

Research

Response of marine communities to local temperature changes

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As global climate change and variability drive shifts in species' distributions, ecological communities are being reorganized. One approach to understand community change in response to climate 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, important questions remain about whether and how responsive communities are to changes in their local thermal environments. We used CTI to analyze changes in 160 marine assemblages (fish and invertebrates) across the rapidly-changing Northeast U.S. Continental Shelf Large Marine Ecosystem and calculated expected community change based on historical relationships between species presence and temperature from a separate training dataset. We then compared interannual and long-term temperature changes with expected community responses and observed community responses over both temporal scales. For these marine communities, we found that community composition as well as composition changes through time could be explained by species associations with bottom temperature. Individual species had non-linear responses to changes in temperature, and these nonlinearities scaled up to a nonlinear relationship between CTI and temperature. On average, CTI increased by 0.36°C (95% CI: 0.34–0.38°C) for every 1°C increase in bottom temperature, but the relationship between CTI and temperature also depended on community composition. In addition, communities responded more strongly to interannual variation than to long-term trends in temperature. We recommend that future research into climate-driven community change accounts for nonlinear responses and examines ecological responses across a range of temporal and geographical scales.

Keywords: climate change, community assembly, marine ecology

Introduction

Anthropogenic climate change is altering nearly every natural environment across the planet (Parmesan and Yohe 2003, Cheung et al. 2013, IPCC 2014). Unprecedented trends and fluctuations in the climate are contributing to complex and unanticipated changes in biotic and abiotic environments (Walther et al. 2002, Hoegh-Guldberg and Bruno 2010, Urban et al. 2012, IPCC 2014). Recent research has shown that many



species are responding to climate change by shifting their distributions (Parmesan et al. 1999, Davis and Shaw 2001, Parmesan and 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 assemblage (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 curve: an increase in temperature may be detrimental for a cold-adapted species, but beneficial for a warm-adapted species in the same location (Menéndez et al. 2006, Moritz et al. 2008, Bertrand et al. 2011, Kordas et al. 2011). In addition to long-term changes in mean temperature, fluctuations in temperature can also play an important role in determining species and community responses to change (Paaijmans et al. 2013, Vasseur et al. 2014, Morley et al. 2017).

As climate change drives increases in 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 and shrinking populations of 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 on regional and global scales (Devictor et al. 2008, Cheung et al. 2013, Zografou et al. 2014, Stuart-Smith et al. 2015). While we may broadly expect communities and CTIs to change in response to temperature change, we have a poor understanding of the shape of those responses and the rates at which they will change (Menge and Olson 1990, Levin 1992, Leibold et al. 2004).

Previous studies have measured community response to temperature change at regional and global scales by directly comparing CTI and temperature. This comparison is based on the (sometimes implicit) assumption that species turnover and community change should occur linearly and one-to-one with temperature change if dispersal or other factors don't prevent or alter such community change (e.g. Fig. 1b) (Devictor et al. 2008, 2012, Cheung et al. 2013, Bowler and Böhning-Gaese 2017). However, species' thermal performance curves are typically dome-shaped functions of temperature (Huey and Stevenson 1979), and these curves are both asymmetric and variable among species. Changes in environmental temperature may thus lead to nonlinear responses in abundance among species (Pörtner and Knust 2007, Deutsch et al. 2008) (e.g. Fig. 1d, f). Since communities are comprised of multiple species with unique thermal performance curves, 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 could 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.

We chose to examine community responses to temperature change in the northeast U.S. continental shelf, a large marine ecosystem (LME) that has warmed over the last three decades ($0-0.03^{\circ}\text{C yr}^{-1}$) (Friedland and Hare 2007, Belkin 2009, Shearman and Lentz 2009). This change has led to a general shift in isotherms and in the species assemblage towards the northeast (Pinsky et al. 2013). Previous studies have also found that warming has 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 (Lucey and Nye 2010). While these large-scale and long-term climate and ecological changes are evident across the region, species interactions and communities are formed at finer spatial scales, and it is not clear whether the same responses to climate change can be detected at a finer scale.

In this manuscript, we investigated 1) how marine communities of fish and invertebrates have changed over the last 25 yr, 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 either decadal or interannual time-scales. To answer these questions, we evaluated temperature and community change in 160 spring and fall assemblages, compared interannual variations and long-term trends in each, and analyzed whether marine communities in this region are changing at the same rates and in the same direction as their local thermal environments.

Material and methods

Survey method and study extent

We used 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. This ecological survey captures a wide range of demersal species and some pelagic species, including groundfishes, crustaceans, sharks, herring, and squid (Supplementary material Appendix 1 Table A1). The survey design divided the survey area into 198 strata (Fig. 2) (methodology described in Azarovitz 1981). Survey

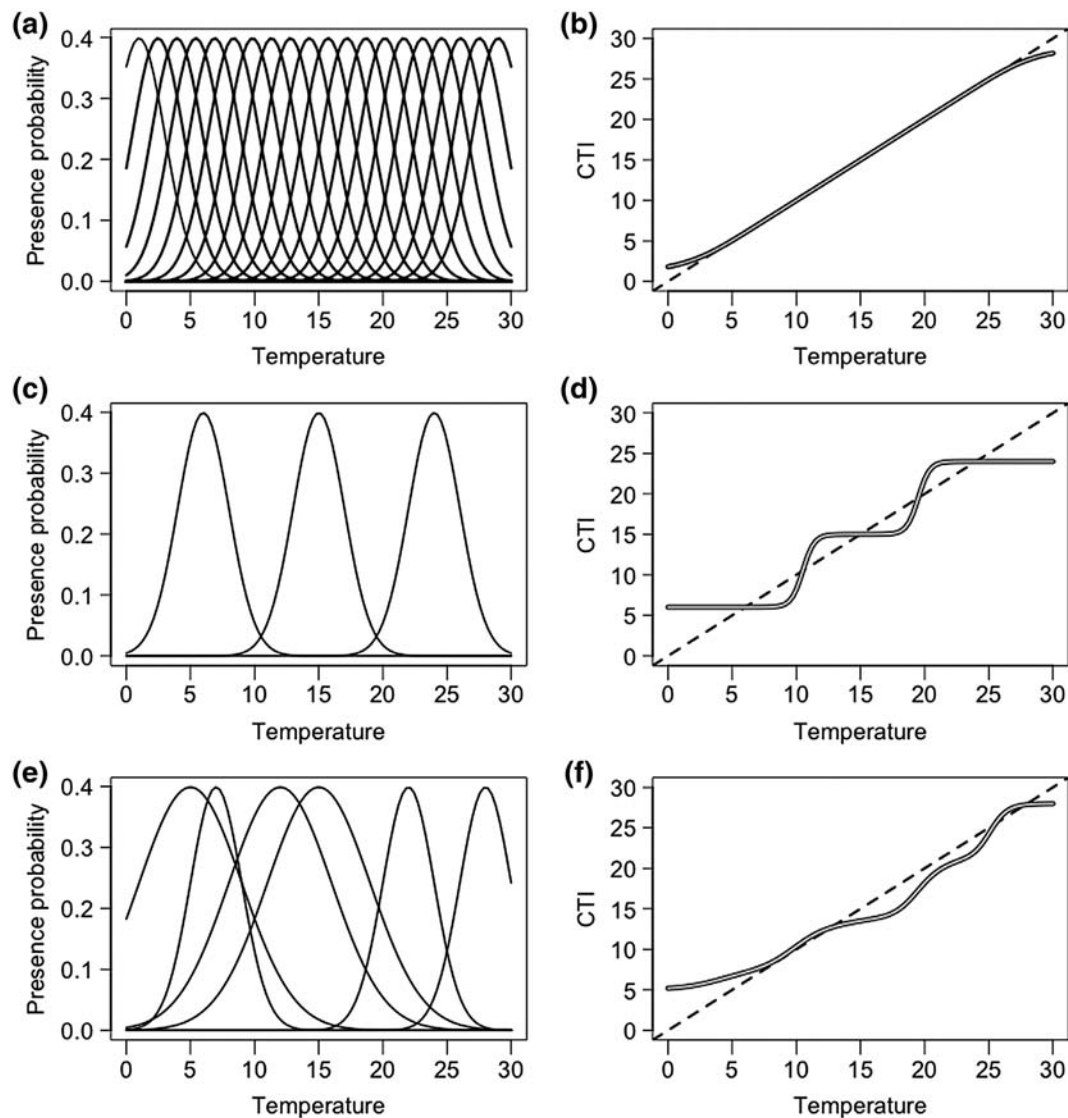


Figure 1. If species' thermal distribution curves are uniform in shape, height, and closely spaced, (a), expected CTI changes are linear and 1:1 with temperature (b), assuming other ecological factors remain constant. If thermal distribution curves are uniform but spaced farther part (c), CTI changes in a stepwise fashion (d). However, species' thermal distributions are rarely symmetrical, have varying degrees of overlap, and include both rare and common species (e), suggesting that CTI may not change linearly or 1:1 with temperature (f).

strata represented the smallest spatial units of the statistical sampling design. Strata ranged in area from 178 to 13 956 km² (median 2503 km²), and in mean depth from 10 to 472 m. The median range of depths within a stratum was 36.5 m. Each trawl recorded the presence of each species, trawl depth, in-situ bottom temperature, and other data. Each year, the survey trawls no more than 0.005% of the northeast U.S. continental shelf area, having a negligible but non-zero effect on community composition.

The timing of the fall survey changed over time from the 1960s to the 1980s, which could create artificial trends in observed temperatures and communities (Supplementary material Appendix 1 Fig. A1). To avoid this possibility, we restricted our analysis of temperature and community change to 1990–2014.

Species temperature index (STI) and community temperature index (CTI) calculations

As a measure of realized thermal niche, we fit a statistical model to the relationship between species presence and bottom temperature. In order to estimate more complete thermal distributions, our training dataset was 97 535 bottom trawl survey hauls with spatial coverage from the Gulf of Mexico to Newfoundland across multiple seasons (Pinsky et al. 2013, Morley et al. 2017, Selden et al. 2018). Our training dataset therefore covered a much wider geographic region than do the time-series of interest in this paper. While some of our focal species have geographical ranges that extend beyond those of these surveys, the most common species in the northeast U.S. had thermal ranges that fell well within the range of

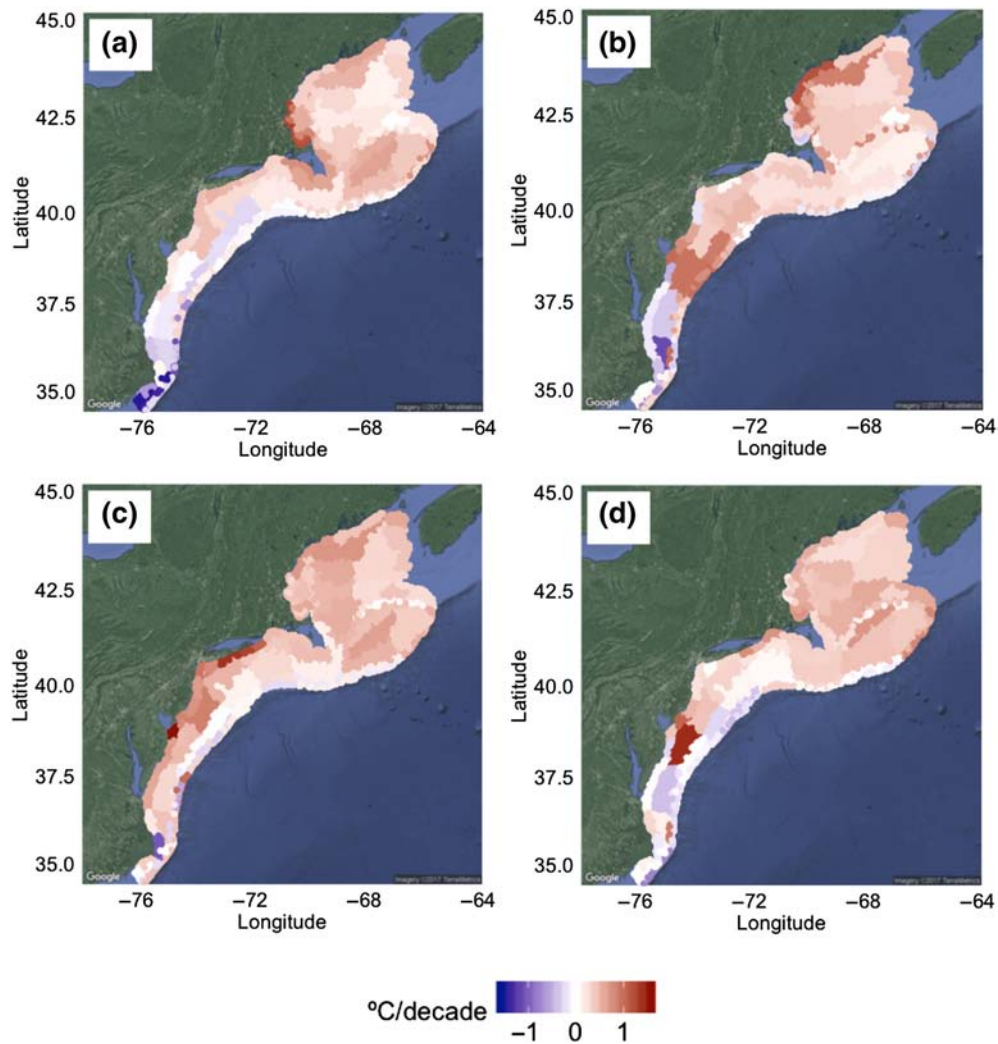


Figure 2. Map of survey area with strata colored by magnitude of long-term change in bottom temperature in spring (a) and fall (b), and by long-term change in CTI in spring (c) and fall (d).

temperatures sampled by this full database of surveys (-2 to 33°C). To prevent overlap with our subsequent analysis, all data from the northeast region after 1989 were omitted from this training dataset.

For each of the 260 most common species found in at least 250 trawls in the northeast U.S. bottom trawl survey 1968–1989 (Supplementary material Appendix 1 Table A1), we fit a generalized additive model (GAM) (Hastie and Tibshirani 1990) to presence and absence data using binomial errors with the ‘mgcv’ package (Wood 2011) in R (R Core Team). Predictor variables included in-situ bottom temperature, benthic rugosity, sediment grain size and a categorical indicator for survey region to account for differences in methodology and catchability among surveys, following the species distribution modeling methods of Morley et al. (2018). Briefly, we calculated seafloor rugosity as the mean of the absolute differences between a given grid cell depth and the depths of the eight surrounding cells using GEBCO bathymetric data (Becker et al. 2009). Grain size was measured

using the Wentworth Phi scale, where lower values indicate coarser sediments and higher values indicate finer sediments (Morley et al. 2018). The inclusion of non-temperature effects in the models helped to account for other influences on species distributions and therefore helped to refine the fit of the temperature effect. In order to prevent overfitting of the GAMs, gamma (which acts as a penalty against model complexity) was set to the log of the number of observations divided by two (Wood 2006). For each species, we fit a single GAM, which allowed us to calculate comprehensive thermal distributions ranging from 0 to 35°C . The species temperature index (STI) was then calculated as the median temperature of the modeled probability of presence with other predictor variables held constant. Across the 260 most common fishes and invertebrates, species temperature index (STI) values ranged from -0.3°C to 30.5°C and roughly clumped into guilds of species above and below 15°C (Supplementary material Appendix 1 Table A1, Fig. A2). These guilds roughly correspond to the subpolar ($< 14^{\circ}\text{C}$), temperate (14 – 23°C),

and tropical ($> 23^{\circ}\text{C}$) guilds identified by Stuart-Smith et al. (2015), though our data do not show a clear break at 23°C .

We defined a ‘community’ as all species present in tows in a stratum in the same season and year. CTI was calculated in each stratum, season and year from 1990–2014 as the average of STIs of each species present. This definition does not account for differences in species abundance, but a sensitivity test weighting by abundance revealed equivalent results to those we present in this paper.

Temperature-only expectations for CTI change

Given that the shapes of species’ thermal distributions may cause communities to respond to temperature nonlinearly, we calculated the ‘idealized’ community for each temperature in the dataset. This model assumed that there are no barriers to dispersal and that each species would occupy the community in proportion to the probability density at that temperature on its respective thermal distribution curve. In the model communities, we calculated the CTI as the mean of the STIs of each species, weighted by their GAM-predicted probability of presence at that temperature (see example Fig. 1). This model demonstrates how CTI would change if change in temperature was the only driver. Once these temperature-only CTI expectations were calculated for each temperature, we matched observed bottom temperatures with the temperature-only model CTI expectations to generate expected-CTI time series for each stratum and season.

Observed bottom temperature and CTI

Of the 198 strata sampled in the trawl survey, 80 had CTI and bottom temperature data available in at least 20 of the 25 yr in both spring and fall from 1990–2014 (for a total of 160 time series). For each season and year, we aggregated all trawls within each stratum and calculated mean bottom temperature and CTI. In years when bottom temperature was not available for a stratum, we omitted CTI for those same years for consistency.

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). We therefore conducted several analyses: 1) to evaluate static patterns, we compared time-averaged bottom temperature and CTI values with a linear regression model. 2) To evaluate the overall correlation of changes in temperature and CTI, we fit linear mixed-effects models to the biannual bottom temperature and observed CTI data. We used observed CTI as the response variable, bottom temperature as the fixed effect, and survey (fall vs spring) nested within stratum as random effects. We evaluated statistical significance of the temperature term 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). We also evaluated a model where the fixed effect was the temperature-only expectation of CTI. 3) To focus specifically on long-term trends, we fit

linear models to each stratum time-series of bottom temperature, of temperature-only CTI expectation, and of 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 temperature-only CTI expectation 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, as implemented in 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 long-term bottom temperature trends and long-term CTI trends by including them as interactions with bottom temperature trends in separate multiple linear regression models. We report overall p and r^2 values for each model. 5) To focus specifically on interannual variability, we detrended the annual values of bottom temperature, temperature-only CTI expectation, and observed CTI in each stratum by fitting a linear regression to each timeseries and keeping only the residuals. We then calculated the Pearson product-moment correlation between each variable’s annual anomalies in each stratum. We fit a linear mixed effects model with CTI anomalies as the response variable, bottom temperature anomalies or temperature-only CTI expectation anomalies as a fixed effect, and survey nested within stratum as random effects. We again compared to a null model without bottom temperature or temperature-only CTI expectation to evaluate statistical significance. We also tested for lags between temperature anomalies and CTI anomalies by conducting cross-correlation analysis for each stratum in each season.

Data deposition

All data is available for download from <http://oceanadapt.rutgers.edu> and from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.bg08269> (Flanagan et al. 2018).

Results

Time-averaged CTI expectations and observations

The influence of nonlinear species turnover and the switch from subpolar to temperate species around 15°C was evident in the relationship between bottom temperature and our temperature-only CTI expectation (black line, Fig. 3). Overall, time-averaged expected CTI values were strongly correlated with time-averaged bottom temperatures (linear model slope: 1.024 ± 0.032 , $r^2 = 0.96$, $p < 0.001$). However, there were notable deviations from this slope at particular temperatures. At colder temperatures, the temperature-only CTI expectation was higher than bottom temperature, but it was lower than bottom temperature at warmer temperatures.

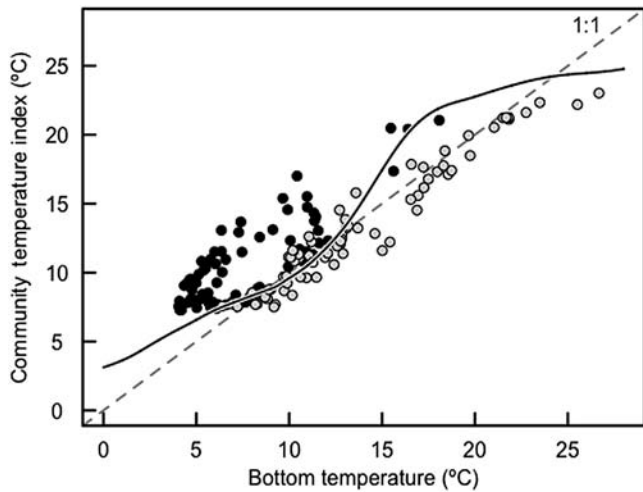


Figure 3. Community temperature index (CTI) in relation to environmental (bottom) temperature. Each point represents an observed stratum mean in either spring (black dots) or fall (gray dots) in the testing dataset (1990–2014). The black line represents the temperature-only expectation of CTI. The dashed gray line indicates what would be a 1:1 correlation between bottom temperature and CTI.

With increasing temperature from 0–10°C, CTI expectations increased in a relatively linear fashion, though with a slope less than one. From 10 to 16°C, the slope of expected CTI change was greater than one. Above 16°C, expected CTI change again had a slope less than one.

Similar to the CTI expectations, time-averaged observed CTI in colder environments (< 16°C) had CTI values somewhat higher than local bottom temperature, while in warmer environments ($\geq 20^\circ\text{C}$), CTI tended to be somewhat lower than bottom temperature (black and gray points, Fig. 3). As with expected CTI, observed CTI was also broadly correlated with bottom temperature (linear regression: slope = 0.710 ± 0.058 , $r^2 = 0.79$, $p < 0.001$). Separating by season, fall time-averaged CTI values were closer to time-averaged bottom temperature values and less variable than spring values (spring linear regression slope 0.826 ± 0.120 , $r^2 = 0.702$, $p < 0.001$, fall: 0.895 ± 0.051 , $r^2 = 0.940$, $p < 0.001$).

Changes in bottom temperature and CTI

Over the period 1990–2014, mean bottom temperature increased by $0.28 \pm 0.10^\circ\text{C decade}^{-1}$ in the fall ($p < 0.0001$) and by $0.20 \pm 0.11^\circ\text{C decade}^{-1}$ in the spring ($p < 0.001$). Some of the southern strata also cooled (Fig. 2a, b). In the same time period, CTI in individual strata also changed substantially (Fig. 2c, d), and across all strata showed similar trends in the fall (mean $0.25 \pm 0.08^\circ\text{C decade}^{-1}$, $p < 0.0001$) and the spring (mean $0.38 \pm 0.09^\circ\text{C decade}^{-1}$, $p < 0.0001$). The strata with decreasing CTI were primarily found in the south, somewhat similar to the spatial distribution of cooling temperatures.

In a mixed-effects model fit to biannual CTI and bottom temperature, we found that for every 1°C increase in bottom temperature, CTI increased by 0.36°C (95% CI: $0.34\text{--}0.38^\circ\text{C}$, $p < 0.0001$). Comparing observations to our temperature-only CTI expectations, observed CTI increased 0.32°C for each 1°C increase in CTI expectation (95% CI: $0.30\text{--}0.34$, $p < 0.0001$).

Long-term trends in bottom temperature and CTI

Long-term bottom temperature and observed CTI trends had similar signs and magnitudes in the same strata, though there was much unexplained variation. Of the two seasons, observed CTI trends were marginally more closely correlated to temperature trends in the spring (slope = 0.626, $r^2 = 0.087$, $p = 0.003$) than in the fall (slope = 0.533, $r^2 = 0.054$, $p = 0.038$) (Fig. 4, Supplementary material Appendix 1 Fig. A3). The temperature-only CTI model provided little additional explanatory power: observed CTI was weakly but significantly correlated to temperature-only CTI expectations (spring $r^2 = 0.066$, $p = 0.022$; fall $r^2 = 0.062$, $p = 0.026$, Supplementary material Appendix 1 Fig. A5). A multiple regression for CTI slope that included bottom temperature slope, depth, and their interaction suggested that CTI trends were more sensitive to bottom temperature trends in shallower strata than in deeper strata ($r^2 = 0.140$, $p < 0.001$). Multiple regressions including latitude and variability suggested that CTI trends were more positive at higher latitudes ($r^2 = 0.131$, $p = 0.001$) and in strata with lower interannual temperature variability ($r^2 = 0.094$, $p < 0.001$).

Interannual changes in bottom temperature and CTI

Individual strata experienced interannual temperature ranges from 1.63 to 14.9°C (detrended) over an entire same-season time-series (average range across strata: 5.63°C). Communities experienced fluctuations in observed CTI of similar but slightly smaller magnitudes, with interannual ranges from 1.13 to 11.5°C (detrended) (average 3.82°C).

Within a majority of individual strata (64%), bottom temperature and observed CTI anomalies were moderately to strongly correlated ($r \geq 0.3$; Supplementary material Appendix 1 Fig. A5a, b). Substituting CTI expectations for bottom temperature revealed a similar effect size (mean $r = 0.376$, Supplementary material Appendix 1 Fig. A5c, d). A mixed effects model supported the conclusion that annual anomalies in CTI and temperature were significantly related, with CTI deviating by 0.31°C (95% confidence interval 0.29–0.33) from its long-term trend for each 1°C deviation in bottom temperature ($p < 0.0001$). Cross-correlation analysis suggested that the majority of communities were most correlated with temperature or temperature-only CTI expectations at time lag zero (Supplementary material Appendix 1 Fig. A6).

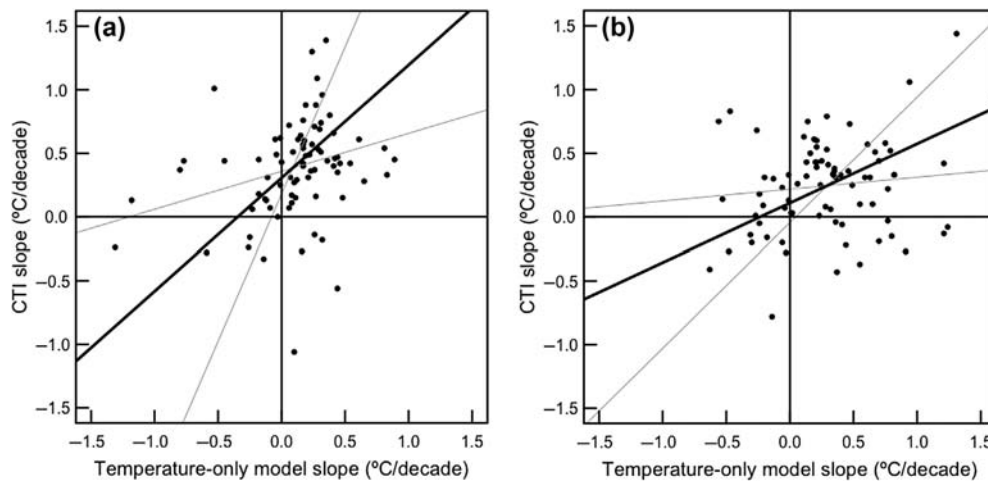


Figure 4. Model II major axis linear regression between 1990–2014 trend in bottom temperature and trend in CTI in spring (a) and fall (b) communities. Major axis regression was used to account for observational error in both temperature and community variables. The black lines indicate major axis regression fits and the gray lines indicate the 95% confidence intervals.

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 yr, with evidence that they are following changes in temperature. We found that temperature effects on community composition were most apparent at inter-annual timescales but were weaker over decadal trends. Our temperature-only modeling approach revealed that CTI responses to temperature will often be non-linear and differ from a 1:1 relationship.

Community implications of nonlinear CTI responses

Species' thermal distributions are rarely symmetrical, which suggests that we should expect the probability of presence of different species to change at different rates, even over relatively narrow temperature ranges. The effects on CTI are likely to be strongest in communities with lower species richness, where changes in the presence or absence of individual species will have a greater impact on the overall CTI (Fig. 1). We therefore need a more nuanced expectation for the relationship of CTI to temperature, and a 1:1 relationship should often not be the null model, even in the absence of factors other than temperature affecting community composition. Further examining the effects of richness and community composition would be an interesting area of future research.

Our temperature-only modeling approach to set CTI expectations presents a first step towards a more appropriate null model (Fig. 1), and it complements other extensions of the CTI method. For example, Bowler and Böhning-Gaese (2017) developed a method to separate temperature change effects from land use change impacts on CTI. Using non-linear species thermal distribution curves to calculate CTI

expectations, we uncovered nonlinear community responses to temperature, even in the absence of land use change, dispersal limitation, or other factors altering community composition. The rate of expected CTI change depended on the initial temperature, with slower turnover expected with warming from colder starting temperatures, and higher turnover expected from warmer starting temperatures.

The step-wise pattern we found in both CTI expectations and the observed CTI values qualitatively echoed global patterns of marine community composition (Stuart-Smith et al. 2015). These global communities 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). Similarly, we found that expectations of CTI change were relatively linear above and below the division between thermal guilds in our dataset (15°C, Supplementary material Appendix 1 Fig. A2), though with a slope less than 1. At intermediate temperatures, communities comprise a mix of subpolar and temperate species, and CTI increased rapidly with increasing temperature as one thermal guild mixed with and replaced another.

Comparing our expected CTI to observed time-averaged CTI, we found that the pattern of observed CTI echoed the pattern of expected CTI, though with more scatter in the relationship, as would be expected with the influence of other factors beyond temperature. Dividing the points by season, the relationship between fall communities and bottom temperature was much closer to the 1:1 line than the relationship for spring communities. We hypothesize that this relationship is due to the nature of seasonal water temperatures and the timing of the surveys. The fall survey occurs towards the end of the warm summer, after community composition has had time to equilibrate to environmental conditions. The spring survey, in contrast, occurs during a season of rapid

environmental change and during a time when community composition is in transition. A similar process of transient dynamics may explain the fact that long-term CTI change was less strongly related to temperature in strata with larger variation in temperature. Further research on seasonality, phenology, and transient dynamics would be a rich area of inquiry.

Thermal impacts on community structure

Previous studies have found that species assemblages follow local temperature changes through geographic or compositional shifts, often with some lag (Menéndez et al. 2006, Lucey and Nye 2010, Bertrand et al. 2011, Devictor et al. 2012, Kleisner et al. 2016). On a temperate continental shelf, we found that CTI change was associated with temperature change, but that the goodness-of-fit depended on temporal scale. While we found evidence that interannual community composition responded predictably to changes in bottom temperature without temporal lags, the relationship between long-term community and environmental changes was weaker. The influence of factors other than temperature on community composition will tend to increase the scatter around the CTI-temperature relationship, reducing both the r^2 and the slope. We did, however, find that long-term community change more closely followed temperature change in the spring season, possibly reflecting the strong impacts of winter temperatures on marine species (Morley et al. 2017) and suggesting that future analyses should examine minimum temperatures.

Effects of spatial scale

Some of the differences between our results and prior studies may arise from differences in spatial and temporal scales. A number of other studies reporting long-term CTI trends have examined change across regions, countries, or entire continents (Bertrand et al. 2011, Devictor et al. 2012, Cheung et al. 2013, Stephens et al. 2016). Climate is often a more dominant influence on population and assemblage dynamics at large spatial scales, while at finer spatial scales, species interactions are thought to more strongly mediate community response to climate change (Pascual and Levin 1999, Walther et al. 2002). We note, however, that our ‘communities’ of analysis had a median area of 2500 km², which were large areas compared to typical communities on land, but which represented the smallest areas consistently sampled. Differences in spatial scale may explain why previous analyses in the northeast U.S. revealed reasonably strong connections between temperature and long-term and wide-scale shifts in species distributions or assemblages (Lucey and Nye 2010, Nye et al. 2013, Pinsky et al. 2013, Kleisner et al. 2016). At finer spatial scales, other studies have emphasized the role of species interactions in mediating the impacts of temperature on long-term CTI change, including in temperate reef communities (Bates et al. 2014, 2017). Changes in land use and microclimate are

also important influences on community composition at fine spatial scales that may hide the effects of temperature change (De Frenne et al. 2013). We look forward to future studies of community change across a broader range of geographic scales.

Effects of time

In addition, most studies focus on long-term trends (Bertrand et al. 2011, Devictor et al. 2012, Bowler and Böhning-Gaese 2017). However, the magnitude of interannual fluctuations in CTI can be larger than long-term changes in temperature or CTI, and particularly at fine spatial scales, the variability from these fluctuations may mask long-term climate signals. Indeed, by comparing interannual and long-term changes, our analysis revealed a higher degree of community responsiveness (less scatter in the CTI to temperature relationship) on an interannual basis than across long-term trends.

The greater role of temperature change at interannual timescales may reflect the strong influence of temperature on marine ectotherm physiology and the high dispersal potential in marine environments (Kinlan and Gaines 2003, Pörtner and Knust 2007, Somero 2012). Compared to terrestrial ectotherms, marine ectotherm body temperatures are largely in thermal equilibrium with their environment due to high rates of convection and conduction (Denny 1993), so temperature changes may therefore quickly drive the emigration of individuals or the extinction of populations. This hypothesis is supported by the close relationship between marine species range edges and their thermal tolerances (Sunday et al. 2012). In addition, compared to terrestrial environments, the relative lack of dispersal barriers and the ability of ocean currents to carry offspring long distances create many opportunities for colonization by new species in response to temperature change. In fact, marine species are colonizing new territory an order of magnitude faster than terrestrial species (Poloczanska et al. 2013). These factors facilitate rapid increases and decreases in species occurrence and may help explain why marine community composition responded quickly to interannual temperature changes in the northeast U.S. Indeed, as found in other marine systems, temperature shapes not only distributions, but also relative abundance of marine animals (Southward et al. 1995, Day et al. 2018). Interannual responses to temperature for individual species were apparent in a similar dataset for the southeast U.S., though in a study that did not address community composition (Morley et al. 2017). The degree to which such rapid responses are general across marine ecosystems and the degree to which they appear in terrestrial and freshwater ecosystems will be interesting to explore further.

Across longer time-scales, however, other factors beyond temperature appeared to play a stronger role in shaping community composition in the northeast U.S., limiting the magnitude of temperature-correlated changes, increasing the scatter, and reducing the slope of the CTI-temperature

relationship. For example, seasonal changes in circulation, including the influx of cool, low-salinity water from the Scotian Shelf in the 1990s, may have contributed to stratification in the Gulf of Maine, driven changes in primary productivity, and altered the distribution and abundance of planktivores, mesopredators, and higher trophic levels (Mountain 2004, Stevenson et al. 2004, Friedland and Hare 2007). In addition, human activities such as harvest, pollution, or habitat destruction can amplify, mediate, or mask the effects of temperature change on species and communities (Anderson et al. 2008, Lucey and Nye 2010, Planque et al. 2010, Bowler and Böhning-Gaese 2017). Fishing pressure in Georges Bank from 1970–2000 changed the abundance of heavily-exploited species like cod and yellowtail flounder, decreasing their spatial and dietary overlap with other species, while allowing minimally-exploited species like spiny dogfish or winter skate to expand into new areas (Garrison and 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 alter marine community composition. The strong role that fishing has had in changing species abundances and occurrences in this ecosystem over the past few decades may explain why long-term CTI and temperature trends were weakly correlated, despite much higher interannual correlations.

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

Conclusion

The use of a single, quantitative measure for evaluating and predicting community change in response to temperature change is an attractive idea. However, interpreting CTI in practice and using it to predict future change requires a nuanced approach. Because CTI is built up from inherently non-linear species responses to temperature, CTI itself will often reveal non-linear responses, particularly in communities with relatively few species. The utility of CTI stretches across scales of time and space, but the importance of temperature change relative to other factors in driving community change will vary across these scales. In the northeast U.S. continental shelf ecosystem, we found that temperature was particularly important in driving community turnover at fine spatial and short (interannual) temporal scales, while previous research has highlighted the important role of temperature at wide spatial scales across a range of temporal scales. Marine ecosystems may be particularly sensitive to temperature at a range of temporal scales given the physics, physiology, and ecological dynamics of these systems.

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Supplementary material (Appendix ECOG-03961 at <www.ecography.org/appendix/ecog-03961>). Appendix 1.