rarely symmetrical, and in many cases, mean temperature was below or above the temperature of peak predicted abundance. Consolidating these thermal distributions into a single STI value that over- or underestimates species' peak preferred temperature has consequences for the calculated community thermal preference. These abundance curves also influence the rate of community change as temperature changes: rather than seeing a linear turnover of species in the community, we can expect the relative abundance of each species to change at substantially different rates over narrow temperature ranges. Overlaying these species thermal distributions to create a null model of CTI, we uncovered this nonlinear community response to temperature. The slope of community change with warming temperatures depended on the starting temperature, with slower turnover at colder starting temperatures and higher turnover at warmer starting temperatures. There was a notable drop-off in CTI change across the highest temperatures, but this may have appeared because these temperatures exceeded the STI of most species we sampled. This

pattern may also have resulted from the limits of our data: with fewer samples at the highest temperatures and no samples in the training dataset above 28.3 °C, we likely underestimated the STI of the warmest-water species.

The step-wise pattern we found in both the null model and observed CTI qualitatively echoes global patterns of marine community composition (Stuart-Smith *et al.*, 2015). These communities tend to fall into thermal guilds, with CTI higher than habitat temperatures in cooler environments (below approximately 18 °C) and lower than habitat temperatures in environments warmer than approximately 27 °C (Stuart-Smith et *al.*, 2015). At intermediate temperatures, communities comprise a mix of cold-water and warm-water species, and CTI increases rapidly with temperature change. The nonlinear CTI-temperature relationship we saw in our null model and in our observed CTI may represent a cold-water extension of these guilds below 15 °C. As temperatures rise, this division into thermal guilds would lead communities to be resistant to change over colder or warmer temperature regimes, while changes at intermediate temperatures may result in rapid change as one thermal guild mixes with and replaces another.

Regardless of cause, the implications for predicting future community change remain clear: whether considering idealized communities or real-world communities affected by fishing and other ecological changes, our expectation should be that climate-driven community change will often occur at very different rates than environmental change.

*Thermal impacts on community structure*

Previous studies have often found that species assemblages follow local temperature changes through geographic or compositional shifts, though often with some degree of lag (Lucey & Nye, 2010; Bertrand *et al.*, 2011; Devictor *et al.*, 2012; Menendez *et al.*, 2006; Stuart-Smith *et al.*, 2015; Kleisner *et al.*, 2016). In our examination of fine-scale community composition changes on a temperate continental shelf, we find that CTI change is associated with environmental temperature, but that the strength of this relationship depends on temporal scale. While we found evidence that interannual community composition responded to changes in bottom temperature without lags, the relationship between long-term community and environmental changes was weak and limits our ability to anticipate future change from temperature alone.

The contrast between our results and those of prior studies may arise from differences in scales of space and time, and the nature of our ecological system. Other studies have examined change at geographic scales of countries, regions, or entire continents (Bertrand *et al.*, 2011; Devictor *et al.*, 2012; Stuart-Smith *et al.*, 2015). While this approach is good for general observations of ecological phenomena, it is less applicable to specific habitats (e.g. shallow vs. deep, sandy-bottom vs. rocky-bottom), where species interact and communities are formed (Menge & Olson, 1990; Levin, 1995; Leibold *et al.*, 2004). Community analysis on finer geographic scales is also particularly important for management, especially when applied to specific ecosystem types or legal jurisdictions. Finally, some studies have examined community change at two distinct time periods rather than every year across a time series (Zografou *et al.,* 2014; Stuart-Smith *et al.*,

2015). This "before and after" snapshot method may reveal long-term changes, but loses detail about seasonality and interannual variability, and, depending on the time frame chosen, may result in different conclusions about the rates of environmental and community change (*sensu* Pershing *et al.,* 2015). Indeed, by comparing interannual and long-term changes, our analysis reveals that weak long-term trend correlations may mask a higher degree of community responsiveness on an interannual basis.

While not explicitly discussed, interannual variability in both temperature and community thermal preference is apparent in similar studies of climate and community change in this region (Lucey & Nye, 2010; Kleisner *et al.*, 2016). The magnitude of interannual fluctuations is often much larger than long-term changes in temperature or CTI. At the smaller geographic and ecological scale of our analysis, the nuances of interannual variation may mask a long-term climate signal. This effect is in line with previous work suggesting that climate may influence large-scale population and assemblage dynamics across large spatial scales, but at smaller spatial scales, particular species interactions more strongly mediate community response to climate change (Pascual & Levin, 1999; Walther *et al.*, 2002).

One potential explanation for interannual variation in the community and temperature time series is the survey method, given the challenge of repeating measurements through random trawls in large strata. However, we found that large strata were somewhat less variable than small strata in both mean bottom temperature and CTI from year to year, possibly because large strata often received greater sampling effort. Alternatively, large

strata may be less variable because they are less influenced by inter-annual changes in the position of sharp temperature breaks, such as the edge of the Gulf Stream.

It appears that other ecological factors beyond temperature are playing a substantial role in shaping community composition from year to year. Temperature is merely one element of a diverse set of biotic and abiotic factors that shape species' ideal niches into their realized ones and influence community dynamics (Hutchinson, 1957; Dunson & Travis, 1991; Kordas *et al.*, 2011). Though the thermal environment may change, a variety of other factors govern (and may buffer) the responses of species and their communities.

Other physical features may also shape community composition (Dunson & Travis, 1991). The abiotic environment of the Northeast U.S. continental shelf ecosystem is highly diverse, with bathymetric features ranging from submarine canyons to seamounts, and substrates from bedrock to gravel to fine silt (Stevenson *et al.,* 2004). For species closely tied to certain habitats, the spatial distribution of these physical features may inhibit or enable migration in response to temperature change and partially determine which species are available to enter an assemblage. Furthermore, during the time period we studied, the non-thermal physical environment also underwent changes in circulation. Shifts in the Gulf Stream were associated with anomalous temperatures that altered cod migration times, exposing them to greater predation risk and decreased recruitment (Pershing *et al.,* 2015). Seasonal changes in circulation, such as the influx of cool, low-salinity water from the Scotian Shelf, may have contributed to stratification in the Gulf of Maine that drove changes in primary productivity and the distribution and abundance of

higher trophic levels (Mountain, 2004; Stevenson *et al.,* 2004; Friedland & Hare, 2007). Beyond long-term temperature trends, these changes in circulation may have contributed to changes in local food webs and community composition.

Interactions among species have direct and indirect effects that also shape the realized distributions of each species and the communities they form (Gilman *et al.,* 2010; Link *et al.*, 2010; Kordas *et al.,* 2011, HilleRisLambers, 2013). Competition may limit the communities that otherwise thermally suited species can inhabit, while positive interactions may allow other species to persist longer in environments at the extremes of their thermal preferences (Gilman *et al.,* 2010; Kordas *et al.,* 2011; HilleRisLambers, 2013; Milazzo *et al.,* 2013). Indeed, Liu *et al.* (2012) found a spectrum of nonlinear dynamic relationships, ranging from strongly positive to strongly negative, in an assemblage of 26 fish species in Georges' Bank. The low correlation between our null model (only temperature) and observed CTI change suggests that species interactions may have strongly mediated the responsiveness of marine communities to changing temperatures. The tendency for observed CTI to be higher than the null model prediction may indicate that existing communities are already capable of persisting in warmer environments, and may continue to show lagged responses to future temperature change.

Layered on top of the "natural" influences of the abiotic and biotic environment are the strong effects of fishing in this ecosystem, which has been highly variable in location, intensity, and selectivity over this time period. Throughout the course of this study, fisheries have shifted in response to changes in species' distributions, stock sizes, and

management practices (Stevenson *et al.*, 2004; Lucey & Nye, 2010; Link *et al.,* 2011; Pinsky & Fogarty, 2012; Pershing *et al.*, 2015). Fishing activity has been shown to change trophic interactions and alter species', communities', and even entire assemblages' ability to respond to climate change (Lucey & Nye, 2010; Planque *et al.*, 2010). Fishing pressure in Georges Bank from 1970-2000 changed the abundance and distribution of both heavily-exploited species, decreasing their spatial and dietary overlap with other species, while allowing minimally-exploited species to expand into new areas at greater rates and overlap with more species (Garrison & Link, 2000). In addition, Nye *et al.* (2013) showed that, depending on the trophic level, the removal of top predators in this system works synergistically or antagonistically with climate change to dramatically alter marine community dynamics. Of the many influences mediating community response to temperature change in this ecosystem, fishing may have been the strongest.

The use of a single quantitative measure for evaluating climate-community fit is an attractive idea. But while CTI has been used effectively to quantify community change in some systems, this analytical approach carries several assumptions about the rate and linearity of community response to temperature change and may be highly dependent on the scale of time and space. Our findings suggest that ecologists should use caution when applying CTI-based analyses to other systems, particularly when projecting community dynamics into the future at the local scales of community assembly and species interactions.

The northeast U.S. continental shelf ecosystem has been one of the longest and most intensely studied of any marine system in the world, yet quantifying and anticipating how communities will respond to change remains a challenge. It is clear that temperature plays an important role in shaping community assembly, and interannual and long-term trends and fluctuations will certainly influence community reorganization. However, we must account for variables beyond temperature when anticipating community response to future climate change.
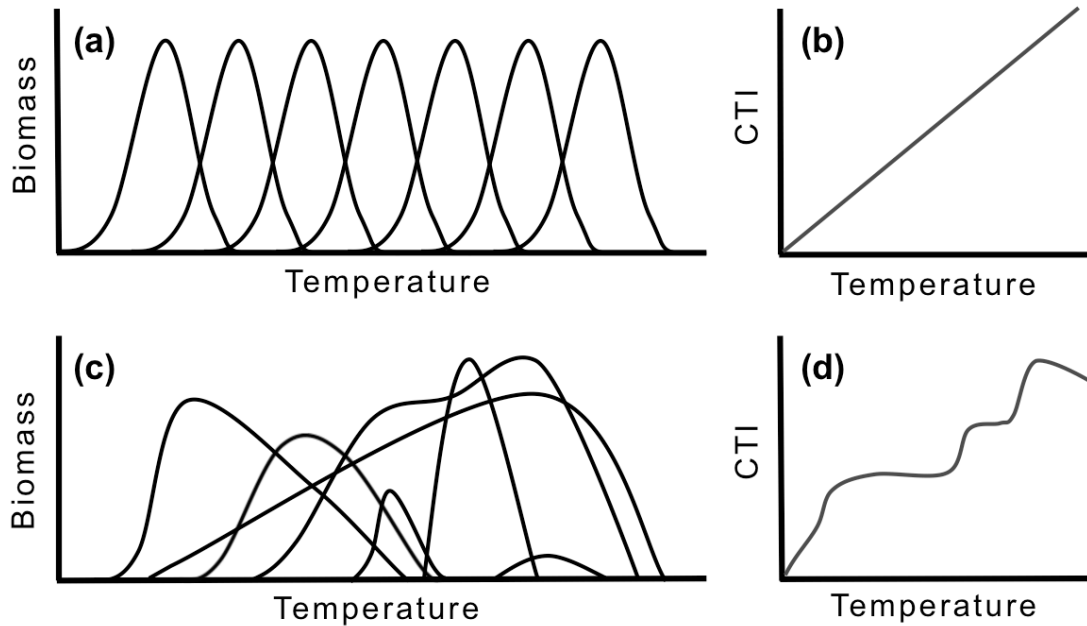
Figure 1. Example species' thermal distributions and change in CTI. The standard null expectation of change in CTI with change in temperature is that, independent of other ecological factors, CTI will change linearly with temperature (b). This would be true if species' thermal distribution curves were uniform in shape, height, and spacing (a). However, species' thermal distributions are rarely symmetrical, have varying degrees of overlap, and constitute a range of proportions of the community (c), suggesting that the null expectation may not be a linear change in CTI with changing temperature (d).
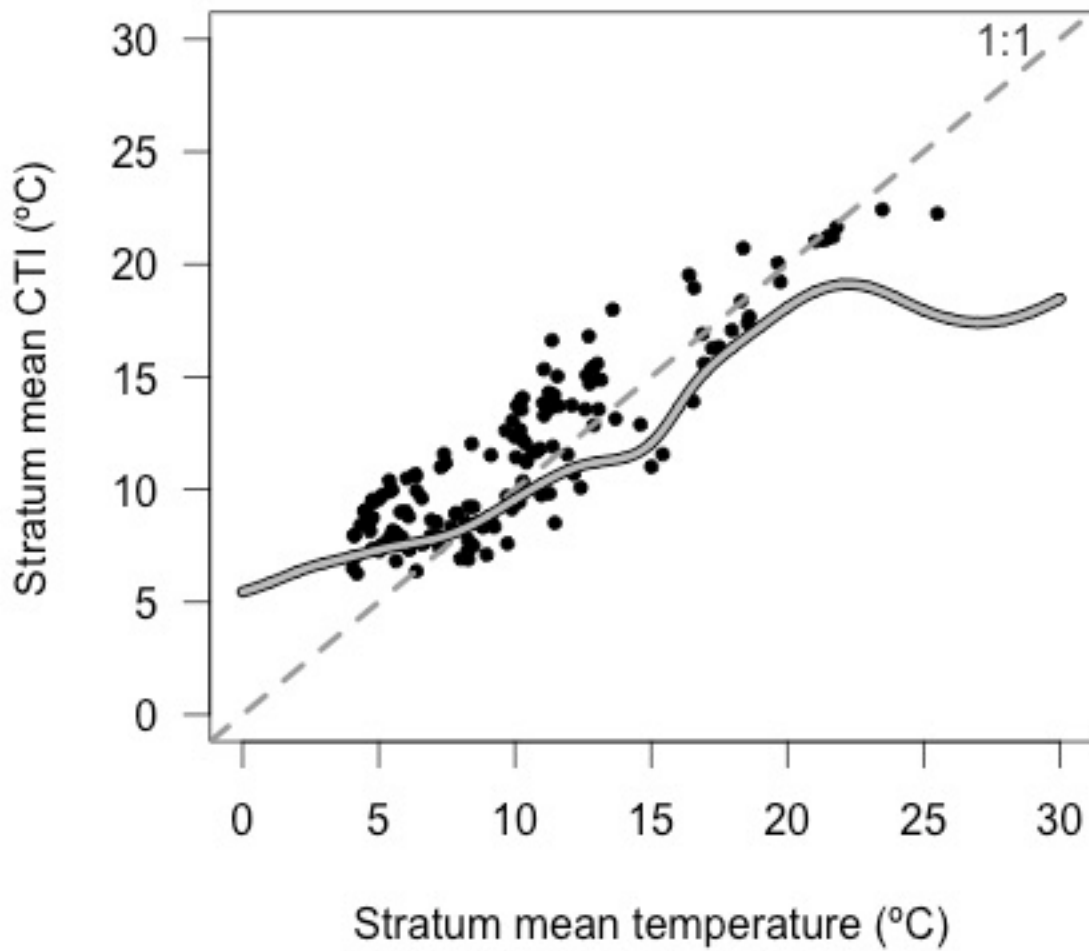
Figure 2. Community temperature index (CTI) in relation to environmental (bottom)

temperature. Each point represents a stratum mean in either spring or fall for 1990-2014.

The gray line represents null model predicted CTI for each temperature from 0–30 ºC.

Dashed gray line indicates what would be a 1:1 correlation between bottom temperature
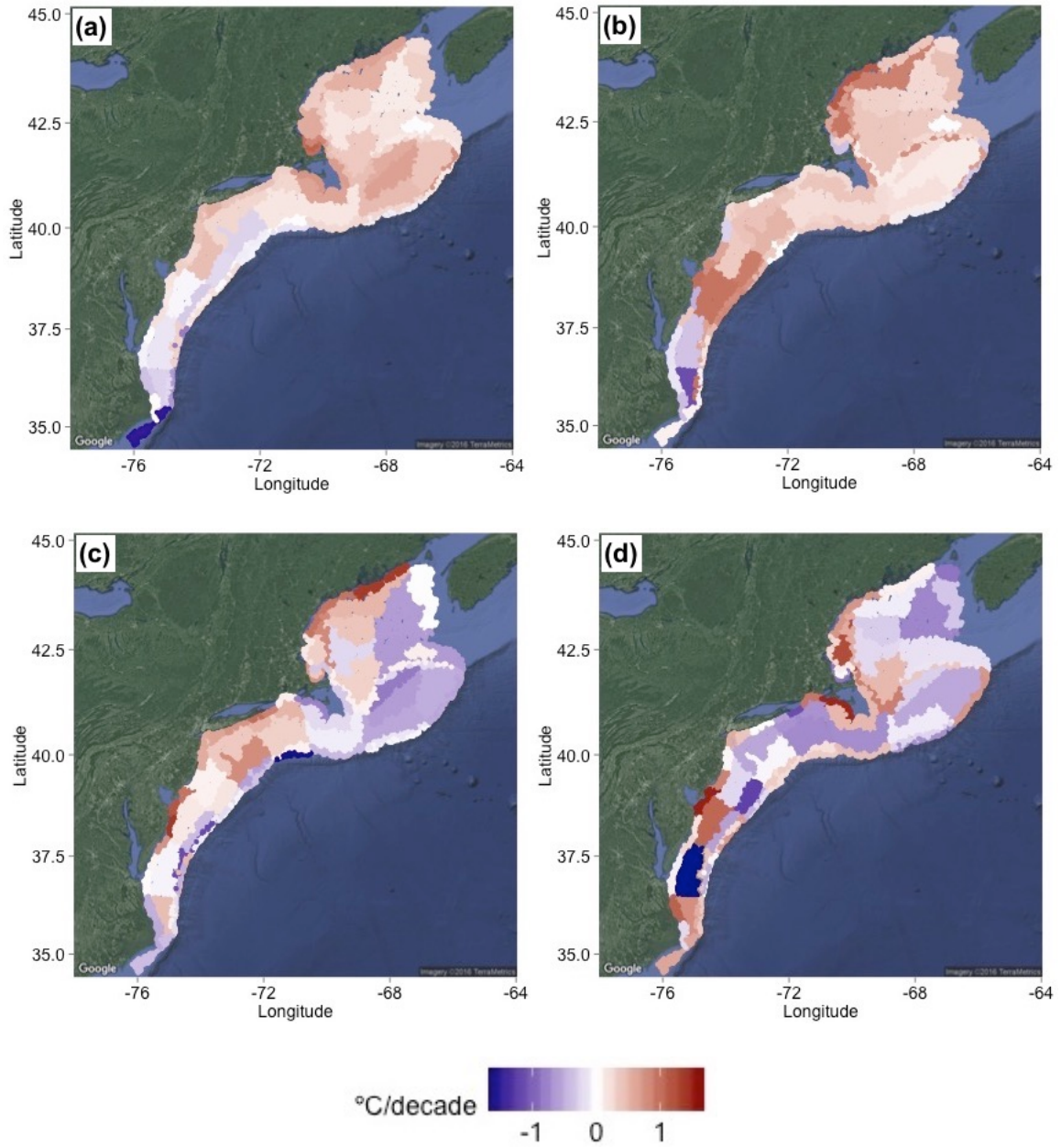
and CTI.

Figure 3. Map of survey area with strata colored by magnitude of long-term change in bottom temperature in spring (a) and fall (b), and CTI in spring (c) and fall (d).
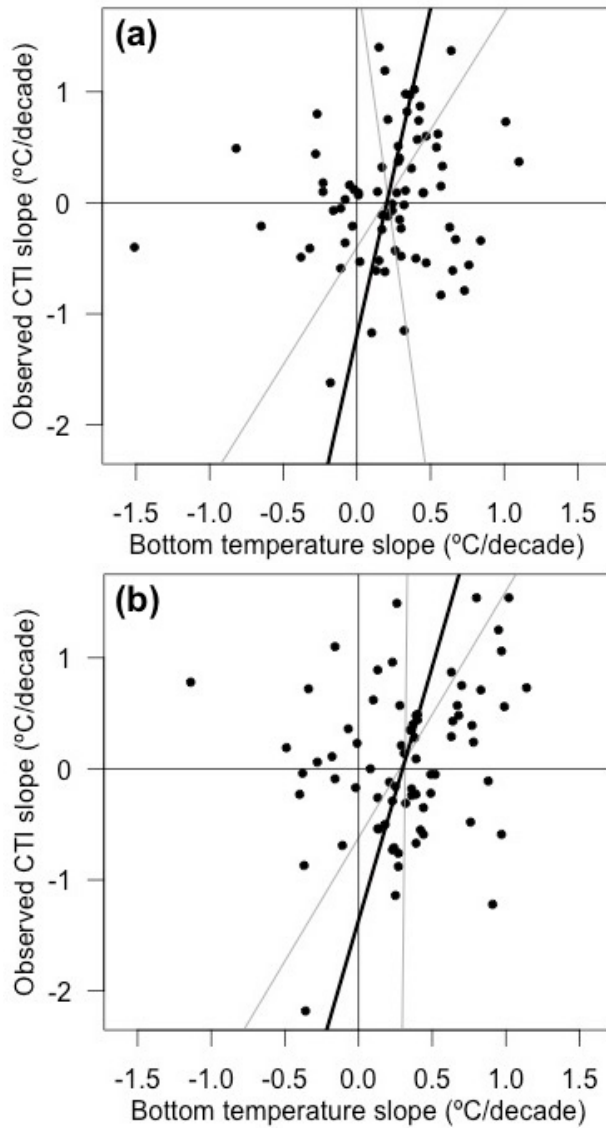
Figure 4. Relationships between change in bottom temperature and observed change in CTI. Model II major axis linear regression using Ordinary Least Squares in spring (a) and fall (b) communities. Black line indicates Major Axis OLS regression fit, gray lines indicate 95% confidence interval.

**Appendices**
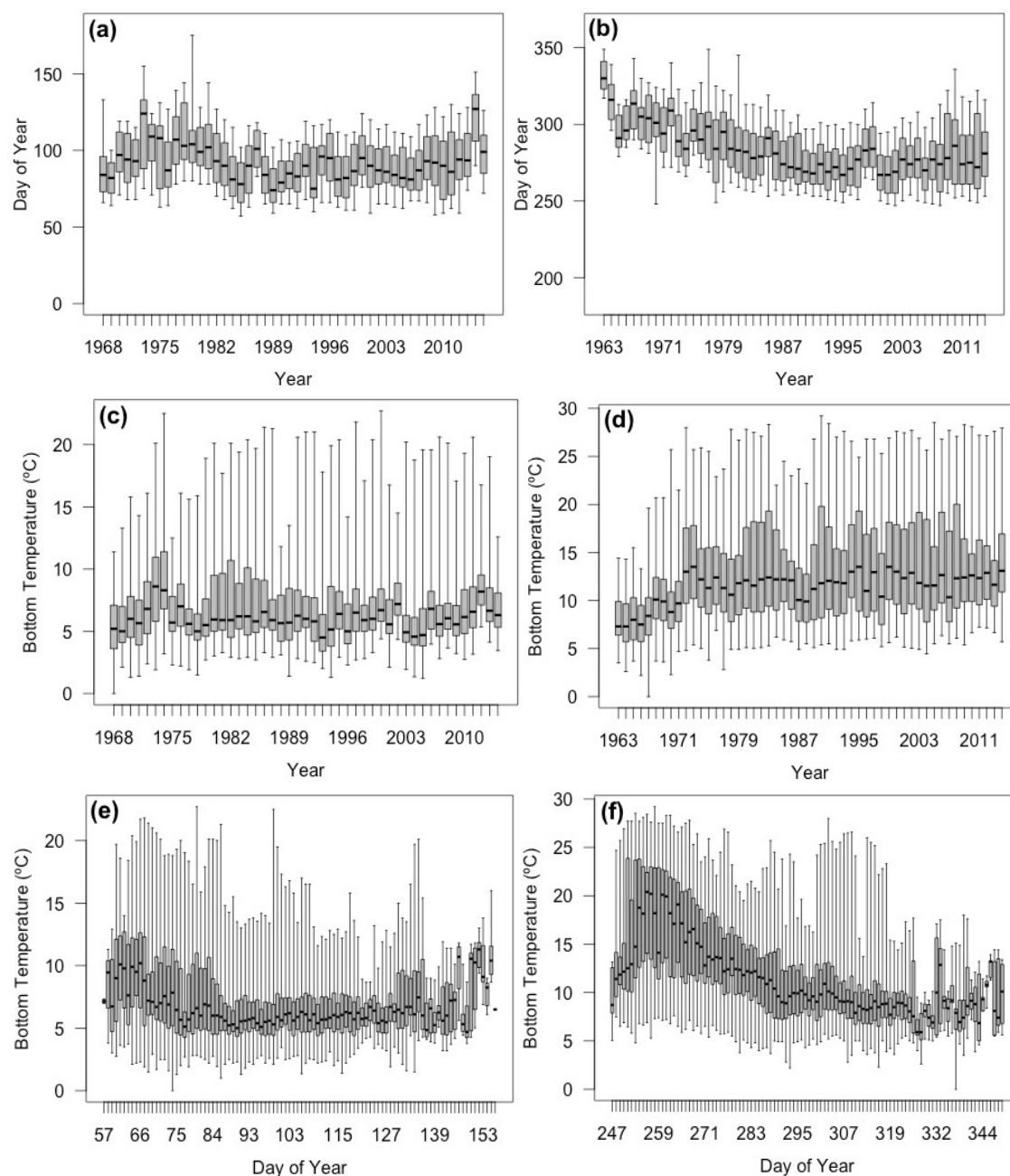


Figure S1. Survey characteristics over time. Boxplots of survey day of year per year in spring (a) and fall (b), bottom temperature per year in spring (c) and fall (d), and bottom temperature per day of year in spring (e) and fall (f) time series. Black bars indicate mean, gray boxes include 95% of range, and whiskers include entire range of data points.
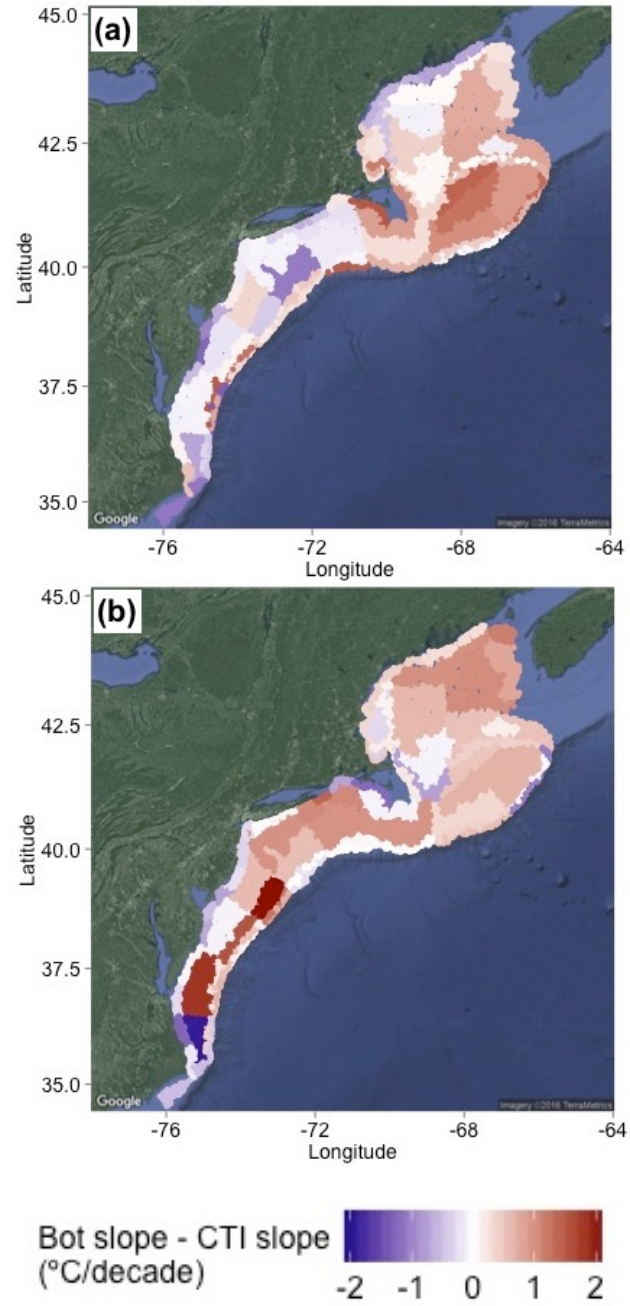
Figure S2. Maps of the difference in slopes of long-term trends in bottom temperature and CTI. Bottom temperature slope minus CTI slope in (a) spring and (b) fall strata.

Figure S3. Relationships between change in null model CTI and change in observed CTI. Model II major axis linear regression between change in null model CTI and change in observed CTI in spring (a) and fall (b) communities. Spring slope = 15.405, $r^2$ = 0.017, $P$ = 0.126; fall slope = 7.824, $r^2$ = 0.060, $P$ = 0.015.
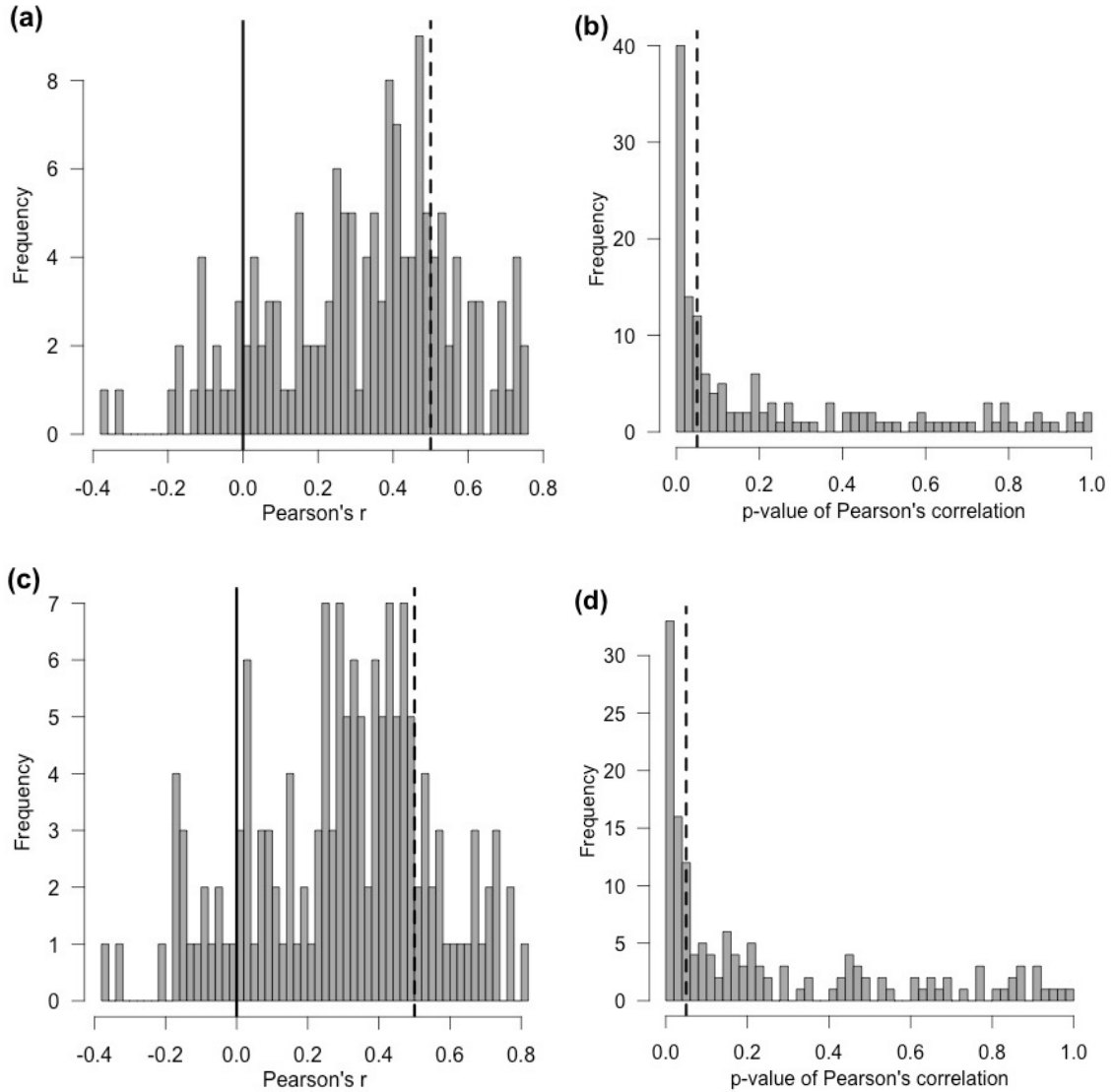
Figure S4. Pearson's correlations between interannual values of bottom temperature or null model CTI and observed CTI in each stratum and season. (a) Histogram of *r* values between bottom temperature and observed CTI, with dashed line denoting *r* of 0.5 (*n* = 146, mean *r* = 0.327). (b) Histogram of *P* values between bottom temperature and observed C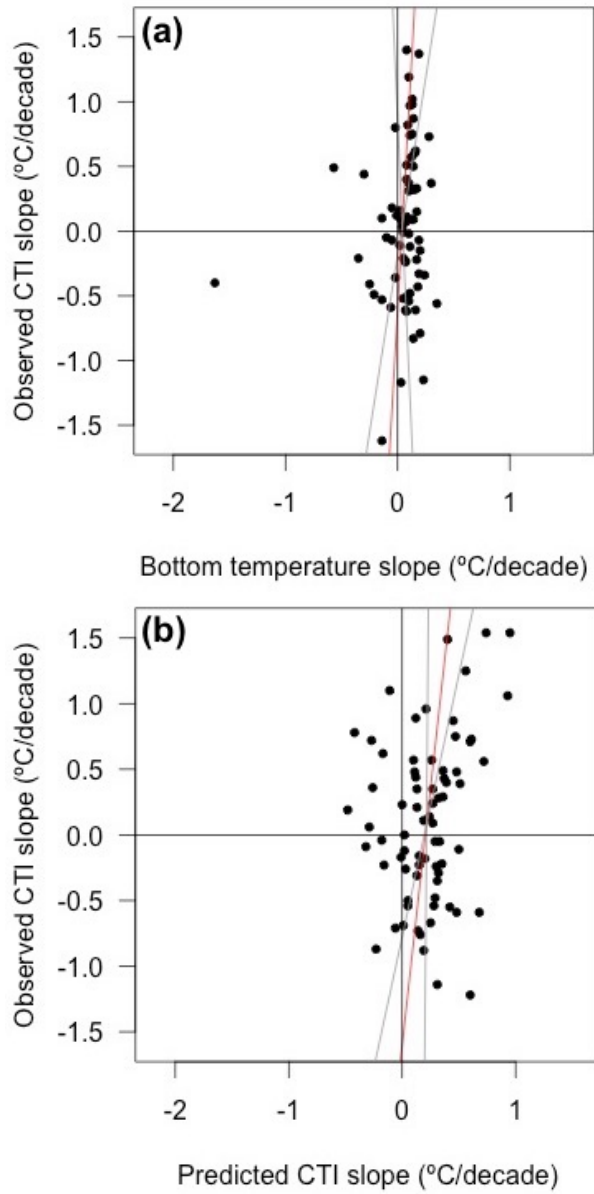TI, with dashed line denoting $P = 0.05$ (*n* = 146, $n(P \leq 0.05) = 21$). (c) Histogram of *r* values between null model and observed CTI, with dashed line denoting *r* of 0.5 (*n* = 146, mean = 0.308). (d) Histogram of *P* values between null model and observed CTI, with dashed line denoting $P = 0.05$ (*n* = 146, $n(P \leq 0.05) = 25$).

Figure S5. Histograms of the lag with the highest cross-correlation between detrended time series. (a and b) Frequency of lags between bottom temperature and observed CTI in (a) spring and (b) fall time series. (c and d) Frequency of lags between null model and observed CTI in (a) spring and (b) fall time series.

Table S1. Species temperature index (STI) values and number of observations in training and testing data sets for 92 species found in the 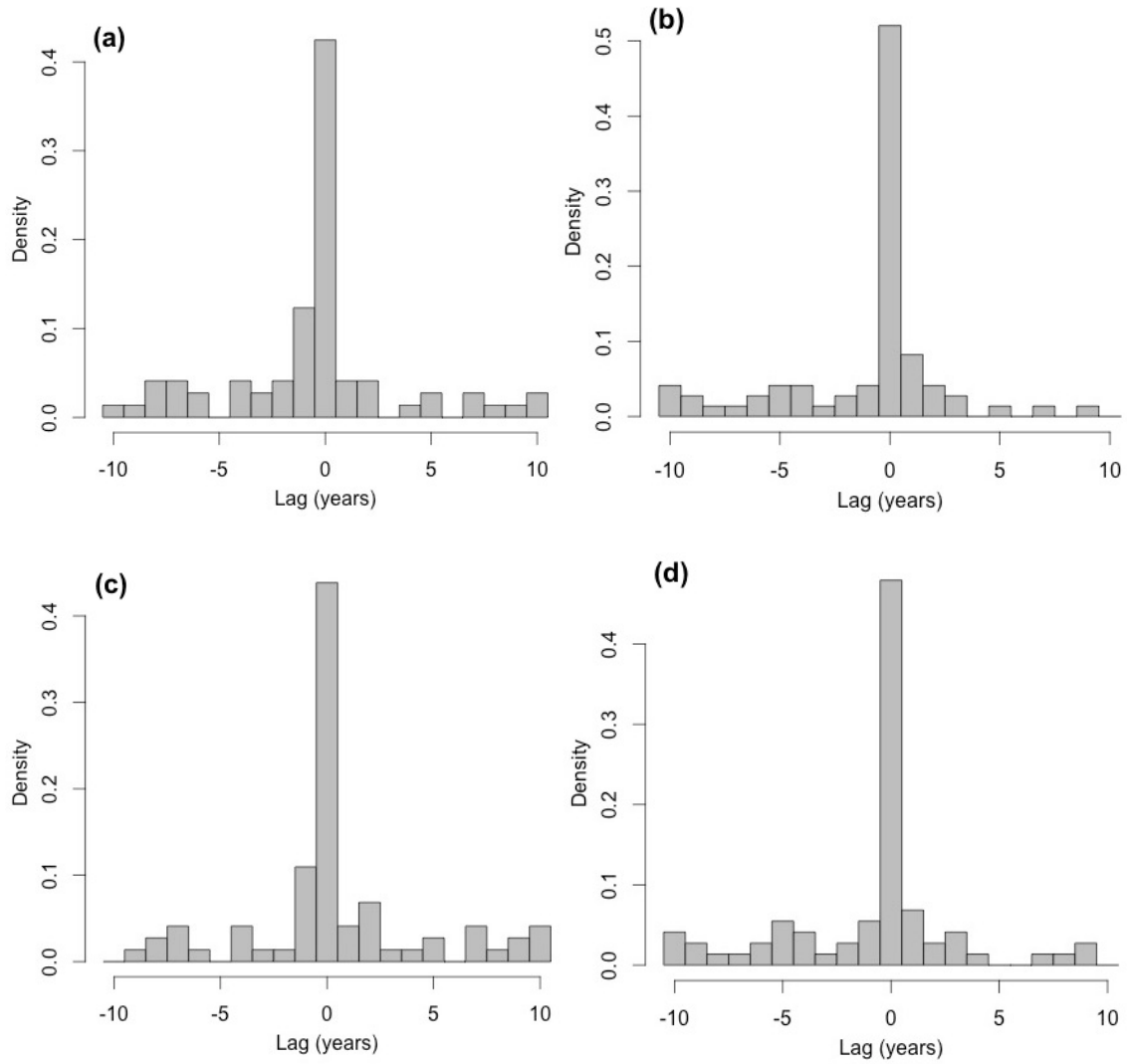Northeast U.S. Continental Shelf ecosystem. Thermal preferences were calculated by fitting a two-part GAM of presence/absence and abundance to trawl data in spring and fall from 1963-1989 (training set) and then calculating the biomass-weighted mean temperature of model predictions across 0.00-30.00 °C. The training set was 1963-1989, and the testing set was 1990-2015.

| Scientific name | Common name | Species temperature index ( ºC) | Obs. (training set) | Obs. (testing set) |
|---|---|---|---|---|
| *Alosa aestivalis* | Blueback herring | 7.09 | 741 | 2112 |
| *Alosa pseudoharengus* | Alewife | 7.46 | 2534 | 4353 |
| *Alosa sapidissima* | American shad | 9.08 | 563 | 1546 |
| *Amblyraja radiata* | Thorny skate | 5.68 | 3160 | 1633 |
| *Ammodytes dubius* | Northern sand lance | 8.13 | 864 | 802 |
| *Anarhichas lupus* | Atlantic wolffish | 2.39 | 782 | 268 |
| *Anchoa hepsetus* | Striped anchovy | 22.83 | 396 | 720 |
| *Anchoa mitchilli* | Bay anchovy | 19.14 | 508 | 961 |
| *Argentina silus* | Atlantic argentine | 8.10 | 295 | 229 |
| *Brevoortia tyrannus* | Atlantic menhaden | 18.66 | 169 | 251 |
| *Brosme brosme* | Cusk | 6.84 | 1040 | 367 |
| *Calamus leucosteus* | Whitebone porgy | 26.30 | 162 | 6 |
| *Callinectes sapidus* | Blue crab | 22.71 | 141 | 261 |
| *Cancer borealis* | Jonah crab | 10.55 | 909 | 2407 |

| *Caranx crysos* | Blue runner | 25.11 | 156 | 312 |
|---|---|---|---|---|
| *Centropristis striata* | Black sea bass | 21.54 | 911 | 1681 |
| *Citharichthys arctifrons* | Gulf stream flounder | 11.08 | 442 | 2246 |
| *Clupea harengus* | Atlantic herring | 3.94 | 1820 | 6364 |
| *Conger oceanicus* | Conger eel | 14.25 | 226 | 201 |
| *Cyclopterus lumpus* | Lumpfish | 7.99 | 121 | 216 |
| *Cynoscion regalis* | Weakfish | 21.00 | 877 | 1161 |
| *Dasyatis centroura* | Roughtail stingray | 23.83 | 168 | 333 |
| *Dasyatis say* | Bluntnose stingray | 19.94 | 295 | 391 |
| *Decapterus punctatus* | Round scad | 26.23 | 361 | 411 |
| *Diplectrum formosum* | Sand perch | 25.09 | 143 | 18 |
| *Dipturus laevis* | Barndoor skate | 8.48 | 288 | 1447 |
| *Enchelyopus cimbrius* | Fourbeard rockling | 5.87 | 308 | 1108 |
| *Gadus morhua* | Atlantic cod | 5.37 | 4658 | 3161 |
| *Glyptocephalus cynoglossus* | Witch flounder | 5.82 | 2708 | 2859 |
| *Gymnura altavela* | Spiny butterfly ray | 20.88 | 175 | 320 |
| *Haemulon aurolineatum* | Tomtate | 24.29 | 168 | 21 |
| *Hemitripterus americanus* | Sea raven | 5.36 | 2630 | 3101 |
| *Hippoglossoides platessoides* | American plaice | 4.68 | 3658 | 3561 |
| *Hippoglossus hippoglossus* | Atlantic halibut | 5.71 | 383 | 317 |
| *Homarus americanus* | American lobster | 10.72 | 3397 | 4932 |

| | | | | |
|---|---|---|---|---|
| *Illex illecebrosus* | Northern shortfin squid | 11.15 | 3278 | 3904 |
| *Lagodon rhomboides* | Pinfish | 27.66 | 185 | 129 |
| *Larimus fasciatus* | Banded drum | 24.72 | 118 | 207 |
| *Leiostomus xanthurus* | Spot | 22.64 | 886 | 965 |
| *Lepophidium profundorum* | Fawn cusk-eel | 12.62 | 450 | 1014 |
| *Leucoraja erinacea* | Little skate | 10.00 | 5008 | 6993 |
| *Leucoraja garmani* | Rosette skate | 14.26 | 182 | 608 |
| *Leucoraja ocellata* | Winter skate | 8.81 | 2563 | 4480 |
| *Limanda ferruginea* | Yellowtail flounder | 5.54 | 3722 | 3305 |
| *Limulus polyphemus* | Horseshoe crab | 17.78 | 926 | 718 |
| *Loligo pealeii* | Longfin squid | 16.77 | 5239 | 7535 |
| *Lophius americanus* | Goosefish | 9.41 | 3663 | 3968 |
| *Malacoraja senta* | Smooth skate | 6.17 | 1081 | 1463 |
| *Melanogrammus aeglefinus* | Haddock | 6.31 | 3960 | 3329 |
| *Menticirrhus americanus* | Southern kingfish | 22.41 | 238 | 423 |
| *Menticirrhus saxatilis* | Northern kingfish | 21.51 | 243 | 459 |
| *Merluccius bilinearis* | Silver hake | 9.30 | 7646 | 9035 |
| *Micropogonias undulatus* | Atlantic croaker | 22.05 | 704 | 1118 |
| *Mustelus canis* | Smooth dogfish | 17.59 | 1266 | 1704 |
| *Myoxocephalus octodecemspinosus* | Longhorn sculpin | 6.19 | 3514 | 4190 |
| *Myxine glutinosa* | Atlantic hagfish | 7.48 | 268 | 543 |
| *Ophidion marginatum* | Striped cusk-eel | 19.38 | 166 | 192 |

| *Opisthonema oglinum* | Atlantic thread herring | 26.68 | 163 | 310 |
|---|---|---|---|---|
| *Orthopristis chrysoptera* | Pigfish | 26.42 | 186 | 232 |
| *Ovalipes ocellatus* | Lady crab | 17.89 | 357 | 607 |
| *Ovalipes stephensoni* | Coarsehand lady crab | 24.25 | 100 | 265 |
| *Pandalus borealis* | Northern shrimp | 3.93 | 368 | 1078 |
| *Paralichthys dentatus* | Summer flounder | 18.00 | 2514 | 3933 |
| *Peprilus triacanthus* | Butterfish | 18.06 | 3516 | 5959 |
| *Peristedion miniatum* | Armored searobin | 11.41 | 174 | 239 |
| *Placopecten magellanicus* | Sea scallop | 10.17 | 1616 | 3737 |
| *Pollachius virens* | Pollock | 6.96 | 2153 | 1589 |
| *Pomatomus saltatrix* | Bluefish | 19.56 | 1153 | 1590 |
| *Porichthys plectrodon* | Atlantic midshipman | 25.57 | 103 | 36 |
| *Prionotus carolinus* | Northern searobin | 17.95 | 1677 | 2632 |
| *Prionotus evolans* | Striped searobin | 18.53 | 772 | 1106 |
| *Pseudopleuronectes americanus* | Winter flounder | 8.53 | 3343 | 4164 |
| *Raja eglanteria* | Clearnose skate | 18.35 | 780 | 1527 |
| *Rhizoprionodon terraenovae* | Atlantic sharpnose shark | 25.45 | 158 | 240 |
| *Rhomboplites aurorubens* | Vermilion snapper | 25.45 | 101 | 19 |
| *Scomber scombrus* | Atlantic mackerel | 9.81 | 1021 | 2605 |
| *Scomberomorus maculatus* | Spanish mackerel | 26.13 | 145 | 163 |

| | | | | |
|---|---|---|---|---|
| *Scophthalmus aquosus* | Windowpane | 12.03 | 3628 | 4439 |
| *Scyliorhinus retifer* | Chain dogfish | 11.77 | 110 | 730 |
| *Sebastes fasciatus* | Acadian redfish | 6.22 | 2585 | 2672 |
| *Sphoeroides maculatus* | Northern puffer | 20.61 | 229 | 530 |
| *Squalus acanthias* | Spiny dogfish | 10.89 | 6031 | 7143 |
| *Squatina dumeril* | Atlantic angel shark | 18.55 | 287 | 261 |
| *Stenotomus chrysops* | Scup | 23.22 | 1667 | 2333 |
| *Synodus foetens* | Inshore lizardfish | 25.85 | 467 | 448 |
| *Tautogolabrus adspersus* | Cunner | 10.62 | 343 | 515 |
| *Trachinocephalus myops* | Snakefish | 24.01 | 127 | 115 |
| *Trachurus lathami* | Rough scad | 24.62 | 135 | 398 |
| *Triglops murrayi* | Moustache sculpin | 5.77 | 153 | 205 |
| *Urophycis chuss* | Red hake | 9.13 | 4918 | 6377 |
| *Urophycis regia* | Spotted hake | 14.48 | 1893 | 4664 |
| *Urophycis tenuis* | White hake | 7.92 | 3923 | 3415 |

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