Range edges of North American marine species are tracking temperature over decades

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Abstract

Understanding range edges is key to addressing fundamental biogeographic questions about abiotic and biotic drivers of species distributions. Range edges are where colonization and extirpation happen, so their dynamics are also important for natural resource management and conservation. We quantified positions for 153 range edges of marine fishes and invertebrates from three US continental shelf regions using decades of survey data and a spatiotemporal model to account for changes in survey design. We analyzed whether range edges maintained their edge thermal niches—temperature extremes at the range edge—over time. Most range edges (86%) maintained either cold or warm temperature extremes; 73% maintained both. However, the substantial fraction of range edges that altered their thermal niche underscore the multiplicity of relevant drivers. This study suggests that temperate marine species largely maintained their edge thermal niches during rapid change and provides a blueprint for testing temperature tracking of species range edges.

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ABSTRACT

Understanding range edges is key to addressing fundamental biogeographic questions about abiotic and biotic drivers of species distributions. Range edges are where colonization and extirpation happen, so their dynamics are also important for natural resource management and conservation. We quantified positions for 153 range edges of marine fishes and invertebrates from three US continental shelf regions using decades of survey data and a spatiotemporal model to account for changes in survey design. We analyzed whether range edges maintained their edge thermal niches—temperature extremes at the range edge—over time. Most range edges (86%) maintained either cold or warm temperature extremes; 73% maintained both. However, the substantial fraction of range edges that altered their thermal niche underscore the multiplicity of relevant drivers. This study suggests that temperate marine species largely maintained their edge thermal niches during rapid change and provides a blueprint for testing temperature tracking of species range edges.

INTRODUCTION

Human-caused global climate change now affects, directly or indirectly, all biomes and levels of biological organization (Scheffers et al. 2016). One of the most profound effects has been changes in the spatial distributions of species that align with shifting climates—up mountains, deeper in the oceans, and generally toward the poles(Parmesan and Yohe 2003, Pecl et al. 2017). A strong correlation between regional climate change and shifting species ranges has been documented in many taxa (Chen et al. 2011, Pinsky et al. 2013). However, individualistic responses and "ecological surprises" are also common (Poloczanska et al. 2011, Zhu et al. 2012, La Sorte and Jetz 2012), underscoring the need to consider the interplay of climatic constraints and non-climate processes in determining the edges of species ranges (Sexton et al. 2009, Urban et al. 2016).

Range edges often arise where biotic or abiotic conditions prevent persistence of a species. We use the definition of the fundamental niche as the range of environments in which a species could theoretically persist in the absence of biotic interactions, and the realized niche as the range of environments in which the species is actually found (Godsoe et al. 2017). Changing environments provide an opportunity to test whether niches are conserved through time. If a species is shifting its geographic range to track temperature, for example, it will occur at the same temperature over time and the realized thermal niche will be conserved. Conversely, if a species does not shift in concert with temperature change, the geographic range may remain stable but the realized thermal niche will change (La Sorte and Jetz 2012). In addition, temperature extremes are more likely to be range-limiting than means (Sunday et al. 2019), but either poleward or equatorward range edges can theoretically be limited by either cold or warm temperature extremes; e.g., a poleward range

edge might occur where it becomes too cold in winter for adults to survive, or where summers are not warm enough for reproduction and/or juvenile survival (Hutchins 1947). We define the *edge thermal niche* as the thermal extremes found at a species' range edge. Testing which temperature extreme is important for which range edges has rarely been examined across full assemblages of species (Ma et al. 2015, Urban et al. 2016). In this study, we test whether range edges of marine species in three continental shelf regions in the United States have conserved their edge thermal niches over decades of environmental change.

Marine continental shelf species are ideal for studying these biogeographical questions: they are shifting rapidly, experience relatively few barriers to dispersal, and large-scale, long-term datasets of their historical distributions and abundances exist (Pinsky et al. 2020). Some studies on range edges and climate have predicted that marine species should track temperature readily throughout their range, because marine range edges occur on average at the limits of species' thermal tolerances (Sunday et al. 2012, Stuart-Smith et al. 2017). Other theory—primarily developed in terrestrial systems but supported by a recent test using marine data (Fredston-Hermann et al. 2020)—suggests that one or both range edges are driven by other processes like species interactions and will not shift as much in response to temperature change (Connell 1961, MacArthur 1972, Sax and Gaines 2003, Poloczanska et al. 2011, Cahill et al. 2014, Louthan et al. 2015).

The extension of these tests to more regions and taxa is partially limited by data availability, because quantifying range edge dynamics requires large-scale and long-term biodiversity surveys (Parmesan et al. 2005). To date, very few studies have measured range edge dynamics at high temporal resolution—a necessary prerequisite to understanding the relationship between range edges and temperature change, particularly because using too few time points can create misleading trends (La Sorte and Jetz 2012, Brown et al. 2016, Fredston-Hermann et al. 2020). Biodiversity survey programs also often use different sampling methods and schedules, further complicating cross-regional comparative biogeography. To address both of these constraints, we used large-scale biodiversity survey data from the National Oceanic and Atmospheric Administration (NOAA) beginning as early as 1968. We then fitted spatiotemporal models to estimate biomass density and then range edge positions through time, which allowed us to estimate range edge uncertainty and to more clearly compare results across species and regions.

Overall, we quantified conservatism of species' edge thermal niches over time, drawing on repeated large-scale biodiversity surveys in three North American marine regions to describe shifts in poleward and equatorward range edges across 153 fish and invertebrate species. The three study regions have divergent climatic histories that allowed us to test for edge thermal niche conservatism in different temperature change regimes: the Northeast US has warmed rapidly and almost continuously, the Eastern Bering Sea has warmed episodically, and the US West Coast has not warmed overall but periodically experiences dramatic temperature fluctuations among years.

MATERIALS AND METHODS

Temperature and species distribution data sources

We used National Oceanic and Atmospheric Administration (NOAA) long-term surveys from three temperate marine continental shelf regions in the US: the Northeast (annual spring survey 1968-2018), the West Coast (triennial fall survey 1977-2004 and annual fall survey 2003-2018), and the Eastern Bering Sea (annual summer survey 1989-2018; earlier years omitted due to limited spatial extent (Lauth and Conner 2014)). These surveys use trawl gear and a random stratified or fixed station sampling design to target demersal and benthic fishes and invertebrates on the continental shelf, up to several hundred meters deep. The West Coast and Eastern Bering Sea raw datasets were downloaded using the R package "FishData", and the Northeast data were obtained from the 2019 OceanAdapt release (Stuart and Pinsky 2019), a data portal to access NOAA trawl survey records (Lauth and Conner 2014, Politis et al. 2014, Keller et al. 2017). The Northeast dataset, which was pre-processed by OceanAdapt for quality control and taxonomic accuracy, contained records for 74 species. We limited our West Coast analysis to the 54 species that were recorded in both the triennial and the annual surveys. In the Eastern Bering Sea dataset, we downloaded data on the 100

most frequently observed taxa and proceeded with analysis for the 81 taxa that were identified to species. We retrieved higher taxonomy for all species using the R package "taxize" (Chamberlain and Szöcs 2013) and grouped species as either fishes (belonging to classes Actinopterygii or Elasmobranchii) or invertebrates (everything else). All data processing and analyses were conducted in R version 3.6.0 (R Core Team 2018). All code used is available at: https://github.com/afredston/range-edge-niches.

Throughout our analysis, we compared distribution data for a given species with temperature data from the preceding 12 months—specifically, the 12 months preceding the earliest possible start month for each region's survey for analysis (March in the Northeast, May in the West Coast, and July in the Eastern Bering Sea). For example, range edges derived from the spring 1999 Northeast survey were compared to temperature records from March 1998 to February 1999.

We used two historical sea surface temperature (SST) datasets. The NOAA NCEI Optimum Interpolation Sea Surface Temperature dataset (NOAA NCEI 2018) is available daily from 1982 onward at 0.25°x0.25° resolution; we downloaded this dataset for all regions. We also downloaded the Hadley Centre Global Sea Ice and Sea Surface Temperature dataset, available monthly at 1° resolution from 1870 (Rayner 2003) to fill in earlier years for the Northeast and West Coast regions. To ensure comparability between the two data sources, we performed mean bias correction and converted the daily SST records from the higher-resolution OISST dataset into monthly means for each grid cell (see Appendix 1); all temperature metrics described henceforth are based on monthly mean SSTs. We tested for change in mean, minimum, and maximum monthly regional SSTs over time by calculating the annual region-wide mean of grid cell-specific mean, minimum (coldest month), and maximum (warmest month) SSTs, and performing a linear regression of those region-wide means over time for each region with a significance threshold of $\alpha = 0.05$.

Range edge positions were compared to warm and cold temperature extremes, defined as the warmest and coldest months of the 12 months preceding the survey (i.e., coldest month the previous winter and warmest month the previous summer). To generate edge-specific estimates of warm and cold extreme temperatures (see *Range edge analysis*), we constructed generalized additive models (GAMs) of maximum and minimum monthly temperatures in each year along the axis of measurement for each region (see *Spatiotemporal reconstruction of species ranges*) using the "mgcv" package in R (Wood 2017). Each regional GAM predicted warm or cold temperature extremes in each year, given a position along the axis (one GAM was fit for all years in a given region with axis position as a smoothed predictor estimated separately for each year, as well as a separate year factor).

Spatiotemporal reconstruction of species ranges

We estimated annual species range edges from the trawl survey data using the spatial generalized linear mixed model implemented in the R package VAST (Thorson and Barnett 2017, Thorson 2019). This model was designed to estimate total abundance and spatial variation in density of species using spatially referenced biomass observations. We fit VAST to data that follow either stratified-random or fixed-station designs; in both cases, VAST predicted densities over a fixed spatial domain. This analysis enabled comparison across years even when survey methodologies were revised and across regions with distinct survey protocols. In addition, this approach controlled for differences in catchability, enabling us to combine the two historical West Coast surveys (Thorson et al. 2016a). The model structure is described in detail in the supplementary materials (Appendix 2).

Of the 209 species-region combinations, VAST models converged for 205 of them (72 of 74 in the Northeast, 53 of 54 on the West Coast, and 80 of 81 in the Eastern Bering Sea). This set included five species found in both the West Coast and the Eastern Bering Sea (*Atheresthes stomias, Bathyraja interrupta, Clupea pallasii, Glyptocephalus zachirus,* and *Hippoglossoides elassodon*), and one found in both the Northeast and the West Coast (*Alosa sapidissima*), so the total number of unique species was 199.

Range edge analysis

We quantified species range edges as the 0.01 and 0.99 quantiles of density along spatial axes running the

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length of each study region. We chose these quantiles to capture the extremes of each species' distribution; because edges were calculated from VAST's spatiotemporal biomass estimates and not from the raw data, they were unlikely to be influenced by the rare, high biomass observations that are common in shoaling species such as fishes (Thorson et al. 2011). Species range edges are conventionally measured in units of degrees latitude along a north-south axis (e.g., Hickling *et al.* 2005). However, in marine regions with complex coastline topographies and/or coastlines that are not oriented parallel to lines of longitude, coastal distance is a more accurate metric of range edge position than latitude (Hare et al. 2010, Bell et al. 2015, Fredston-Hermann et al. 2020). We therefore developed a coastal distance metric for the West Coast and the Northeast (Figure 1A, 1B; methods in Appendix 2). We then associated points along the coastline with the grid of VAST knots (see Appendix 2) by finding the points with the minimum Euclidean distances. Matching points along the coastline to the VAST knots enabled us to estimate density, and thus range edge position, along the coastal distance axis. In the Eastern Bering Sea, the coastal distance axis was less applicable because the shelf is so wide that many species fall quite far from the coast and also because the presence of islands makes the delineation of a smoothed coastline more complex. In the Eastern Bering Sea, we therefore estimated density along a line drawn from the Aleutian Islands (56ºN, 161ºW) to the edge of the US Exclusive Economic Zone (62ºN, 176.5ºW) through the Middle Domain, a hydrographic region with similar bathymetry defined as lying between two oceanographic mixing zones that partition the middle from inner and outer domains (Coachman 1986, Ortiz et al. 2016).

To ensure that the species analyzed had at least one range edge in the study region, we eliminated range edges with mean positions over time that fell close to the boundary of the study region, defined as less than 10% from the end of the axis of measurement in either direction (Northeast axis length = 1368 km, West Coast axis length = 2037 km, Eastern Bering Sea axis length = 1102 km). This removed 18 Northeast species, 24 West Coast species, and 13 Eastern Bering Sea species. After this filter, we proceeded with 153 range edges—55 in the Northeast, 25 on the West Coast, and 73 in the Eastern Bering Sea—across 145 fishes and invertebrates from 17 taxonomic classes (eight had both equatorward and poleward range edges; see Appendix 3). We note that for almost all species, only one range edge fell within the study region (see Appendix 3). Thus, our analysis evaluated the evidence for our different hypotheses by evaluating many isolated range edges, not by evaluating both range edges of a single species.

We tested whether range edge positions had shifted significantly over time with single-species Bayesian linear regressions of range edge position on time ($n = 151$ models; two models were removed that did not estimate standard errors around range edge position due to parameter reduction to aid convergence in VAST). Single-species models were fitted using the "rstanarm" package (Goodrich et al. 2018) with four chains, 40,000 iterations including 10,000 burn-in draws, and a target average proposal acceptance probability of 0.99. We selected a normally distributed vague prior with a mean of 0 and standard deviation of 50 km/year; this standard deviation was chosen to exceed the upper range of climate velocities in the oceans (Burrows et al. 2011). Range positions were weighted by VAST-estimated standard errors ($\frac{1}{\mathrm{SE}^2}$) for each year so that estimated edge positions with higher associated uncertainties were less influential (Thorson et al. 2016b). All of these models converged, as evaluated by Gelman-Rubin convergence statistic below 1.1.

Edge thermal niche conservation

We measured the edge thermal niche—the temperatures found at the range edge—by predicting annual warm and cold temperature extremes at the range edge position using region-specific GAMs (see *Temperature and distribution data sources*). We then fitted Bayesian linear regressions to test whether either the warm or cold extreme temperature at a species' range edge had changed over time ($n = 306$, 153 range edges for each of two temperature extremes). Single-species Bayesian linear regressions were fitted using the "rstanarm package" (Goodrich et al. 2018) with four chains, 40,000 iterations including 10,000 burn-in draws, and a target average proposal acceptance probability of 0.99. We selected a normally distributed vague prior with a mean of 0 and standard deviation of 0.1 °C/year; this standard deviation was chosen to exceed the largest rates of SST change across all study regions (see *Results*). Models were weighted by GAM-estimated standard errors ($\frac{1}{\mathrm{SE}^2}$), so that estimated temperatures with higher associated uncertainties were less influential. Models

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converged for all range edges (Gelman-Rubin convergence statistic below 1.1). We calculated the mean and 90% Bayesian credible interval from each single-species posterior distribution of the year coefficient for either warm or cold temperature extremes.

If at least one of the two temperature metrics we measured at a range edge—cold or warm extremes—was constant over time, the range edge could be tracking that temperature and exhibiting edge thermal niche conservatism (Hutchins 1947). We categorized range edges according to whether the range edge maintained a constant warm extreme temperature at the edge over time, a constant cold extreme temperature, both, or neither, based on 90% Bayesian credible intervals (Figure 2). In this method, edge thermal niche conservatism could arise either from the range edge shifting in space to track temperature, or the range edge remaining stationary in a location where temperatures have not changed over time. To disentangle these processes, we compared changes in the edge thermal niche to changes in the range edge position (Figure 2).

RESULTS

From 1967 to 2018, minimum, mean, and maximum SST in the Northeast all increased (Figure 1A), translating to more than one degree Celsius of warming in every SST metric over the fifty years measured (respectively, 0.023 ± 0.007 °C/year, $p = 1.4 \times 10^{-3}$; 0.03 ± 0.004 °C/year, $p = 3.7 \times 10^{-9}$; 0.033 ± 0.006 °C/year, $p = 4.4 \times 10^{-7}$). On the West Coast (Figure 1B), no significant trends occurred in any temperature metric from 1976-2018, despite variation of ± 2 °C for individual years (minimum SST 0.004 ± 0.008 °C/year, $p = 0.65$; mean SST 0.002 ± 0.007 °C/year, $p = 0.77$; maximum SST 0.003 ± 0.009 °C/year, $p = 0.77$). In the Eastern Bering Sea (Figure 1C), warming was evident in maximum SST change from 1988-2018, which increased 0.038 ± 0.018 °C/year ($p = 0.049$). Neither minimum nor mean SST increased significantly in the Eastern Bering Sea, although both had a positive relationship with year (minimum 0.008 ± 0.01 °C/year, $p = 0.48$; 0.022 ± 0.013 °C/year, $p = 0.10$).

Range edge shifts over time

Species' range edge shifts differed substantially, ranging from 24.5 km/year (equatorward edge of *Homarus americanus* in the Northeast) to -26.5 km/year (poleward edge of *Sebastes semicinctus* in the West Coast). Single-species edge positions over time are reported in Appendix 3. When pooled over all species in a region, all regions had a generally northward shift. Range edges shifted 3.9 km/year in the Northeast from 1967-2018 (90% CI 3.6 – 4.2), 5.2 km/year on the West Coast from 1976-2018 (90% CI 4.2 – 6.2), and 0.1 km/year in the Eastern Bering Sea from 1988-2018 (90% CI -0.2 – 0.4; means and credible intervals from single-species Bayesian linear regressions). Separating these posterior distributions by range edge type (poleward or equatorward) revealed opposing shifts in the two groups: equatorward range edges overall shifted 5.3 km/year (90% CI 5.0 – 5.6), but poleward range edges shifted -2.2 km/year (90% CI -2.6 – -1.8; means and credible intervals from single-species Bayesian linear regressions).

The magnitude of range edge shifts was slightly greater in fishes than in invertebrates. When both were pooled across all species and regions, fishes shifted north 2.6 km/year (90% CI 2.3 – 2.9) and invertebrates 1.7 km/year (90% CI 1.3 – 2.1; means and credible intervals from single-species Bayesian linear regressions). This difference in magnitude of shift was driven by equatorward range edges of fishes shifting faster—6.0 km/year *versus* 4.0 km/year—than invertebrates (90% CIs 5.6 – 6.4 and 3.6 – 4.4, respectively), while both groups of poleward edges shifted in the opposite direction at similar rates (fishes -2.3 km/year, 90% CI -2.8 – -1.7, invertebrates -2.0 km/year, 90% CI -2.7 – -1.3; means and credible intervals from single-species Bayesian linear regressions).

Edge thermal niche tracking

We estimated edge thermal niche tracking by testing whether the change in minimum or maximum temperature at the range edge over time was different from zero, based on 90% Bayesian credible intervals from Bayesian linear regressions of temperature on time. Of 153 species range edges, we found that 131 (86%) maintained at least one component of the edge thermal niche (warm or cold extreme temperature) during the study period. Further, for the majority of range edges—111, or 73%—both minimum and maximum tem-

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peratures were maintained over time. Of the 20 range edges consistent with only one temperature metric, 13 were consistent with cold extremes and 7 were consistent with warm extremes.

In the West Coast and the Eastern Bering Sea, almost all range edges tracked both temperature metrics (84% and 97%, respectively; Figure 3B, 3C). By contrast, only 34% of range edges in the Northeast tracked both temperature metrics, and the Northeast also contained 20 of the 22 range edges that did not track either warm or cold temperature extremes (Figure 3A). Lack of tracking arose for different reasons in poleward and equatorward edges: the poleward edges that did not maintain their edge thermal niches often did not shift as the oceans warmed, or even shifted south, while the equatorward edges that did not maintain their edge thermal niches often shifted north faster than expected, into cooler waters (Appendix 4).

DISCUSSION

We quantified temporal dynamics and thermal niche tracking over decades for more than 150 marine range edges while using a novel spatiotemporal modeling approach to standardize among the three study regions and their differing survey methodologies. Across diverse geographies, historical climates, and taxa, range edges of marine species were in general conserving their thermal niches through space and time. Edge thermal niche conservatism suggests that most species range edges are tracking temperature change, consistent with evidence that many species distributions are shifting through space (Pinsky et al. 2013, Hiddink et al. 2015, Day et al. 2018, Lenoir et al. 2020) and supported by theory from thermal ecophysiology (Sunday et al. 2012, Stuart-Smith et al. 2017, Pinsky et al. 2019). However, a non-negligible number of range edges did not shift as predicted—especially in the Northeast, the region with the greatest historical temperature increase—indicating that temperature alone does not explain range edge dynamics for all marine species. This study provides the first large-scale, multi-region analysis of thermal niche tracking at range edges and describes novel statistical approaches that are applicable to a wide range of taxa and systems.

Species ranges are shifting poleward around the globe, both on land and in the sea (Chen et al. 2011, Poloczanska et al. 2013). Local patterns in climate change have helped to explain distributional shifts of many species, especially those that did not shift directly toward the poles (Pinsky et al. 2013, Lenoir and Svenning 2015). These findings suggest that species' range shifts can be at least partially explained by spatial shifts in their climatic niches (Loarie et al. 2009, Burrows et al. 2011). While many global change studies have not measured range edge displacement, those that have often report major poleward shifts in range edges, particularly at the poleward range edge (Parmesan et al. 1999, Hickling et al. 2005). However, most studies on range edges have used a small number of time points (e.g., Hickling et al. 2005)—and often just two—limiting inference about climatic niche tracking. Marine species are predicted to track their climatic niches more closely than terrestrial species: they have exhibited greater range shifts to date, and are more physiologically vulnerable to warming (Pinsky et al. 2019, 2020, Lenoir et al. 2020). Testing for climatic niche tracking is fundamentally related to measuring range edge dynamics, because—especially in the oceans—range edges are expected to coincide with climatic niche limits, specifically thermal limits (Sunday et al. 2012).

By measuring thermal niche conservatism at the range edge, we tested for a relationship between range edge position and the isotherms representing winter and summer temperatures over time (Sunday et al. 2015, Fredston-Hermann et al. 2020). A finding that a range edge remained in the same winter or summer temperatures over time can have several interpretations. It does not necessarily imply that the isotherm moved: an edge may track its thermal niche either by shifting in the same direction and at the same rate as an isotherm, or by remaining in place when the isotherm is stationary. The two regions in our study with high levels of edge thermal niche tracking, the West Coast and the Eastern Bering Sea, both had relatively little temperature change when averaged over the study period; thus, range edges in those regions that did not move much were typically classified as tracking the edge thermal niche.

Recent work on marine heatwaves has underscored the need to move beyond means to measure climatic extremes and variability in studies of global change biology, including in the oceans (Smale et al. 2019). We quantified edge position in relation to temperature extremes precisely for this reason, especially given the

marked recent increases in warm extreme (summer) temperatures in the Northeast and the Eastern Bering Sea. Yet our results revealed that range edges remained in the same cold extreme (winter) temperatures approximately as often as they did for summer temperatures, suggesting that winter temperatures may be an underappreciated covariate of range dynamics at both poleward and equatorward range edges (Dana 1853, Morley et al. 2017). Foundational biogeographic theory provides a hypothesis for this: poleward range edges could be influenced either by summer temperatures limiting reproduction and growth or by winter temperatures limiting survival; and equatorward range edges could be influenced either by summer temperatures limiting survival or by winter temperatures limiting growth and reproduction (Hutchins 1947). Further work could test whether this is a biologically plausible explanation for these temperate marine species. Longer time series, extensive analysis of different dimensions of temperature change, or additional oceanographic data products such as high-resolution hindcast sea bottom temperature data could be used in the future to tease apart more precisely which temperature metrics best explain range edge dynamics and why.

Our finding that the region with the greatest historical temperature increase exhibited the lowest frequency of edge thermal niche tracking underscores the critical importance of considering non-temperature and indirect processes that may influence species distributions. In the Northeast, we documented equatorward range edges that shifted much further north than expected based on temperature—into cooler waters—and poleward range edges that did not shift or shifted south (Appendices 3 and 4). This could arise due to density-dependent habitat selection if these species were declining in abundance, causing each range edge to collapse toward the range center (Blanchard et al. 2005). At the equatorward edge, competition or predation from the south could be driving edge retraction (Kordas et al. 2011); for example, the rapid contraction of the equatorward range edge of American lobster could be due to increased predation from species like black sea bass shifting up the coast (McMahan and Grabowski 2019) or increased mortality from a temperature-related disease (Groner et al. 2018). At the poleward edge, species interactions (HilleRisLambers et al. 2013), priority effects (Fukami 2015), dispersal limitation (Poloczanska et al. 2011), or a lack of non-thermal habitat (McHenry et al. 2019) could all inhibit northward shifts. Sessile invertebrates are particularly vulnerable to dispersal limitation if prevailing currents do not align with local climate velocities, as in the Northeast (Molinos et al. 2017, Fuchs et al. 2020). Changes in non-temperature abiotic drivers such as dissolved oxygen are likely to also influence range edge dynamics (Deutsch et al. 2015, Howard et al. 2020).

This study is the first to use a spatiotemporal modeling approach to estimate range edge dynamics and estimate a standard error around range edge positions, which we see as important methodological advances. Using the VAST model, we calculated rates of range edge shift that were similar in magnitude to those calculated from raw survey data in the Northeast (Fredston-Hermann et al. 2020). Our results are not directly comparable to previous work, however, because—unlike analyses of raw distribution data—VAST attributes some variation in recorded observations and abundances to observation error. Continued extensions of VAST and similar models to distribution data will facilitate more rigorous evaluation of historical range edge dynamics, even for datasets with known inconsistencies and biases in sampling.

While we found that range edge positions almost always maintained their edge thermal niche, year-over-year temperatures at the range edge were often variable (Appendix 4), and near-term (i.e., annual, not multi-decadal) projections of a species' edge thermal niche are unlikely to predict exactly where it will shift. Further, a non-negligible fraction of range edges did not shift at all, shifted opposite the predicted direction, or "overshot" temperature change and shifted into cooler waters. Our methods provide a blueprint for assessing whether range edges have tracked their thermal niches and for identifying species of concern that do not appear to be shifting as expected based on temperature alone. Classifying species by edge thermal niche tracking can inform management and conservation because different interventions are likely required for a species that shifts in response to warming (e.g., transboundary management) than for a species that remains stationary in the face of warming (e.g., assisted migration). To move beyond categorizing all results of no thermal niche tracking as "individualistic responses," future research can test edge thermal niche conservatism against—or jointly with—other biogeographic hypotheses that integrate the influence of species interactions, population dynamics, eco-evolutionary processes, and other important abiotic and biotic

drivers. Future progress on range edge dynamics will be accelerated by mechanistically testing predictions about which temperature and non-temperature processes should be limiting for which range edges against biogeographical data. Testing multiple contemporaneous processes (including density-dependent range expansion and contraction) and their net effects will provide insight into, and ultimately enable prediction of, range edge dynamics in a changing climate.

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FIGURES

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Figure 1. Maps of study regions—Northeast (A), West Coast (B), and Eastern Bering Sea (C)—with the continental shelf shaded in blue (300 m cutoff for Northeast and Eastern Bering Sea, 600 m for West Coast). Inset plots show regional minimum (blue), mean (orange), and maximum (red) monthly SST (annual means). Black dashed lines show axes of measurement for range edges in each region, for which the origin point is marked with an X.

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Figure 2. Example schematic showing range edge position with standard errors over time (first column), edge thermal niche over time (second column), and the posterior distribution of estimated edge thermal niche change (third column) for the equatorward edge of *Gadus morhua* in the Northeast (A), the poleward edge of *Paralithodes camtschaticus* in the Eastern Bering Sea (B), and the equatorward edge of *Sebastes pinniger* on the West Coast (C). Time-series and distributions in blue represent cold extreme temperatures and red represents warm extreme temperatures. Horizontal bars in the third column represent 90% Bayesian credible intervals. A Bayesian credible interval that included zero (the vertical dotted line) was interpreted as no change over time. Canary rockfish icon by Harold N Eyster via phylopic.org under a Creative Commons License http://creativecommons.org/licenses/by/3.0/.

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Figure 3. Distribution of range edge shifts over time (x-axis) grouped by whether the edge thermal niche was conserved over time (y-axis) in the Northeast (A), the West Coast (B), and the Eastern Bering Sea (C). Each point corresponds to a single range edge. Range edges could track cold (blue), warm (red), both (purple), or neither (grey) temperature extremes. The thickness of each horizontal band represents a relative weighting of point densities along the x-axis.