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Cold range edges of marine fishes track climate change better than warm edges

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Abstract

Species around the world are shifting their ranges in response to climate change. To make robust predictions about climate-related colonizations and extinctions, it is vital to understand the dynamics of range edges. This study is among the first to examine annual dynamics of cold and warm range edges, as most global change studies average observational data over space or over time. We analyzed annual range edge dynamics of marine fishes—both at the individual species level and pooled into cold- and warm-edge assemblages—in a multi-decade time-series of trawl surveys conducted on the Northeast US Shelf during a period of rapid warming. We tested whether cold edges show stronger evidence of climate tracking than warm edges (due to non-climate processes or time lags at the warm edge; the *biogeography hypothesis* or *extinction debt hypothesis*), or whether they tracked temperature change equally (due to the influence of habitat suitability; the *ecophysiology hypothesis*). In addition to exploring correlations with regional temperature change, we calculated species- and assemblage-specific sea bottom and sea surface temperature isotherms and used them to predict range edge position. Cold edges shifted further and tracked sea surface and bottom temperature isotherms to a greater degree than warm edges. Mixed-effects models revealed that for a one-degree latitude shift in isotherm position, cold edges shifted 0.47 degrees of latitude, and warm edges shifted only 0.28 degrees. Our results suggest that cold range edges are tracking climate change better than warm range edges, invalidating the ecophysiology hypothesis. We also found that even among highly mobile marine ectotherms in a global warming hotspot, few species are fully keeping pace with climate.

KEYWORDS
biogeography, ecophysiology, fisheries, Northwest Atlantic, range limit, spatial ecology, species distributions, thermal tolerance

1 | INTRODUCTION

Species around the globe are shifting their ranges in response to warming (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Lenoir & Svenning, 2015; Parmesan & Yohe, 2003; Poloczanska et al., 2013). In the 20th century, the land and sea surfaces of our planet warmed 0.85°C on average. By 2100, the planet will almost certainly have warmed at least 2°C relative to the pre-industrial average, and could warm up to 5°C depending on the greenhouse gas emissions trajectory (Pachauri & Mayer, 2015). Robust predictions of which species will move, where they will go, and how fast they will shift are critical for maintaining food security, controlling agricultural pests, managing disease outbreaks, preserving ecosystem function and biodiversity, and many other contributors to human well-being (Pecl et al., 2017). Because species' responses to climate change are highly individualistic and are not solely climate-mediated (Jackson, Betancourt, Booth, & Gray, 2009), they can be difficult to predict.

Better predictions are likely to derive from a better understanding of the relevant processes (Urban et al., 2016) but understanding the ecological processes underlying the shifts in species distributions has been challenging in part because many studies examine shifts in the center of a species distribution (Perry, Low, Ellis, & Reynolds, 2005; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013). However, species shifts consist of colonizations at the leading edge, extirpations at the trailing edge, or both. Each of these processes is likely to be sensitive to different aspects of climate change and to differ from the processes affecting range centers (Sunday et al., 2015). If climate velocities point poleward—that is, the region is warming and cooler climates exist toward the poles, as is the case in most parts of the world (Burrows et al., 2011)—then the leading edge is equivalent to the 'cold' or 'poleward' range edge, and the trailing edge to the 'warm' or 'equatorward' edge.

The fundamental determinants of species range edges, and their sensitivity to climate, have been active areas of ecological research for over a century (Gaston, 2009; MacArthur, 1972; Sexton, McIntyre, Angert, & Rice, 2009; Wallace, 1876). Biogeographic theory developed largely in terrestrial systems suggests that cold range edges are exposed to greater abiotic stress and thus more likely to be climate-mediated than are warm range edges. By contrast, warm range edges encounter less seasonality and higher biodiversity (due to the latitudinal biodiversity gradient), so biotic interactions should have a greater influence (Cahill et al., 2014; Louthan, Doak, & Angert, 2015); we call this the *biogeography hypothesis*. Alternatively, cold edges may respond more immediately to contemporary climate shifts while warm edges may 'lag' climate if extirpation is relatively slow (the *extinction debt hypothesis*). Climate-induced extirpation in terrestrial species can take decades to materialize for short-lived species, and more than a century for long-lived species, due to extinction debt (Fordham et al., 2016). If either of these mechanisms—the biogeography hypothesis or the extinction debt hypothesis—is operating for marine species, we would expect cold range edges to track climate better than warm range edges.

Most biogeographic research has been conducted on land, but the relative importance of climatic and biotic factors in constraining cold and warm range edges may differ systematically between terrestrial and marine ecosystems. Range edges of mobile marine ectotherms are expected to be highly correlated with climate suitability because those species experience few barriers to dispersal and tend to occupy all thermally suitable habitat (Sunday, Bates, & Dulvy, 2011, 2012). In addition, local extirpations as a result of warming were found to be twice as common in the ocean as on land (Pinsky, Eikeset, McCauley, Payne, & Sunday, 2019), suggesting that temperature is an important driver of both extinction and colonization dynamics in marine species. This mechanism would lead to an expectation that warm and cold range edges should track climate equally, which we term the *ecophysiology hypothesis*.

Predictions from theory are therefore equivocal about how marine species range edges are expected to change as ocean temperatures warm. One of the major challenges to testing theory about movements of range edges is the large data requirement: data are ideally collected over large spatial extents with fine-scale resolution for many species and over many years (Thomas, Franco, & Hill, 2006). Consequently, few empirical studies have investigated the relationship between annual range edge positions and climate, and most of them focus on just one edge type (Cavanaugh et al., 2018; La Sorte & Thompson III, 2007). One study that tested annual dynamics of cold and warm range edges for climate tracking—in tree species in the United States—found no evidence of climate-related shifts at either range edge (Zhu, Woodall, & Clark, 2012). The several empirical studies that compared both range edges using two or three time points have reported variable findings, including better climate tracking at the cold edges than the warm edges (Hickling, Roy, Hill, & Thomas, 2005; Parmesan et al., 1999); no climate tracking at either edge (Currie & Venne, 2017); and warm-edge retractions without concordant cold-edge extensions (Coristine & Kerr, 2015; Kerr et al., 2015). Analyzing fewer time points creates greater uncertainty about the shift of any given species and can confound stationary variability in range position with a long-term shift (Bates et al., 2015; Brown et al., 2016).

We address this empirical challenge by examining whether cold and warm range edges of marine fishes have shifted predictably in response to temperature change on the Northeast US Shelf, a global warming hotspot, using annual survey data from 1968 to 2017. We used both sea surface and sea bottom temperatures to predict species-specific and assemblage-wide shifts in edge position, contrasting individual responses with broader trends. On the Northeast US Shelf, severe warming since the mid-20th century has already been linked to marked shifts in distributions of marine fish, including an assemblage-wide northward shift (Bell, Richardson, Hare, Lynch, & Fratantoni, 2015; Hare et al., 2016; Lucey & Nye, 2010; Nye, Link, Hare, & Overholtz, 2009; Pinsky et al., 2013) and novel northward occurrences of many species (Mills et al., 2013). By examining trends in both cold and warm edges under climate change, we tested the ecophysiology hypothesis against the biogeography and extinction debt hypotheses. We found evidence that both cold and warm range edges of marine fishes in the Northeast US shifted north and tracked temperature in our 50-year time-series, but cold edges shifted further and exhibited a stronger relationship with temperature. This contradicts the ecophysiology hypothesis and suggests either that biotic interactions and other non-temperature-related factors are more important at the warm than at the cold range edge or that extinction debt is causing warm range edges to lag behind temperature changes.

2 | MATERIALS AND METHODS

2.1 | Region and historical warming

The Northeast US Shelf is a highly productive, temperate ecosystem with extensive sandy bottom that supports numerous important fisheries. It extends from Cape Hatteras to the Gulf of Maine. The region is considered a global warming hotspot, having warmed over 1°C in the 20th century (Hare et al., 2016). Some high-resolution climate models suggest that this region will continue to warm even more than previously expected (Saba et al., 2016). We used three different temperature datasets to capture three dimensions of temperature change in this region. The National Oceanographic and Atmospheric Administration (NOAA) NCEI optimum interpolation sea surface temperature (NOAA, 2018) is available daily from 1982 onward at 0.25° × 0.25° resolution; we used this to calculate temperature extremes. The Hadley Centre sea surface temperature dataset included the full length of the study period, but only monthly at 1° resolution, from which we calculated average sea surface temperatures (Rayner, 2003). We also obtained hindcast sea bottom temperature values from the Simple Ocean Data Assimilation model (version 3.4.2, available monthly from 1980 at 0.5° resolution) to test whether bottom temperature better explained the dynamics of these demersal fish species than surface temperature. Both sea surface temperature datasets were accessed using the rerddap package (Chamberlain, 2019). Bottom temperature data were provided by J. Carton (pers. comm.). Each dataset was retrieved within a bounding box of 35–45°N and 66–77°W and then cropped to exclude all points deeper than 300 m or beyond the US Exclusive Economic Zone (Bauer, 2018; Flanders Marine Institute, 2019).

2.2 | Survey data

We used data from benthic trawl surveys conducted on the Northeast US Shelf by NOAA's Northeast Fisheries Science Center (NEFSC) from 1968 to 2017 (Politis, Galbraith, Kostovick, & Brown, 2014). The NEFSC's spring survey was historically conducted at more consistent times than their fall survey, so we only used data from the spring survey (Flanagan, Jensen, Morley, & Pinsky, 2019). These surveys are repeated annually as random samples within predefined statistical regions ('strata'). There are over 100 strata across the entire Northeast US Shelf at various depths; hauls ranged from 5 to 542 m deep, with almost all hauls occurring between 10 and 300 m depth. The NEFSC trawl survey records observations regarding both the catch and the environment, including bottom temperature, depth, salinity, species identity, individual length, and individual weight. Data were obtained from OceanAdapt (downloaded May 5, 2019 from https://oceanadapt.rutgers.edu/), a data portal to access NOAA trawl survey records.

We analyzed two distinct groups of species: those with a cold range edge in the Northeast US Shelf and those with a warm range edge in that region. Because marine fish often have large ranges, and because we restricted our study to the Northeast US Shelf, none of the species had both a cold and a warm range edge in the study area (i.e., there is no overlap in species identity between the two groups studied). Most species with warm range edges in the Northeast US Shelf extend past Maine into Canadian waters (beyond the NEFSC survey area), and most species with cold range edges in this region are also found in the South Atlantic, Gulf of Mexico, or Caribbean (also beyond the NEFSC survey area). To distinguish single-species and pooled analyses, we refer to the set of species with a cold or a warm edge as a *group*, and to the set of all observations belonging to cold- or warm-edge species pooled together (without regard to species) as an *assemblage*.

We used three approaches to check that the species to be analyzed had range edges in the study region. First, we eliminated from the warm range edge group any species recorded in the Southeast US survey (using the list of species in that region from the analogous South Atlantic bottom trawl survey conducted by the Southeast Fisheries Science Center, also obtained from OceanAdapt). To ensure that cold-edge species started out well within the survey area (i.e., not already close to the edge of the US Exclusive Economic Zone), we classified species as having a cold edge in the region if they were not found above 42°N in the first year they were observed. Second, we calculated range edges from Aquamaps, a global ecological niche model of marine species ranges that projects into under-sampled areas using environmental variables and known observations of species (Kaschner et al., 2016). Because Aquamaps range edges are imprecise, we calculated the 5th and 95th percentile of latitudes where each of these species occurs in Aquamaps with >80% probability. To eliminate species with range edges far beyond the Northeast US Shelf, we removed a warm-edge species from further analysis if the Aquamaps projections placed its 5th percentile latitude below 30°N, or if Aquamaps placed a cold-edge species' 95th percentile latitude above 50°N. Third, we manually compared the two lists of species to the International Union for Conservation of Nature (IUCN) and/or FishBase range maps (Froese & Pauly, 2019; IUCN, 2019). This third check primarily ruled out species with a cold edge near Nova Scotia or Newfoundland, such as Atlantic menhaden (*Brevoortia tyrannus*) and barndoor skate (*Dipturus laevis*).

We imposed a number of filters to ensure data quality and comparability among species, strata, and years. This study only used data on bony and cartilaginous fishes, which are most frequently and consistently sampled in the NEFSC survey. We excluded all observations that were missing essential data or were otherwise of poor quality (e.g., not identified to species [eliminated 28,504 records], no recorded biomass [eliminated 18,223 additional records], latitude below 36°N where survey does not regularly operate [eliminated 10,533 additional records]). We eliminated species–year combinations where the species was observed fewer than 10 times (eliminating 4,829 additional records) because such limited observations were not sufficient to estimate the edge position. From the remaining data, we excluded species that were observed in fewer than 10 years. The final datasets used for analysis included 105,887 records of warm-edge species, and

14,422 records of cold-edge species. Although many species were observed in far more than 10 years, we did not impose a stricter filter on the number of years because we wanted to include species with range edges that might have shifted into or out of the study region during the time-series.

After imposing these filters on data quality, we examined 14 cold-edge species and 29 warm-edge species that represented a diverse group of benthic-dwelling bony and cartilaginous fish (see Data S1). In addition to including more species, the warm-edge group was better-sampled: the median number of total observations per species was 3,708 (interquartile range: 964–5,034), and over half of the species were present in all 50 years. The median number of observations of each cold-edge species was 568 (interquartile range: 352–1,324), and median years recorded per species was 27 (interquartile range: 12–42).

2.3 | Range edge position analysis

Many methods exist to quantify the edge of a species' range, most of which are based on measuring latitudinal position (Kerr et al., 2015; Lenoir, Gégout, Pierrat, Bontemps, & Dhôte, 2009; Thomas & Lennon, 1999; Zhu et al., 2012). Because climate velocity points northeast along the shelf in this region (Burrows et al., 2011; Pinsky et al., 2013), and latitudinal response variables only capture north/south displacement, we also described range edges using distance along the coastline (Bell et al., 2015; Hare, Alexander, Fogarty, Williams, & Scott, 2010). For the Northeast US Shelf region, we downloaded a coarse outline of the coast using the 'rnaturalearth' package in R (South, 2017) and applied a smoothing function to remove coastal features such as the Chesapeake Bay that would otherwise be counted in a measurement of coastline length. We measured the smoothed coastline using Cape Hatteras as the origin, such that a greater distance along the coastline represented a poleward shift. Each species observation was 'snapped' to the smoothed coastline by minimizing the absolute distance from the point observation (somewhere on the shelf) to the smoothed coastline. For each year, the edge position was calculated as the 95th percentile (cold edge) or 5th percentile (warm edge) of point observation distances along the smoothed coastline. We also calculated a second, independent edge metric as the 95th percentile (poleward) or 5th percentile (equatorward) of *latitudes* of observations, for use in models with isotherms, which were defined in terms of latitude.

We applied the edge calculation approach both to the observations of a single species in a year (species range edge), and to all observations of individuals belonging to species in the cold-edge or warm-edge groups in each year (assemblage range edge). For the assemblage range edges, in other words, we pooled observations across species before calculating the range edge. The assemblage range edge therefore described the range edge of an entire assemblage of species with a cold or warm range edge in this region. These assemblage edges were strongly influenced by the further poleward cold-edge species or the further equatorward warm-edge species in a given year.

We tested for edge displacement over the time-series with a linear model of edge position on year (14 linear models for the cold-edge group of species, 29 models for species in the warm-edge group, and two for the cold- and warm-edge assemblages). Our approach to estimating range edge position relied on presence and absence only. We did not use data on abundance or biomass because our focus was on range edge dynamics. The within-range distribution of abundance is poorly understood for most species (Dallas, Decker, & Hastings, 2017; Sagarin, Gaines, & Gaylord, 2006; Santini, Pironon, Maiorano, & Thuiller, 2019) and will not necessarily shift in concert with range edges (Simpson et al., 2011). Relative to a presence-based edge metric, an abundance-weighted edge metric (see Figures S1 and S2 in Data S1) would estimate less similar (i.e., further apart) edge positions for species with the same overall geographic extent but different within-range distributions of abundance (e.g., one species concentrated toward its geographic center, one toward the edges). Our approach is also consistent with the existing literature on range edge shifts and climate change, which predominantly uses presence-based metrics (Hickling et al., 2005; Sittaro, Paquette, Messier, & Nock, 2017; Tingley & Beissinger, 2009).

2.4 | Relationships between range edge dynamics and temperature

We fitted a series of statistical models to examine the relationship between annual edge position and recent changes in temperature: linear models for each species-specific edge, linear mixed-effects models for all species edges in the warm- or cold-edge group at once, and linear models for the edge positions of each of the two assemblages (all individuals in cold-edge or warm-edge species groups, pooled). We used two groups of predictor variables (Table 1): regional trends in temperature to explore the influence of temperature extremes and longer time-series, and edge-specific isotherms to test spatially explicit temperature tracking. Because the trawl survey occurs in the spring, species may be responding to conditions from the previous calendar year. To address this timing issue, all models used predictor variables calculated from the 12-month period (March–February) before the spring survey in any given year. In other words, the edge position calculated in 1990 was compared to temperatures that occurred from March 1989 to February 1990.

Annual species- or assemblage-specific isotherms were derived from the monthly sea surface and bottom temperature datasets (Sunday et al., 2015). The isotherm analyses were repeated independently with the surface and bottom datasets, so each species and assemblage had a sea surface and a sea bottom temperature isotherm. First, using annual linear models of sea surface or sea bottom temperature on latitude, we derived an equation that calculated the expected temperature given a latitude, or the expected latitude given a temperature. Once a range edge was described (see Section 2.3), we established a baseline temperature for that edge. For the assemblages, the baseline temperature was the sea surface or sea bottom temperature predicted by the linear model at the latitudinal position of the edge in the first year

TABLE 1 Predictor variables used in the analysis

Predictor variable	Data source	Years available
Regional annual sea bottom temperature, mean	SODA	Monthly 1980–2017
Regional annual sea surface temperature, mean	HadISST	Monthly 1968–2017
Regional annual sea surface temperature, 99th percentile (warm extreme)	OISST	Daily 1982–2017
Regional annual sea surface temperature, 1st percentile (cold extreme)	OISST	Daily 1982–2017
Edge-specific sea surface temperature isotherms	HadISST	Monthly 1968–2017
Edge-specific sea bottom temperature isotherms	SODA	Monthly 1980–2017

Abbreviations: HadISST, Hadley Centre Global Sea Ice and Sea Surface Temperature model (Rayner, 2003); OISST, NOAA NCEI optimum interpolation sea surface temperature model (NOAA, 2018); SODA, Simple Ocean Data Assimilation model 3.4.2 (Carton, Chepurin, & Chen, 2018).

for which monthly temperature data were available. For individual species, whose edges are more variable through time, the baseline temperature was the mean of predicted temperatures calculated from the first 3 years when the species was observed. For species that were observed every year, the baseline reference years were 1968–1970 for sea surface temperature and 1980–1982 for sea bottom temperature. With these species- and assemblage-specific isotherms, we then calculated the latitude at which those temperatures occurred in later years, again using annual linear models of sea surface or bottom temperature on latitude. Each time-series of predicted latitudes at which a given temperature was found comprised a species- or assemblage-specific isotherm (sensu Sunday et al., 2015).

For the species-specific linear models, we fit linear regressions to test the correlation between each range edge position and each species' corresponding isotherm position (n = 14 cold range edges and n = 29 warm range edges). For each edge, we examined two models: one with the sea surface temperature isotherm as a predictor, and one with the sea bottom temperature isotherm as a predictor. In total, we fit 86 linear regressions of this type (two models by 43 individual species).

Next, we constructed linear mixed-effects models across all species in a group (cold edge or warm edge) to test our hypotheses in aggregate rather than in a species-by-species manner. We used the lmerTest package in R, which implements linear mixed-effects models and calculates p values using Satterthwaite's degrees of freedom method (Kuznetsova, Brockhoff, & Christensen, 2017). The response variable was a single-species edge position, and the explanatory variables were either sea surface or sea bottom temperature species-specific isotherm positions. Species identity was a random effect. In total, we fit four linear mixed-effects models (two groups for each of two sets of predictor variables).

Finally, to explain the annual position of the assemblage edge, we compared six linear models, each run separately for the cold- and warm-edge assemblages. Each linear model had a different set of explanatory variables: (a) *bottom temperature only*: regional mean annual bottom temperature as the predictor variable, (b) *surface temperature only*: regional mean annual surface temperature, (c) *cold extreme*: 1st percentile regional annual surface temperature, (d) *warm extreme*: 99th percentile regional annual surface temperature, (e) *sea surface isotherms*: the assemblage edge-specific isotherm for sea surface temperature, and (f) *sea bottom isotherms*: the assemblage edge-specific isotherm for sea bottom temperature. The cold and warm extreme models tested for the influence of extreme temperatures on range edges (Pinsky et al., 2019; Sunday et al., 2019), and were based on percentiles of daily mean temperatures across the region; in other words, these predictors represented the warmest and coldest days in the Northeast US in the past year. Depending on the predictor variables in each model, response variables (edge positions) were estimated from either a percentile of distance (for regional temperatures) or of latitude (for isotherms, see Section 2.3). The assemblage models contained no species-specific information. In total, we fit 12 assemblage linear models (two species groups by six sets of explanatory variables).

2.5 | Changes in depth and biomass

Range size is positively correlated with abundance for many species, so a decline in abundance could accelerate equatorward edge shifts or impede poleward edge shifts under climate change (Blanchard et al., 2005; MacCall, 1990; Ralston, DeLuca, Feldman, & King, 2017). We note that because we measured abundance using biomass, we cannot rule out that declining biomass is due to reduced body size in a species, rather than population size (Shackell, Frank, Fisher, Petrie, & Leggett, 2010). Shifting to deeper waters could allow species to stay within their historic thermal conditions, in addition to—or instead of—shifting up the coast (Dulvy et al., 2008). Responses to warming might 'trade off' such that a species shifted *either* north or deeper (negative correlation between depth shift and edge shift across species), or they might have occurred simultaneously (positive correlation between depth shift and edge shift across species). We tested whether range edge shifts were correlated with changing biomass or depth over time.

To estimate biomass, we calculated a standardized total annual biomass for each species from the weight recorded in the survey. Each row in the raw data contained a recorded biomass in kilograms for individuals of each species in each haul. We then averaged those raw biomass values, producing a mean annual biomass value for each species in each stratum that included zeroes for true absences where a haul occurred but a species was not found. Up to this point, all biomass values were in units of kg/tow; to standardize by area towed, we divided the mean annual biomass value for each species in each stratum by the area of a tow (0.01 nmi^2), multiplied it by the area of that stratum (available from OceanAdapt), and summed over all strata to yield a standardized estimate of each species' total annual biomass. Changes in biomass can reflect changes in abundance, changes in body size, or both (Bell et al., 2015; Shackell et al., 2010). We tested for changes in biomass over time using a linear regression of biomass on year for each species (43 species-specific linear regressions).

To estimate depth, we used the depth data from the NEFSC trawl surveys to calculate an annual mean depth for each species based on all its observations in that year—not just the observations at the edge. These annual depth estimates were weighted by the biomass recorded in each haul (the raw biomass values described above). For each species, we performed a linear regression of depth on year (43 species-specific linear regressions). This analysis tested whether the biomass-weighted mean depth of each species had shifted deeper or shallower over the time-series.

We compared coefficients from these linear models and those described in Section 2.3 to explore whether species showed simultaneous changes in range edge position and either biomass or depth. We then calculated the Spearman rank correlation between the coefficients of biomass or depth over time and the coefficients of edge position over time from the linear models (four tests total, for biomass and depth by the two species groups). These tests revealed whether range edge shifts were either positively or negatively associated with changing biomass or depth within the poleward or equatorward edge group.

All data analyses for this project were conducted in R version 3.6.0 (R Core Team, 2018). Code can be accessed on GitHub at: https://github.com/afredstonhermann/neus-range-edges.

3 | RESULTS

3.1 | Region and historical warming

The Northeast US Shelf region (Figure 1a) has a strong thermal gradient along the coast (Figure 1b). From 1968 to 2017, the annual mean of monthly sea surface temperatures on the Northeast US Shelf increased 0.030°C per year (±0.004°C, p = 1.14 × 10^{-8}, linear regression; Figure 1d). From 1982 to 2017, high (99th percentile) daily sea surface temperatures in this region warmed 0.046°C per year (±0.01°C, p = 3.32 × 10^{-5}, linear regression; Figure 1e). Mean annual monthly sea bottom temperatures also increased from 1980 to 2017, at a rate of 0.017°C per year (±0.007°C, p = .024, linear regression). Cold extremes were less affected: the low (1st percentile) daily sea surface temperature from 1982 to 2017 did not significantly change

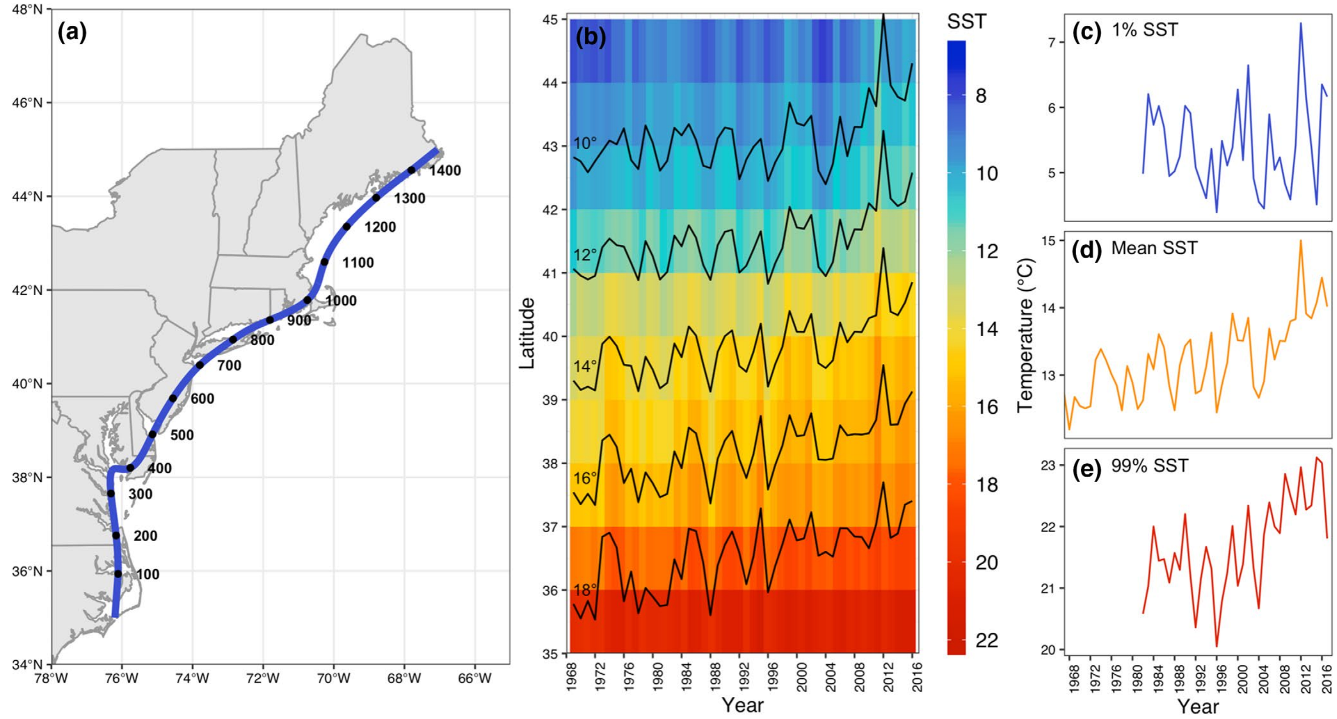

FIGURE 1 Map of study area (a), Hovmöller diagram of change in sea surface temperature during the study period (b), and time-series of 1st percentile (c), mean (d), and 99th percentile (e) sea surface temperature in the study region. The blue line on (a) shows the smoothed coastline, with dots every 100 km. Sea surface temperature data in (b) are presented as shelf-wide annual means of monthly temperatures (°C). The 10°C, 12°C, 14°C, 16°C, and 18°C isotherms plotted in black on (b) are calculated from annual linear regressions of monthly sea surface temperature on latitude

(0.005 ± 0.01°C, *p* = .68, linear regression; Figure 1c). These spatial and temporal changes in temperature translated into isotherms that shifted north at least one degree of latitude during the study period (0.02–0.03 degrees latitude per year; Figure 1b).

3.2 | Range edge position analysis

Of the 14 cold edges studied, 11 (79%) shifted north during the time-series, of which 8 (57%) shifted significantly north ($p \le .05$, linear regression; Figure 2a). Only one of the three species that shifted south was statistically significant: offshore silver hake. Among the significant shifts, the estimated time trend of species edge position ranged from −7.4 to 13.1 km/year, with standard errors ranging from ±0.6 to ±3.5. In other words, over the 50-year time-series, we estimated that species' cold edges shifted up to 370 km south or 655 km north. The cold assemblage edge, calculated from species observations pooled together, moved north at 6.7 km/year ± 0.8 (standard error; $p = 3.7 \times 10^{-11}$, linear regression), or a total of 335 km from 1968 to 2017. See Data S1 for all estimated range edge shifts.

In the warm-edge group, 18 of 29 edges (62%) shifted north, of which 13 (45%) were statistically significant ($p \le .05$, linear regression; Figure 3a). Of the 11 warm edges that shifted south, only winter skate and barndoor skate were significant. Effect sizes of significant shifts ranged from −15.6 km/year (750 km south in total) to 11 km/year (550 km north in total), with standard errors from ±0.1 to ±2.2. A linear model of the warm-edge assemblage position over time revealed a non-significant relationship (*p* = .8) with an effect size close to zero (−0.2 km/year).

For most species in both groups, range edge position was highly dynamic over time; for many species we studied, selecting a random 'old' and 'new' year to compare could result in a finding of a marked

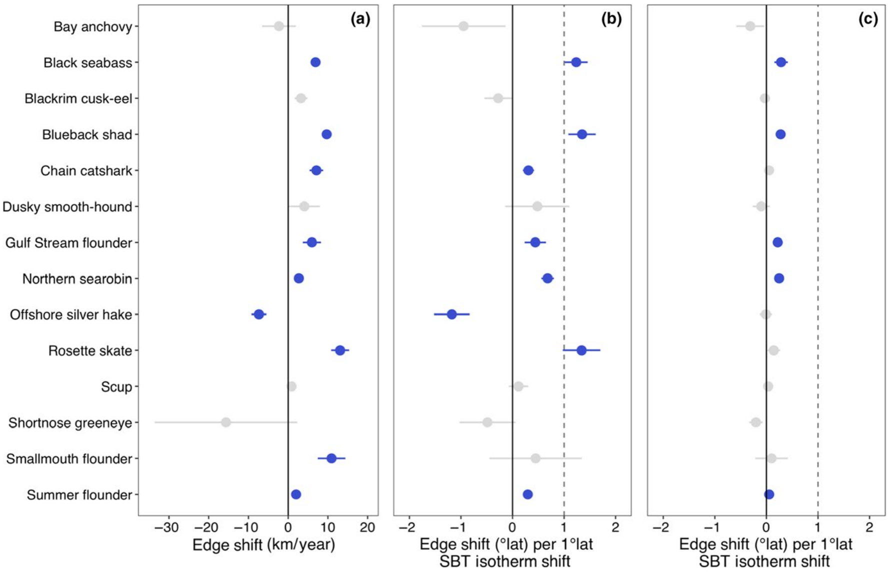

FIGURE 2 Species-specific cold-edge shifts over time (a) and effect of species-specific sea surface (b) and sea bottom (c) temperature isotherms on edge position (linear models). Lines are standard errors from the model output. Blue dots represent significant results ($p \le .05$), and grey dots represent non-significant results ($p > .05$). Points to the left of the vertical black line represent southward shifts (a) or negative relationships with isotherm position (b or c). In (b) and (c), a value of 1 (vertical grey dashed line) represents perfect climate tracking, that is, the range edge shifted one degree in latitude for every degree that the isotherm shifted

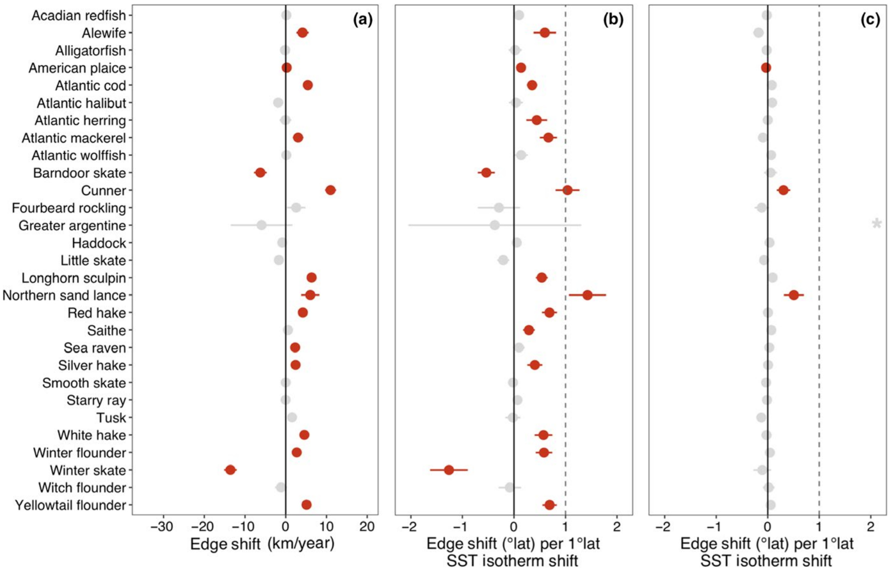

FIGURE 3 Species-specific warm-edge shifts over time (a) and effect of species-specific sea surface (b) and sea bottom (c) temperature isotherms on edge position (linear models). Lines are standard errors from the model output. Red dots represent significant results ($p \le .05$), and grey dots represent non-significant results ($p > .05$). Points to the left of the vertical black line represent southward shifts (a) or negative relationships with isotherm position (b or c). In (b) and (c), a value of 1 (vertical grey dashed line) represents perfect climate tracking, that is, the range edge shifted one degree in latitude for every degree that the isotherm shifted. The grey asterisk for greater argentine in (c) denotes a non-significant outlier (effect size 4.0 ± 2.3)

northward shift, a marked southward shift, or no shift at all, depending on the exact years chosen (Figure 4). All single-species time-series can be viewed in Data S1.

3.3 | Range edge dynamics and temperature

Seven of the 14 cold-edge species and 14 of the 29 warm-edge species had a significant positive association with their sea surface temperature isotherms (Figures 2b and 3b). Fewer species in either group had a significant positive association with their sea bottom temperature isotherms (Figures 2c and 3c), although the fraction was higher in the cold-edge group (5 of 14, 36%) than the warm-edge group (3 of 29, 10%). In both groups, the species that did significantly track sea bottom temperature also tracked sea surface temperature and shifted significantly north. The four linear mixed-effects models across all species in a group suggested similar conclusions, with stronger relationships to surface than to bottom temperatures (Table 2).

In addition, the individual species models and the cross-species mixed-effects models both suggested stronger temperature

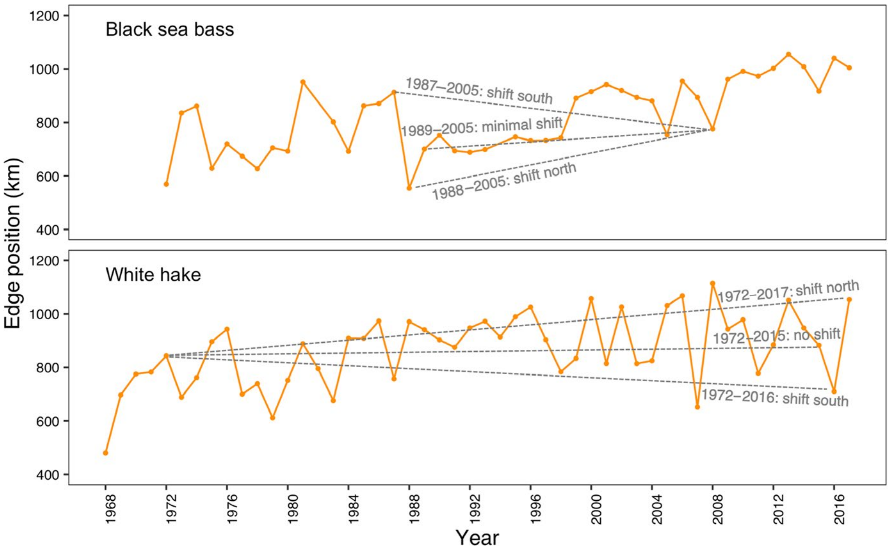

FIGURE 4 Annual cold (black sea bass) and warm (white hake) range edge position; for example, species chosen to represent relatively well-sampled species that show highly variable edge dynamics. Both species shifted significantly north over the time-series. Grey lines show hypothetical observed shifts in each species if only two time points had been observed: a baseline in 1987, 1988, and 1989 with a resurvey in 2005 for black sea bass, and a baseline in 1972 with a resurvey in 2015, 2016, or 2017 for white hake. See Data S1 for all species' time-series

TABLE 2 Results of models explaining range edge position with temperature

Model	Response variable	Predictor variable(s)	Coefficient(s)	*p* value
Cold edge				
LMEM	Species edges (latitude)	SST isotherm	0.47 ± 0.07°lat/°lat	**7.96×10^{-10}**
LMEM	Species edges (latitude)	SBT isotherm	0.13 ± 0.03°lat/°lat	**5.51×10^{-6}**
LM	Assemblage edge (distance)	Mean SST	105.88 ± 25.15 km/°C	**1.11×10^{-4}**
LM	Assemblage edge (distance)	Mean SBT	37.55 ± 38.93 km/°C	0.34
LM	Assemblage edge (distance)	1% SST	−12.48 ± 34.20 km/°C	0.72
LM	Assemblage edge (distance)	99% SST	90.35 ± 21.04 km/°C	**1.45×10^{-4}**
LM	Assemblage edge (latitude)	SST isotherm	0.60 ± 0.24°lat/°lat	**0.016**
LM	Assemblage edge (latitude)	SBT isotherm	0.18 ± 0.10°lat/°lat	0.075
Warm edge				
LMEM	Species edges (latitude)	SST isotherm	0.28 ± 0.04°lat/°lat	**4.69×10^{-15}**
LMEM	Species edges (latitude)	SBT isotherm	0.014 ± 0.016°lat/°lat	0.40
LM	Assemblage edge (distance)	Mean SST	18.65 ± 12.05 km/°C	0.13
LM	Assemblage edge (distance)	Mean SBT	14.62 ± 14.06 km/°C	0.31
LM	Assemblage edge (distance)	1% SST	13.54 ± 12.37 km/°C	0.28
LM	Assemblage edge (distance)	99% SST	26.54 ± 8.47 km/°C	**0.0036**
LM	Assemblage edge (latitude)	SST isotherm	0.23 ± 0.10°lat/°lat	**0.027**
LM	Assemblage edge (latitude)	SBT isotherm	0.02 ± 0.05°lat/°lat	0.73

Note: Model acronyms: linear model (LM), linear mixed-effects model (LMEM). Temperature acronyms: sea bottom temperature (SBT), sea surface temperature (SST). Coefficients are presented with standard errors. *p* values below 0.05 are in bold text, and very small *p* values are expressed in scientific notation.

relationships for cold range edges than for warm range edges. The isotherm coefficients represent how far the range edge shifted in relation to a shift in the isotherm. Coefficients were larger for cold-edge species in the single-species models: the median edge shift for a one-degree latitude shift in isotherm position was 0.38 for sea surface temperature versus median estimates of only 0.14 for warm-edge species (0.05 and 0.006, respectively, for sea bottom temperature). We found similar results in the mixed-effects models: coefficients for cold-edge species were 0.47 and 0.13 for sea surface and sea bottom temperature isotherms, respectively, versus 0.28 and 0.014 for warm-edge species. However, the edges for only a small percentage of species fully kept pace with that of climate (dashed line in Figures 2b and 3b).

Sea surface temperature also emerged as a stronger predictor of the cold assemblage edge than of the warm assemblage edge (Figure 5, Table 2). The cold assemblage edge was positively and significantly associated with regional mean sea surface temperature, regional warm extreme sea surface temperature, and the sea surface temperature isotherm (Figure 5a, Table 2). It was also marginally associated with the sea bottom temperature isotherm (*p* = .075, Figure 5a, Table 2). The cold assemblage edge shifted 0.6 degrees of latitude for every one-degree latitude shift in its sea surface temperature isotherm. The warm assemblage edge was only significantly associated with the sea surface temperature isotherm and the regional warm extreme sea surface temperature (Figure 5b, Table 2), and it only shifted 0.23 degrees north for every one-degree latitude shift in the sea surface temperature isotherm. Sea bottom temperature and cold extreme sea surface temperature were both poor predictors of edge position.

3.4 | Changes in depth and biomass

In the cold-edge group, five of 14 species had significant shifts in depth over time (*p* ≤ .05, linear regressions). These shifts were all

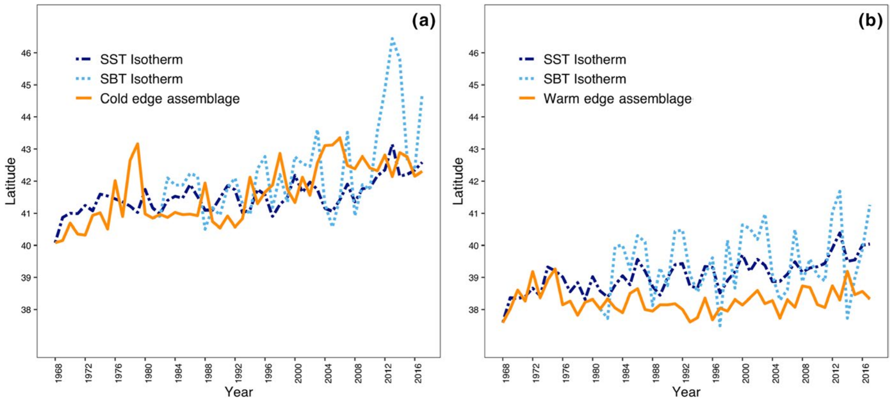

FIGURE 5 Assemblage-wide edge position (solid orange line), mean sea surface temperature isotherm position (dashed dark blue line), and mean sea bottom temperature isotherm position (dashed light blue line) for cold edge (a) and warm edge (b) species

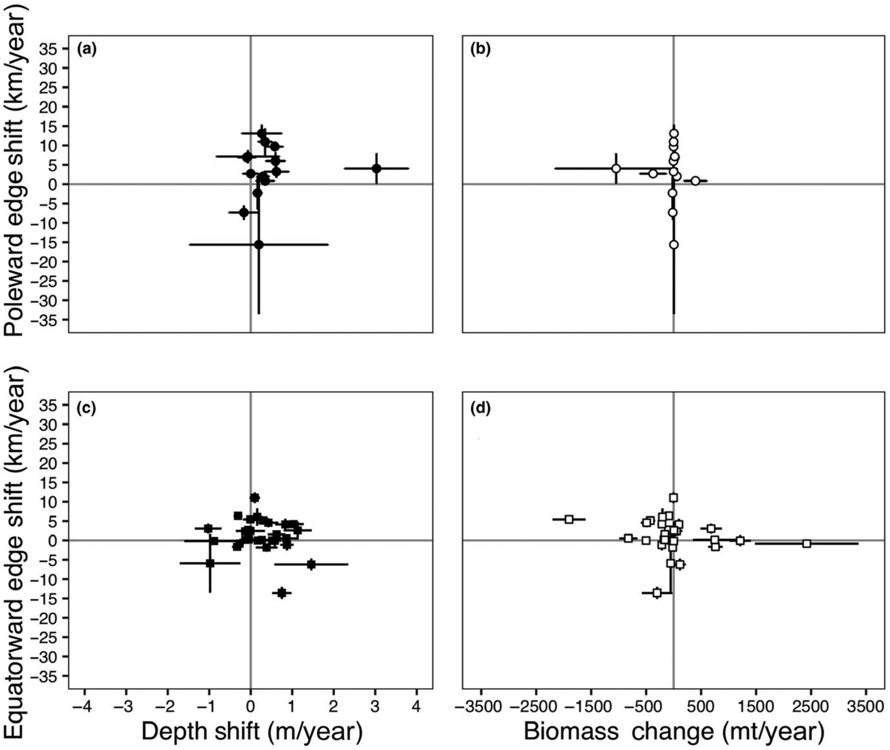

FIGURE 6 Relationships between changes in depth (m/year; filled points) and abundance (metric tons/year; open points), and edge shifts (km/year). (a) and (b) show cold-edge species (circles) and (c) and (d) show warm-edge species (squares). Spearman's rank correlations: (a) 0.22, *p* = .44, (b) 0.13, *p* = .65, (c) −0.06, *p* = .75, and (d) −0.26, *p* = .18. Positive depth shifts are toward deeper water, and positive edge shifts are northward up the shelf. Each point is a single species, and the lines are standard errors

positive (i.e., deeper); one species shifted 3 m/year deeper (dusky smooth-hound), and the other four (blueback shad, Gulf Stream flounder, summer flounder, and blackrim cusk-eel) all shifted less than 0.7 m/year (Figure 6a). Six of the cold-edge species showed significant changes in biomass over time ($p \le .05$; linear regressions); offshore silver hake and Gulf Stream flounder declined in biomass, and rosette skate, summer flounder, chain catshark, and shortnose greeneye all increased (Figure 6b). See Data S1 for single-species time-series of depth and abundance.

The warm-edge group had stronger evidence for a depth shift, which was significant in 14 of the 29 species ($p \le .05$; linear regressions). Four species shifted significantly shallower (Atlantic mackerel, longhorn sculpin, haddock, and little skate), and the remaining 10 shifted deeper; in either direction, significant shifts ranged from about 0.3 to 1.1 m/year in magnitude (Figure 6c). This group also had stronger evidence for biomass shifts: 18 of 29 species had significant biomass changes over the time-series ($p \le .05$; linear regressions). Thirteen of these species declined in biomass, and only five increased (Figure 6d). Estimated biomass changes were also greater in magnitude than in the cold-edge group. In either group, we did not find any evidence for a relationship between the rate of edge shifts and changes in either depth or biomass over time (Spearman's rank correlation, Figure 6).

4 | DISCUSSION

By analyzing 50 years of range edge dynamics of marine fishes, we found that both warm and cold range edges have shifted significantly over time. However, species' cold edges shifted further north with warming were more strongly associated with temperature, and tracked isotherms better than species' warm edges. These results suggest that cold edges are tracking ocean temperature change more readily than warm edges in the same region, lending support to either the biogeography or the extinction debt hypotheses.

Our findings of faster range edge expansions than range edge contractions are consistent with previous work demonstrating that the range sizes of North American marine fishes are expanding (Batt, Morley, Selden, Tingley, & Pinsky, 2017), which could be explained by cold-edge shifts outpacing warm-edge shifts. At the single-species level, approximately half of each group shifted north and had a significant positive association with their sea surface temperature isotherms, underscoring the highly individualistic response of fishes to the same history of warming. We also documented a number of range expansions and local extirpations in Northeast US Shelf marine fishes; some are consistent with previous literature and news reports, such as black sea bass and Atlantic cod (Bell et al., 2015; Nye et al., 2009), and others have not yet been widely highlighted, such as the warm-edge retraction in Northern sand lance (a forage fish).

Cold edges of marine fishes in the Northeast US responded positively and quite consistently to historical warming in our analysis. Cold range edges predominantly shifted north, as did the cold-edge assemblage as a whole (which was unlikely to be driven by a single outlier, as several species had range edges near one another in the northern part of the study region; see Data S1). Cold-edge species also tracked their sea surface and sea bottom temperature isotherms to a greater degree than warm-edge species. In contrast, the warm assemblage edge was associated with sea surface temperature but not with sea bottom temperature, and northward shifts were only evident at the species-specific (not assemblage wide) scale. The warm assemblage edge did not shift north because many of the most abundant species in that assemblage moved north slightly or not at all or even shifted south. The assemblage edge represents the frontier of all species colonizing or becoming locally extirpated, so its position along the coastline is strongly influenced by the furthest (i.e., most distal) species in each assemblage. Notably, although the warm assemblage edge did not significantly shift north, it showed a positive relationship with sea surface temperature, suggesting that the range edge was responding to interannual temperature variation but that longer-term changes were counterbalanced by changing species interactions or other factors that offset range contractions.

Our finding that warm-edges track isotherms poorly relative to cold edges is consistent with either a localized extinction debt or with the warm edge being mediated more strongly by species interactions, adaptation (Doak & Morris, 2010), or other non-temperature processes. The lags we find are similar to the 'climatic debts' defined as the differential between regional climate velocities and realized shifts of species, an approach that also cannot distinguish between extinction debt, species interactions, and other processes (Devictor et al., 2012). Few studies have explored whether species interactions mediate range edges of demersal fishes (Louthan et al., 2015). A bioclimate envelope model applied to marine fishes predicted lesser range shifts when trophic interactions were incorporated (Fernandes et al., 2013). Evidence for delayed range contractions from localized extinction debt processes is also less clear in fishes. Many species in our dataset are relatively long-lived, but adults are also quite mobile and able to move in response to temperature change (Freitas, Olsen, Knutsen, Albretsen, & Moland, 2016). Formally testing for the presence of an extinction debt may be possible with models that include lags or life-history information to explain the length of time lags (Orensanz, Ernst, Armstrong, Stabeno, & Livingston, 2004). Similarly, testing for the role of antagonistic species interactions in mediating warm-edge dynamics may be possible by identifying strong interactors for each study species and then comparing the study species' warm-edge position to the distribution of its competitor, predator, or prey (García-Valdés, Gotelli, Zavala, Purves, & Araújo, 2015; Sanín & Anderson, 2018). While both of those lines of inquiry are beyond the scope of this study, we can conclude that our results contradict the hypothesis that warm and cold edges of marine fishes will track climate change equally (Sunday, Bates, & Dulvy, 2012).

Across a number of tests, we found that the demersal species in our analysis appeared to respond to sea surface temperature more strongly than to sea bottom temperature. We examined sea bottom temperature because the bottom trawl survey catches primarily demersal species, and yet our results suggested that sea surface temperature is a better predictor of range edge positions. Two possible explanations are that the longer time-series available for sea surface temperature aided in detecting a relationship or that the hindcast sea bottom temperatures were not be sufficiently accurate or precise for the Northeast US Shelf. However, it is also possible that a real sensitivity to sea surface temperature exists in these species, most likely in the larval phase. Temperature affects larval duration and survival (O'Connor et al., 2007), and some marine species' range edges are driven by larval distributions (Gaylord & Gaines, 2000; Hutchins, 1947; Orensanz et al., 2004; Sanford, Holzman, Haney, Rand, & Bertness, 2006; Zacherl, Gaines, & Lonhart, 2003). While this mechanism has primarily been described in invertebrates, the distributions of fish species may also be constrained by juvenile survival (Hare, Wuenschel, & Kimball, 2012; Wuenschel, Hare, Kimball, & Able, 2012). Further research using improved hindcast temperature models and species with different dispersal capacities and different stage-specific thermal tolerances may shed light on this result.

Analyzing our data at the species as well as the assemblage scale, using two different metrics for edge position, and numerous temperature datasets as predictor variables allowed us to tease apart broad- and fine-scale patterns and to address common sources of error in studying range shifts (Brown et al., 2016). For example, measuring edge shifts only using latitude and not using our alongshore distance metric might have masked some range shifts that occurred in sections of the coast that slant eastward. Had we examined only northward shifts and regional warming, we might have been biased toward finding cold-edge shifts because cold edges tend to fall further north in this region which is also where the most warming has occurred. By conducting the isotherm analysis, we were able to detect that some warm edges are tracking local changes in temperature. We also tested for changes in depth, another possible response to warming. While some species—approximately one-third of each group—shifted deeper over the time-series, we did not find evidence either that depth and edge shifts were positively correlated or that species were only shifting in one dimension or the other (negative correlation).

This is one of a very small number of studies to examine range edge dynamics at the annual scale (Cavanaugh et al., 2018; La Sorte & Thompson III, 2007; Zhu et al., 2012). The vast majority of studies documenting the displacement of a cold or warm range edge in the Anthropocene use relatively few time points as a result of either binning time-series data (Alheit et al., 2012; Kerr et al., 2015) or a 'resurvey' approach that revisits the site of a historic dataset and conducts a second survey for comparison (Franco et al., 2006; Freeman, Scholer, Ruiz-Gutierrez, & Fitzpatrick, 2018; Wernberg et al., 2011). These studies provide a valuable snapshot of change and useful baselines for historic species distributions. However, the resurvey and binning approaches mask the complexity of range edges that is only apparent in time-series analyses. In our data, using two or three time points to estimate an edge shift would have yielded results that are inconsistent with the magnitude and even the direction of change revealed by the complete time-series (Figure 4).

Given that our estimates of edge shifts are based on up to 50 years of data, it is surprising that we found several warm-edge species that shifted south during the study period (little skate, barndoor skate, and winter skate), or had a negative relationship with isotherm position (American plaice, tusk, alewife, and all three southward-shifting skates). Offshore hake, a cold-edge species, also shifted significantly south. In other systems, shifts against the direction of climate velocity have been attributed to a positive abundance–area relationship (Blanchard et al., 2005; Thorson, Rindorf, Gao, Hanselman, & Winker, 2016) or the species tracking a non-temperature climate factor, for example, water availability in plants (Crimmins, Dobrowski, Greenberg, Abatzoglou, & Mynsberge, 2011). However, the warm-edge species that we studied generally decreased in biomass over the time-series or did not change (see Figure 6 and Data S1). If a positive abundance–area relationship was responsible for these observed southward shifts, biomass should have increased, not decreased. The non-temperature climate factors most likely to influence the distributions of marine fishes include pH and dissolved oxygen; but ocean acidification in this region is primarily considered a risk to coastal marine invertebrates, not demersal fish (Hare et al., 2016). High-resolution time-series data are not readily available to test for the role of oxygen limitation (Deutsch, Ferrel, Seibel, Pörtner, & Huey, 2015).

In addition to mechanistic explanations, there may be methodological reasons why individual species do not appear to be tracking climate change. Species distributions in this region fluctuate over the year due to seasonal migrations as well as a response to seasonal stratification (Kleisner et al., 2016). The spring survey may not capture the absolute furthest position of each species' range edge. By comparing data from the same season across years, we have described the range edge position at one point in the year, but the data may miss possible climate-related spatial shifts in species distributions in other seasons. We included several predictor variables for temperature, including sea surface and bottom temperatures, and extreme values as well as means. However, these predictors are annual summary statistics that may do a poor job of capturing the thermal conditions that are actually influencing species fitness (Helmuth et al., 2014). We avoided some of the most common sources of methodological error in detecting range shifts using a long time-series, focusing on abundant species, and calculating edge position as a percentile rather than from the most extreme values (Bates et al., 2015; Brown et al., 2016). However, the high degree of variability that we observed in species' range edge dynamics may be as much or more due to imperfect sampling than to actual fluctuations in the species range. Range edges are difficult to quantify, and even using a 50-year survey conducted annually at a large spatial scale, our estimates are imperfect. This underscores the need to both continue these types of large-scale biodiversity surveys and intensify efforts to sample large areas at fine spatial and temporal scales. Empirical research in this field is limited by available datasets, and we strongly support the continuation of traditional biodiversity surveys such as the trawl survey we used in addition to more non-traditional programs such as citizen science efforts aimed at detecting novel colonizations (Pecl et al., 2019), recognizing, however, that efforts to document local extinctions are also needed (Thomas et al., 2006).

We found consistent evidence that cold range edges of marine fishes in the Northeast US tracked climate better than warm range edges during 50 years of historical warming. Not only do these results invalidate the ecophysiology hypothesis, they also challenge the assumption that marine fishes are shifting as fast as climate velocities: very few range edges from either group perfectly tracked an isotherm. If warm edges are lagging cold edges in marine systems as well as terrestrial systems, we may expect widespread increases in range size—at least in the short term—with cascading consequences for ecological communities both on land and in the oceans. Our findings underscore the importance of studying non-climate processes at range edges of all taxa, including those that are often expected to keep pace with climate change.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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