

DR. ALEXA FREDSTON (Orcid ID : 0000-0002-5449-7054)

DR. MALIN PINSKY (Orcid ID : 0000-0002-8523-8952)

Article type : Primary Research Article

TITLE:

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

SHORT RUNNING TITLE: Thermal niche tracking of species range edges

AUTHORS:

Alexa Fredston<sup>1,2\*</sup>, Malin Pinsky<sup>2</sup>, Rebecca L. Selden<sup>3</sup>, Cody Szuwalski<sup>4</sup>, James T. Thorson<sup>4</sup>, Steven D. Gaines<sup>1</sup>, and Benjamin S. Halpern<sup>1,5</sup>

<sup>1</sup> Bren School of Environmental Science & Management, University of California, Santa Barbara, Santa Barbara, CA, United States

<sup>2</sup> Department of Ecology, Evolution, and Natural Resources, Rutgers, The State University of New Jersey, New Brunswick, NJ, United States

<sup>3</sup> Department of Biological Sciences, Wellesley College, Science Center, Wellesley, MA, United States

<sup>4</sup> Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA, United States

<sup>5</sup> National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, Santa Barbara, CA, United States

\* *Corresponding author*: Email: fredston@rutgers.edu. Phone: (914) 960-3230. ORCID: 0000-0002-5449-7054.

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/GCB.15614](https://doi.org/10.1111/GCB.15614)

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KEYWORDS: biogeography, climate change, global warming, thermal tolerance, range limit, range margin, thermal niche

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1 ABSTRACT

2 Understanding the dynamics of species range edges in the modern era is key to addressing  
3 fundamental biogeographic questions about abiotic and biotic drivers of species distributions.  
4 Range edges are where colonization and extirpation processes unfold, and so these dynamics are  
5 also important to understand for effective natural resource management and conservation.  
6 However, few studies to date have analyzed time series of range edge positions in the context of  
7 climate change, in part because range edges are difficult to detect. We first quantified positions  
8 for 165 range edges of marine fishes and invertebrates from three U.S. continental shelf regions  
9 using up to five decades of survey data and a spatiotemporal model to account for sampling and  
10 measurement variability. We then analyzed whether those range edges maintained their edge  
11 thermal niche—the temperatures found at the range edge position—over time. A large majority  
12 of range edges (88%) maintained either summer or winter temperature extremes at the range  
13 edge over the study period, and most maintained both (76%), although not all of those range  
14 edges shifted in space. However, we also found numerous range edges—particularly poleward  
15 edges and edges in the region that experienced the most warming—that did not shift at all,  
16 shifted further than predicted by temperature alone, or shifted opposite the direction expected,  
17 underscoring the multiplicity of factors that drive changes in range edge positions. This study  
18 suggests that range edges of temperate marine species have largely maintained the same edge  
19 thermal niche during periods of rapid change and provides a blueprint for testing whether and to  
20 what degree species range edges track temperature in general.

21 INTRODUCTION

22

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

31 climatic constraints and non-climate processes in determining the edges of species ranges  
32 (Sexton et al., 2009; Urban et al., 2016).

33 Range edges often arise where biotic or abiotic conditions prevent persistence of a  
34 species. We use the definition of the fundamental niche as the range of environments in which a  
35 species could theoretically persist in the absence of biotic interactions, and the realized niche as  
36 the range of environments in which the species is actually found (Godsoe et al., 2017). Changing  
37 environments provide an opportunity to test whether niches are conserved through time. If a  
38 species is shifting its geographic range to track temperature, for example, it will occur at the  
39 same temperature over time and the realized thermal niche will be conserved. Conversely, if a  
40 species does not shift in concert with temperature change, the geographic range may remain  
41 stable but the realized thermal niche will change (La Sorte & Jetz, 2012). In addition,  
42 temperature extremes are more likely to be range-limiting than means (Sunday et al., 2019), but  
43 either poleward or equatorward range edges can theoretically be limited by either summer or  
44 winter extreme temperatures; e.g., a poleward range edge might occur where it becomes too cold  
45 in winter for adults to survive, or where summers are not warm enough for reproduction and/or  
46 juvenile survival (Hutchins, 1947). We define the *edge thermal niche* as the thermal extremes  
47 found at a species' range edge. Testing which temperature extreme is important for which range  
48 edges has rarely been examined across full assemblages of species (Ma et al., 2015; Urban et al.,  
49 2016). In this study, we test whether range edges of marine species in three continental shelf  
50 regions in the United States have conserved their edge thermal niches over decades of  
51 environmental change.

52 Marine continental shelf species are ideal for studying these biogeographical questions:  
53 they are shifting rapidly, experience relatively few barriers to dispersal, and large-scale, long-  
54 term datasets of their historical distributions and abundances exist (Pinsky et al., 2020). Some  
55 studies on range edges and climate have predicted that marine species should track temperature  
56 readily throughout their range, because marine range edges occur on average at the limits of  
57 species' thermal tolerances (Stuart-Smith et al., 2017; Sunday et al., 2012). Other theory—  
58 primarily developed in terrestrial systems, but supported by recent tests using marine data  
59 (Fredston-Hermann et al., 2020; Thorson et al., 2017)—suggests that one or both range edges  
60 can be commonly driven by other processes like species interactions and will not shift as much in

61 response to temperature change (Cahill et al., 2014; Connell, 1961; Louthan et al., 2015;  
62 MacArthur, 1972; Poloczanska et al., 2011; Sax & Gaines, 2003).

63 The extension of these tests to more regions and taxa is partially limited by data  
64 availability, because quantifying range edge dynamics requires large-scale and long-term  
65 biodiversity surveys (Parmesan et al., 2005). To date, very few studies have measured range edge  
66 dynamics at high temporal resolution—a necessary prerequisite to understanding the relationship  
67 between range edges and temperature change, particularly because using too few time points can  
68 create misleading trends (Brown et al., 2016; Fredston-Hermann et al., 2020; La Sorte & Jetz,  
69 2012). Biodiversity survey programs also often use different sampling methods and designs,  
70 further complicating cross-regional comparative biogeography. To address both of these  
71 constraints, we used large-scale biodiversity survey data from the National Oceanic and  
72 Atmospheric Administration (NOAA) beginning as early as 1968. We then fitted spatiotemporal  
73 models to estimate biomass density and then range edge positions through time, which allowed  
74 us to estimate range edge uncertainty and to more clearly compare results across species and  
75 regions.

76 Overall, we quantified conservatism of species' edge thermal niches over time, drawing  
77 on repeated large-scale biodiversity surveys in three North American marine regions to describe  
78 shifts in 165 poleward and equatorward range edges of fish and invertebrate species. The three  
79 study regions have divergent climatic histories that allowed us to test for edge thermal niche  
80 conservatism in different temperature change regimes: the Northeast US has warmed rapidly and  
81 almost continuously, the Eastern Bering Sea has warmed episodically, and the US West Coast  
82 has not warmed overall but periodically experiences dramatic temperature fluctuations among  
83 years.

84

## 85 MATERIALS AND METHODS

86

### 87 *Temperature and species distribution data sources*

88 We used National Oceanic and Atmospheric Administration (NOAA) long-term surveys from  
89 three temperate marine continental shelf regions in the US: the Northeast (annual spring survey  
90 1968-2018), the West Coast (triennial fall survey 1977-2004 and annual fall survey 2003-2018),  
91 and the Eastern Bering Sea (annual summer survey 1989-2018; earlier years omitted due to

92 limited spatial extent (Lauth & Conner, 2014)). These surveys use trawl gear and a random  
93 stratified or fixed station sampling design to target demersal and benthic fishes and invertebrates  
94 on the continental shelf, up to several hundred meters deep. The West Coast and Eastern Bering  
95 Sea raw datasets were downloaded from data portals for Alaska and Northwest Fisheries Science  
96 Centers, and the Northeast data were obtained from the 2019 OceanAdapt release (Stuart &  
97 Pinsky, 2019), a data portal to access NOAA trawl survey records (Keller et al., 2017; Lauth &  
98 Conner, 2014; Politis et al., 2014). The Northeast dataset, which was pre-processed by  
99 OceanAdapt for quality control and taxonomic accuracy, contained records for 74 species. For  
100 the other regions, we used an API in the “FishData” R package (Thorson, 2015) to download  
101 datasets for the West Coast groundfish bottom trawl survey  
102 ([https://www.webapps.nwfsc.noaa.gov/data/api/v1/source/trawl.catch\\_fact/selection.json?filters=  
103 project=Groundfish%20Slope%20and%20Shelf%20Combination%20Survey,performance=Satis  
104 factory](https://www.webapps.nwfsc.noaa.gov/data/api/v1/source/trawl.catch_fact/selection.json?filters=project=Groundfish%20Slope%20and%20Shelf%20Combination%20Survey,performance=Satisfactory)), the West Coast triennial survey  
105 ([https://www.webapps.nwfsc.noaa.gov/data/api/v1/source/trawl.catch\\_fact/selection.json?filters=  
106 project=Groundfish%20Triennial%20Shelf%20Survey,performance=Satisfactory](https://www.webapps.nwfsc.noaa.gov/data/api/v1/source/trawl.catch_fact/selection.json?filters=project=Groundfish%20Triennial%20Shelf%20Survey,performance=Satisfactory)), and the  
107 Eastern Bering Sea bottom trawl survey  
108 ([http://www.afsc.noaa.gov/RACE/groundfish/survey\\_data/downloads/ebsYEAR\\_INTERVAL.zi  
109 p](http://www.afsc.noaa.gov/RACE/groundfish/survey_data/downloads/ebsYEAR_INTERVAL.zip), where YEAR\_INTERVAL was one of the following: 1982\_1984, 1985\_1989, 1990\_1994,  
110 1995\_1999, 2000\_2004, 2005\_2008, 2009\_2012, 2013\_2016, 2017\_2018). We limited our West  
111 Coast analysis to the 54 species that were recorded in both the triennial and the annual surveys.  
112 In the Eastern Bering Sea dataset, we downloaded data on the 100 most frequently observed taxa  
113 and proceeded with analyses for the 81 taxa that were identified to species. We retrieved higher  
114 taxonomy for all species using the R package “taxize” (Chamberlain & Szöcs, 2013) and  
115 grouped species as either fishes (belonging to classes Actinopterygii or Elasmobranchii) or  
116 invertebrates (everything else). All data processing and analyses were conducted in R version  
117 3.6.0 (R Core Team, 2018). All code used is available at: [https://github.com/afredston/range-  
118 edge-niches](https://github.com/afredston/range-edge-niches).

119 Throughout our analysis, we compared distribution data for a given species with  
120 temperature data from the preceding 12 months—specifically, the 12 months preceding the  
121 earliest possible start month for each region’s survey for analysis (March in the Northeast, May  
122 in the West Coast, and July in the Eastern Bering Sea). For example, range edges derived from

123 the spring 1999 Northeast survey were compared to temperature records from March 1998 to  
124 February 1999.

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

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

147

#### 148 *Spatiotemporal reconstruction of species ranges*

149 We estimated annual species range edges from the trawl survey data using the spatio-  
150 temporal model implemented in the R package VAST (Thorson, 2019; Thorson & Barnett,  
151 2017). This model was designed to estimate total abundance and spatial variation in density of  
152 species using spatially referenced biomass observations. We fit VAST to data that follow either  
153 stratified-random or fixed-station designs; in both cases, VAST predicted densities over a fixed

154 spatial domain. This analysis enabled comparison across years even when survey methodologies  
155 were revised and across regions with distinct survey protocols. In addition, this approach  
156 controlled for differences in catchability, enabling us to combine the two historical West Coast  
157 surveys (Thorson et al., 2016). The model also predicted densities (and resulting ranges) after  
158 controlling for measurement variability (expected variance in replicated sampling at the same  
159 location-season) and sampling variability (randomized or systematic variation in sampling  
160 locations in spatially unbalanced or randomized designs). The model structure is described in  
161 detail in the supplementary materials (Appendix 2).

162 VAST models converged for all 209 species-region combinations. This set included six  
163 species found in both the West Coast and the Eastern Bering Sea (*Atheresthes stomias*, *Bathyraja*  
164 *interrupta*, *Clupea pallasii*, *Glyptocephalus zachirus*, *Hippoglossoides elassodon*, and  
165 *Hippoglossus stenolepsis*), and one found in both the Northeast and the West Coast (*Alosa*  
166 *sapidissima*), so the total number of unique species was 202.

#### 167 168 *Range edge analysis*

169 We quantified species range edges as the 0.01 and 0.99 quantiles of density along spatial  
170 axes running the length of each study region. We chose these quantiles to capture the extremes of  
171 each species' distribution; because edges were calculated from VAST's spatiotemporal biomass  
172 estimates and not from the raw data, they were less sensitive to rare, high biomass observations  
173 that are common in shoaling species such as fishes (Thorson et al., 2011). Species range edges  
174 are conventionally measured in units of degrees latitude along a north-south axis (e.g., Hickling  
175 et al., 2005). However, in marine regions with complex coastline topographies and/or coastlines  
176 that are not oriented parallel to lines of longitude, coastal distance is a more accurate metric of  
177 range edge position than latitude (Bell et al., 2015; Fredston-Hermann et al., 2020; Hare et al.,  
178 2010). We therefore developed a coastal distance metric for the West Coast and the Northeast  
179 (Fig. 1a,c; methods in Appendix 2). We then associated points along the coastline with the grid  
180 of VAST knots (see Appendix 2) by finding the points with the minimum Euclidean distances.  
181 Matching points along the coastline to the VAST knots enabled us to estimate density, and thus  
182 range edge position, along the coastal distance axis. In the Eastern Bering Sea, the coastal  
183 distance axis was less applicable, because the shelf is so wide that many species fall quite far  
184 from the coast and also because the presence of islands makes the delineation of a smoothed



185 coastline more complex. In the Eastern Bering Sea, we therefore estimated density along a line  
186 drawn from the Aleutian Islands (56°N, 161°W) to the edge of the US Exclusive Economic Zone  
187 (62°N, 176.5°W) through the Middle Domain (Fig. 1b), a hydrographic region with similar  
188 bathymetry defined as lying between two oceanographic mixing zones that partition the middle  
189 from inner and outer domains (Coachman, 1986; Ortiz et al., 2016).

190 To ensure that the species analyzed had at least one range edge in the study region, we  
191 eliminated range edges with mean positions over time that fell close to the boundary of the study  
192 region, defined as less than 10% from the end of the axis of measurement in either direction  
193 (Northeast axis length = 1368 km, West Coast axis length = 1823 km, Eastern Bering Sea axis  
194 length = 1102 km). This removed 18 Northeast species, 20 West Coast species, and 14 Eastern  
195 Bering Sea species. We also removed one additional species in the Northeast, *Mustelus canis*, for  
196 which VAST did not estimate a standard error of the range edge position. After these filters, we  
197 proceeded with 165 range edges—56 in the Northeast, 36 on the West Coast, and 73 in the  
198 Eastern Bering Sea—across 154 fishes and invertebrates from 17 taxonomic classes. Nine had  
199 both equatorward and poleward range edges (see Appendix 3). We note that for almost all  
200 species, only one range edge fell within the study region (see Appendix 3); tracking both range  
201 edges would likely require synthesizing results across many surveys (Maureaud et al., 2021).  
202 Thus, our analysis evaluated the evidence for our different hypotheses by evaluating many  
203 isolated range edges, not by evaluating both range edges of a single species.

204 We tested whether range edge positions had shifted significantly over time with single-  
205 species Bayesian linear regressions of range edge position on time ( $n = 165$  models). Single-  
206 species models were fitted using the “rstanarm” package (Goodrich et al., 2018) with four  
207 chains, 40,000 iterations including 10,000 burn-in draws, and a target average proposal  
208 acceptance probability of 0.99. We selected a normally distributed vague prior with a mean of 0  
209 and standard deviation of 50 km/year; this standard deviation was chosen to exceed the upper  
210 range of climate velocities in the oceans (Burrows et al., 2011). Range positions were weighted  
211 by VAST-estimated standard errors ( $1/SE^2$ ) for each year so that estimated edge positions with  
212 higher associated uncertainties were less influential (Thorson et al., 2016). All of these models  
213 converged, as evaluated by Gelman-Rubin convergence statistic below 1.1.

214

215 *Edge thermal niche conservation*

216 We measured the edge thermal niche—the temperatures found at the range edge—by  
217 predicting annual summer and winter temperature extremes at the range edge position using  
218 region-specific GAMs (see *Temperature and distribution data sources*). We then fitted Bayesian  
219 linear regressions to test whether either the summer and winter extreme temperature at a species'  
220 range edge had changed over time ( $n = 330$ , 165 range edges for each of two temperature  
221 extremes). Single-species Bayesian linear regressions were fitted using the “rstanarm package”  
222 (Goodrich et al., 2018) with four chains, 40,000 iterations including 10,000 burn-in draws, and a  
223 target average proposal acceptance probability of 0.99. We selected a normally distributed vague  
224 prior with a mean of 0 and standard deviation of 0.1 °C/year; this standard deviation was chosen  
225 to exceed the largest rates of SST change across all study regions (see *Results*). Models were  
226 weighted by GAM-estimated standard errors ( $1/SE^2$ ), so that estimated temperatures with higher  
227 associated uncertainties were less influential. Models converged for all range edges (Gelman-  
228 Rubin convergence statistic below 1.1). We calculated the mean and 90% Bayesian credible  
229 interval from each single-species posterior distribution of the year coefficient for either summer  
230 or winter temperature extremes.

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

## 241 242 RESULTS

243  
244 Each region experienced distinct temperature trends, from warming in the Northeast to  
245 variability on the West Coast and warm-cold stanzas in the Eastern Bering Sea. More  
246 specifically, from 1967 to 2018, minimum, mean, and maximum SST in the Northeast all

247 increased (Fig. 1a), translating to more than one degree Celsius of warming in every SST metric  
248 over the fifty years measured (respectively,  $0.023 \pm 0.007$  °C/year,  $p = 1.4 \times 10^{-3}$ ;  $0.03 \pm 0.004$   
249 °C/year,  $p = 3.7 \times 10^{-9}$ ;  $0.033 \pm 0.006$  °C/year,  $p = 4.4 \times 10^{-7}$ ). On the West Coast (Fig. 1b), no  
250 significant trends occurred in any temperature metric from 1976-2018, despite variation of  $\pm 2$   
251 °C for individual years (minimum SST  $0.004 \pm 0.008$  °C/year,  $p = 0.65$ ; mean SST  $0.002 \pm 0.007$   
252 °C/year,  $p = 0.77$ ; maximum SST  $0.003 \pm 0.009$  °C/year,  $p = 0.77$ ). In the Eastern Bering Sea  
253 (Fig. 1c), warming was evident in maximum SST change from 1988-2018, which increased  
254  $0.038 \pm 0.018$  °C/year ( $p = 0.049$ ). Neither minimum nor mean SST increased significantly in the  
255 Eastern Bering Sea, although both had a positive relationship with year (minimum  $0.008 \pm 0.01$   
256 °C/year,  $p = 0.48$ ;  $0.022 \pm 0.013$  °C/year,  $p = 0.10$ ), and recent warm-cold stanzas (warm: 1999-  
257 2005; cold: 2006-2013; warm: 2014-2018) that were evident in all temperature measurements.

258

### 259 *Range edge shifts over time*

260 Species exhibited a wide variety of shifts, including a 10.8 km/year shift of the  
261 equatorward edge of canary rockfish (*Sebastes pinniger*) on the West Coast, a -5.2 km/year shift  
262 in the poleward edge of longhead dab (*Limanda proboscidea*) in the Eastern Bering Sea, and a  
263 24.5 km/year shift in the equatorward edge of American lobster (*Homarus americanus*) in the  
264 Northeast (Fig. 2; negative values indicate southward/equatorward shifts). Indeed, *Homarus*  
265 *americanus* had one of the greatest of all range edge shifts we documented. The most extreme  
266 shifts across all species and regions ranged from 24.7 km/year (poleward edge of *Porichthys*  
267 *notatus* on the West Coast) to -26.6 km/year (poleward edge of *Sebastes semicinctus* on the West  
268 Coast; Fig. 3). It was striking that the two largest range shifts occurred in the region with the  
269 smallest average temperature shifts. All single-species edge positions over time are reported in  
270 Appendix 3.

271 When pooled over all species in a region, all regions had a generally northward shift.  
272 Range edges shifted 4.4 km/year in the Northeast from 1967-2018 (90% CI 4.0 – 4.7), 1.3  
273 km/year on the West Coast from 1976-2018 (90% CI 0.7 – 2.0), and 0.1 km/year in the Eastern  
274 Bering Sea from 1988-2018 (90% CI -0.2 – 0.4; means and credible intervals from single-species  
275 Bayesian linear regressions). Separating these posterior distributions by range edge type  
276 (poleward or equatorward) revealed opposing shifts in the two groups: equatorward range edges  
277 overall shifted 4.1 km/year (90% CI 3.8 – 4.4), but poleward range edges shifted -1.8 km/year

278 (90% CI -2.2 – -1.4; means and credible intervals from single-species Bayesian linear  
279 regressions).

280 The magnitude of range edge shifts was slightly greater in fishes than in invertebrates.  
281 When both were pooled across all species and regions, fishes shifted north 2.0 km/year (90% CI  
282 1.7 – 2.2) and invertebrates 1.5 km/year (90% CI 1.1 – 1.9; means and credible intervals from  
283 single-species Bayesian linear regressions). This difference in magnitude of shift was driven by  
284 equatorward range edges of fishes shifting faster—4.5 km/year *versus* 3.4 km/year—than  
285 invertebrates (90% CIs 4.2 – 4.8 and 2.9 – 3.9, respectively), while both groups of poleward  
286 edges shifted in the opposite direction at similar rates (fishes -1.9 km/year, 90% CI -2.4 – -1.3,  
287 invertebrates -1.8 km/year, 90% CI -2.4 – -1.1; means and credible intervals from single-species  
288 Bayesian linear regressions).

289

#### 290 *Edge thermal niche tracking*

291 We estimated edge thermal niche tracking by testing whether the change in minimum or  
292 maximum temperature at the range edge over time was different from zero, based on 90%  
293 Bayesian credible intervals from Bayesian linear regressions of temperature on time. Of 165  
294 species range edges, we found that 145 (88%) maintained at least one component of the edge  
295 thermal niche (summer or winter extreme temperature) during the study period. Further, for the  
296 majority of range edges—126, or 76%—both minimum and maximum temperatures were  
297 maintained over time. Of the 19 range edges consistent with only one temperature metric, 12  
298 were consistent with winter extremes and 7 were consistent with summer extremes.

299 On the West Coast and in the Eastern Bering Sea, almost all range edges tracked both  
300 temperature metrics (100% and 97%, respectively; Fig. 4b,c). By contrast, only 34% of range  
301 edges in the Northeast tracked both temperature metrics, and the Northeast also contained all of  
302 the 20 range edges that did not track either summer or winter temperature extremes (Fig. 4a).  
303 Lack of tracking arose for different reasons in poleward and equatorward edges: the poleward  
304 edges that did not maintain their edge thermal niches often typically did not shift, or even shifted  
305 south, as the oceans warmed, while the equatorward edges that did not maintain their edge  
306 thermal niches often shifted north faster than expected, into cooler waters (Appendix 4). Among  
307 fishes (the group with more readily available trait data) we did not find evidence that dispersal-  
308 related traits were related to the degree of thermal niche tracking (Appendix 5).

309

310 DISCUSSION

311

312 We quantified temporal dynamics and thermal niche tracking over decades for 165  
313 marine range edges while using a novel spatiotemporal modeling approach to standardize among  
314 the three study regions and their differing survey methodologies. Across diverse geographies,  
315 historical climates, and taxa, range edges of marine species were in general conserving their  
316 thermal niches through space and time. Edge thermal niche conservatism suggests that most  
317 species range edges are tracking temperature change, consistent with evidence that many species  
318 distributions are shifting through space (Hiddink et al., 2015; Lenoir et al., 2020; Pinsky et al.,  
319 2013; Poloczanska et al., 2013) and supported by theory from thermal ecophysiology (Pinsky et  
320 al., 2019; Stuart-Smith et al., 2017; Sunday et al., 2012). However, a non-negligible number of  
321 range edges did not shift as predicted—especially in the Northeast, the region with the greatest  
322 historical temperature increase—indicating that temperature alone does not explain range edge  
323 dynamics for all marine species. Changing predator or prey distributions, temperature-dependent  
324 hypoxia, dispersal limitation, population dynamics, evolutionary adaptation, and other biotic or  
325 abiotic processes could all be affecting species distributions in addition to temperature (Angert et  
326 al., 2020; Deutsch et al., 2015; Ellingsen et al., 2020; Louthan et al., 2015; Molinos et al., 2017).  
327 Deviations from temperature driven predictions came in multiple forms – larger range shifts in  
328 the predicted direction, lack of movement, and substantial shifts in the “wrong” direction. This  
329 study provides the first large-scale, multi-region analysis of thermal niche tracking at range  
330 edges and describes novel statistical approaches that are applicable to a wide range of taxa and  
331 systems.

332 Species ranges are shifting poleward around the globe, both on land and in the sea (Chen  
333 et al., 2011; Poloczanska et al., 2013). Local patterns in climate change have helped to explain  
334 distributional shifts of many species, especially those that did not shift directly toward the poles  
335 (Lenoir & Svenning, 2015; Pinsky et al., 2013). These findings suggest that species’ range shifts  
336 can be at least partially explained by spatial shifts in their climatic niches (Burrows et al., 2011;  
337 Loarie et al., 2009). While many global change studies have not measured range edge  
338 displacement, those that have often report major poleward shifts in range edges, particularly at  
339 the poleward range edge (Fredston-Hermann et al., 2020; Hickling et al., 2005; Parmesan et al.,

1999). 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. This  
“resurvey” method and other approaches that use a small number of time points may lead to  
inaccurate or spurious conclusions about ecological responses to climate change (McCain et al.,  
2016; Stuble et al., 2021). Given the degree of variability we observed in some species’ range  
edge positions over time (Appendix 3), long time-series were important for detecting trends  
(Fredston-Hermann et al., 2020). 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 (Lenoir et al., 2020; Pinsky et al., 2019, 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 (Fredston-Hermann et al., 2020; Sunday et al., 2015). 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. Ironically, the West  
Coast, however, also had the two species that showed the largest shifts in both poleward and  
equatorward distributions.

Recent work on marine heatwaves has underscored the need to move beyond temperature  
means to measure climatic extremes and variability in studies of global change biology,  
including in the oceans (Day et al., 2018; Smale et al., 2019). We quantified edge position in  
relation to temperature extremes precisely for this reason, especially given the marked recent  
increases in summer extreme temperatures in the Northeast and the Eastern Bering Sea. Yet our  
results revealed that range edges remained in the same winter extreme temperatures  
approximately as often as they did for summer temperatures, suggesting that winter temperatures

371 may be an underappreciated covariate of range dynamics at both poleward and equatorward  
372 range edges (Dana, 1853; Morley et al., 2017). Foundational biogeographic theory provides a  
373 hypothesis for this: poleward range edges could be influenced either by summer temperatures  
374 limiting reproduction and growth or by winter temperatures limiting survival; and equatorward  
375 range edges could be influenced either by summer temperatures limiting survival or by winter  
376 temperatures limiting growth and reproduction (Hutchins, 1947). Further work could test  
377 whether this is a biologically plausible explanation for these temperate marine species. Longer  
378 time series, extensive analysis of different dimensions of temperature change, or additional  
379 oceanographic data products such as high-resolution hindcast sea bottom temperature data could  
380 be used in the future to tease apart more precisely which temperature metrics best explain range  
381 edge dynamics and why.

382 Our finding that the region with the greatest historical temperature increase exhibited the  
383 lowest frequency of edge thermal niche tracking—and the region with the smallest historical  
384 temperature increase exhibited the two most extreme range shifts—both underscore the critical  
385 importance of considering non-temperature, indirect, and non-linear processes that may influence  
386 species distributions. In the Northeast, we documented equatorward range edges that shifted  
387 much further north than expected based on temperature—into cooler waters—and poleward  
388 range edges that did not shift or shifted south (Appendices 3 and 4). This could arise due to  
389 density-dependent habitat selection if these species were declining in abundance, causing each  
390 range edge to collapse toward the range center (Blanchard et al., 2005). At the equatorward edge,  
391 competition or predation from the south could be driving edge retraction (Kordas et al., 2011);  
392 for example, the rapid contraction of the equatorward range edge of American lobster could be  
393 due to increased predation from species like black sea bass shifting up the coast (McMahan &  
394 Grabowski, 2019) or increased mortality from a temperature-related disease (Groner et al.,  
395 2018). At the poleward edge, species interactions (HilleRisLambers et al., 2013), priority effects  
396 (Fukami, 2015), dispersal limitation (Poloczanska et al., 2011), or a lack of non-thermal habitat  
397 (McHenry et al., 2019) could all inhibit northward shifts. Exploited species such as those  
398 analyzed here may also exhibit range shifts due to spatial variation in fishing and/or population  
399 rebuilding (Selden et al., 2020), as well as associated density-dependent range shifts (Thorson et  
400 al., 2016). Sessile invertebrates are particularly vulnerable to dispersal limitation if prevailing  
401 currents do not align with local climate velocities, as in the Northeast (Fuchs et al., 2020;

402 Molinos et al., 2017). On the West Coast, threshold responses to non-linear temperature change  
403 may also structure species distributions; El Niño events sometimes cause the transport of  
404 anomalously warm water up the coastline, facilitating transient poleward range extensions of  
405 species—some of which have persisted after these warm events ended (Leising et al., 2015;  
406 Tanaka et al., 2021; Zacherl et al., 2003). The Eastern Bering Sea system’s high degree of edge  
407 thermal niche tracking may be partly due to sea ice causing fairly stable winter temperatures  
408 there (Stabeno et al., 2001). Changes in non-temperature abiotic drivers such as dissolved  
409 oxygen (Deutsch et al., 2015; Howard et al., 2020) and ontogenetic differences in temperature  
410 sensitivity (Barbeaux & Hollowed, 2018; Dahlke et al., 2020) are likely to also influence range  
411 edge dynamics.

412 This study is the first to use a spatiotemporal modeling approach to estimate range edge  
413 dynamics and estimate a standard error around range edge positions, which we see as important  
414 methodological advances. Using the VAST model, we calculated rates of range edge shift that  
415 were similar in magnitude to those calculated from raw survey data in the Northeast  
416 (Fredston-Hermann et al., 2020). Our results are not directly comparable to previous work,  
417 however, because—unlike analyses of raw distribution data—VAST attributes some variation in  
418 recorded observations and abundances to both measurement variability (the tendency for fine-  
419 scale gear and habitat-selection processes to affect survey biomass for replicated samples at the  
420 same location and season) and sampling variability (random or systematic variation in selected  
421 stations within a stratified random design). Accounting for sampling variability can greatly  
422 improve precision for inference about population density for habitat-structured species (Cao et  
423 al., 2017; Shelton et al., 2014). In other cases, surveys sometimes do not follow a consistent  
424 design (e.g., the West Coast triennial survey from 1977-2004), and using a spatio-temporal  
425 model can mitigate biases arising from random or systematic changes in the area sampled  
426 (Thorson et al., 2016). In all regions, fish availability to the trawl survey likely varies depending  
427 on the thermal conditions in which the survey is conducted (Nichol et al., 2019). Continued  
428 extensions of VAST and similar models to distribution data will facilitate more rigorous  
429 evaluation of historical range edge dynamics, even for datasets with known inconsistencies and  
430 biases in sampling.

431 While we found that range edge positions almost always maintained their edge thermal  
432 niche, year-over-year temperatures at the range edge were often highly variable (Appendix 4),



433 and near-term (i.e., annual, not multi-decadal) projections of a species' edge thermal niche are  
434 unlikely to predict exactly where it will shift. Further, a non-negligible fraction of range edges  
435 did not shift at all, shifted opposite the predicted direction, or "overshot" temperature change and  
436 shifted further than expected. Our methods provide a blueprint for assessing whether range edges  
437 have tracked their thermal niches and for identifying potential species of concern that have  
438 reached a thermal limit yet do not appear to be shifting as expected based on temperature alone.  
439 Classifying species by edge thermal niche tracking can inform management and conservation,  
440 because different interventions are likely required for a species that shifts in response to warming  
441 (e.g., transboundary management) than for a species that remains stationary in the face of  
442 warming (e.g., assisted migration if there are barriers to movement). To move beyond  
443 categorizing all results of no thermal niche tracking as "individualistic responses," future  
444 research can test edge thermal niche conservatism against—or jointly with—other biogeographic  
445 hypotheses that integrate the influence of dispersal limitation, species interactions, population  
446 dynamics, eco-evolutionary processes, and other important abiotic and biotic drivers. Future  
447 progress on range edge dynamics will be accelerated by mechanistically testing predictions about  
448 which temperature and non-temperature processes should be limiting for which range edges  
449 against biogeographical data. Testing multiple contemporaneous processes (including density-  
450 dependent range expansion and contraction) and their net effects will provide insight into, and  
451 ultimately enable prediction of, range edge dynamics in a changing climate.

452

#### 453 ACKNOWLEDGMENTS

454 We thank current and past NOAA staff for collecting, curating, and publishing the data used in  
455 this study. E. M. Howard and R. Mendelsohn provided expert advice regarding oceanographic  
456 and spatial data analysis. We also thank A. J. Allyn and D. Ovando for code review and  
457 feedback, and D. Stevenson, L. Rogers, and two anonymous reviewers for comments on a  
458 previous draft.

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757 **Figure 1.** Maps of study regions—Northeast (A), Eastern Bering Sea (B), and West Coast (C)—  
758 with the continental shelf shaded in blue (300 m cutoff for Northeast and Eastern Bering Sea,  
759 600 m for West Coast). Plots show regional minimum (blue), mean (orange), and maximum  
760 (red) monthly sea surface temperature (SST; annual means) for the Northeast, the Eastern Bering  
761 Sea, and the West Coast (left to right). Black dashed lines show axes of measurement for range  
762 edges in each region, for which the origin point is marked with an X. Waypoints along the axis  
763 of measurement are marked with white dots every 100 km for the Northeast and Eastern Bering  
764 Sea, and every 200 km for the West Coast.

765

766

767 **Figure 2.** Example schematic showing range edge position with standard errors over time (first  
768 column), edge thermal niche over time (second column), and the posterior distribution of  
769 estimated edge thermal niche change (third column) for the equatorward edge of *Sebastes*  
770 *pinniger* in the West Coast (A), the poleward edge of *Limanda proboscidea* in the Eastern Bering  
771 Sea (B), and the equatorward edge of *Homarus americanus* in the Northeast (C). Time-series and  
772 distributions in blue represent winter extreme temperatures and red represents summer extreme  
773 temperatures. Horizontal bars in the third column represent 90% Bayesian credible intervals. A  
774 Bayesian credible interval that included zero (the vertical dotted line) was interpreted as no

775 change over time. Images by Harold N. Eyster and others via phylopic.org  
776 (<https://creativecommons.org/licenses/by-nc-sa/3.0/>).

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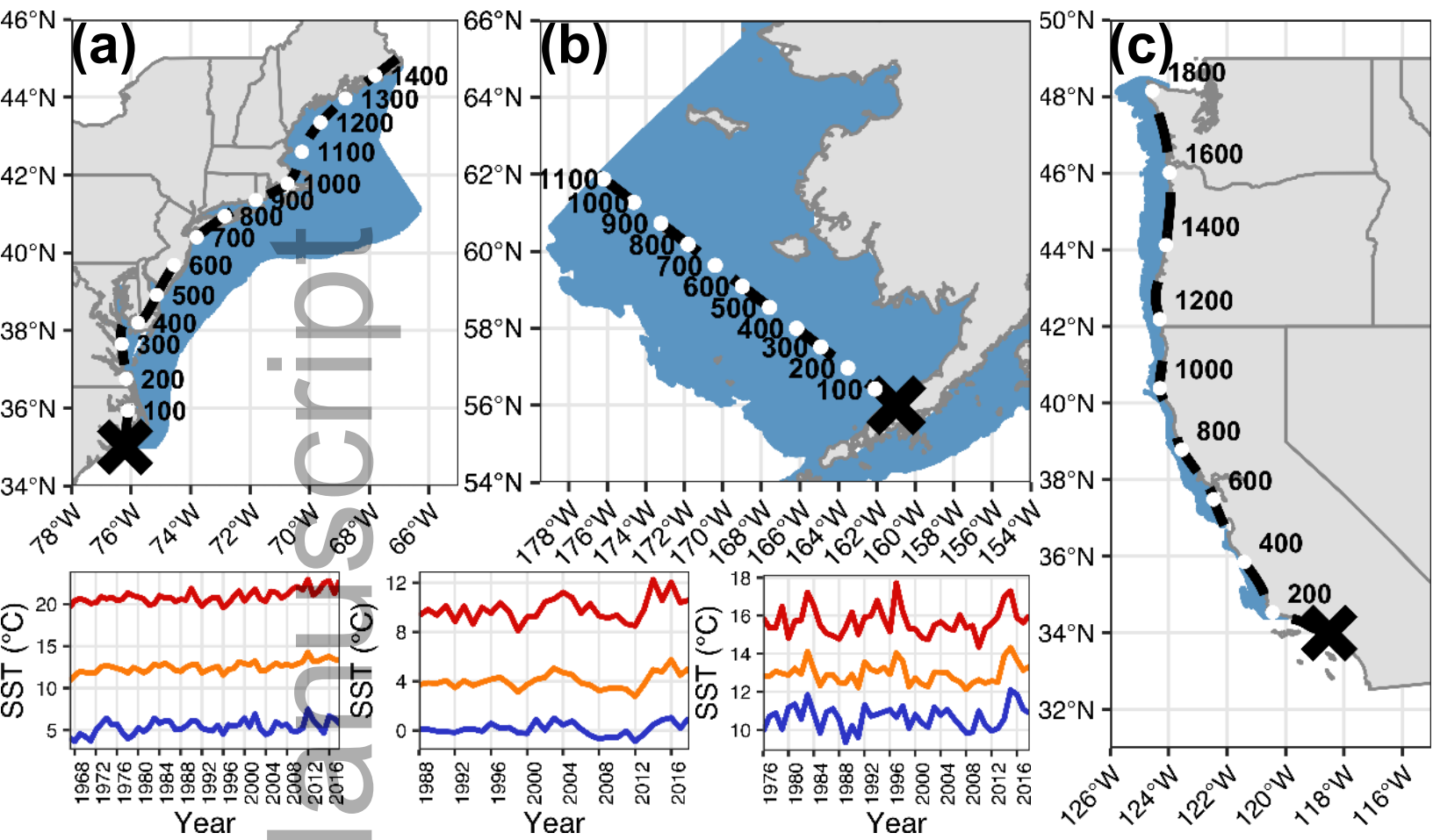
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779 Figure 3. Distribution of range edge shifts over time (x-axis) and niche shifts (y-axis) in summer  
780 and winter temperature extremes for all range edges and regions, from Bayesian linear  
781 regressions. Each point is an equatorward (black) or poleward (grey) range edge ( $n=164$  on each  
782 plot), and bars represent 90% Bayesian credible intervals. One outlier was omitted: the poleward  
783 edge of *Merluccius albidus* in the Northeast, which exhibited a  $0.21\text{ }^{\circ}\text{C}/\text{year}$  increase in the  
784 warm extreme (summer) temperature component of its edge thermal niche. Point shapes  
785 represent the region where the range edge was measured.

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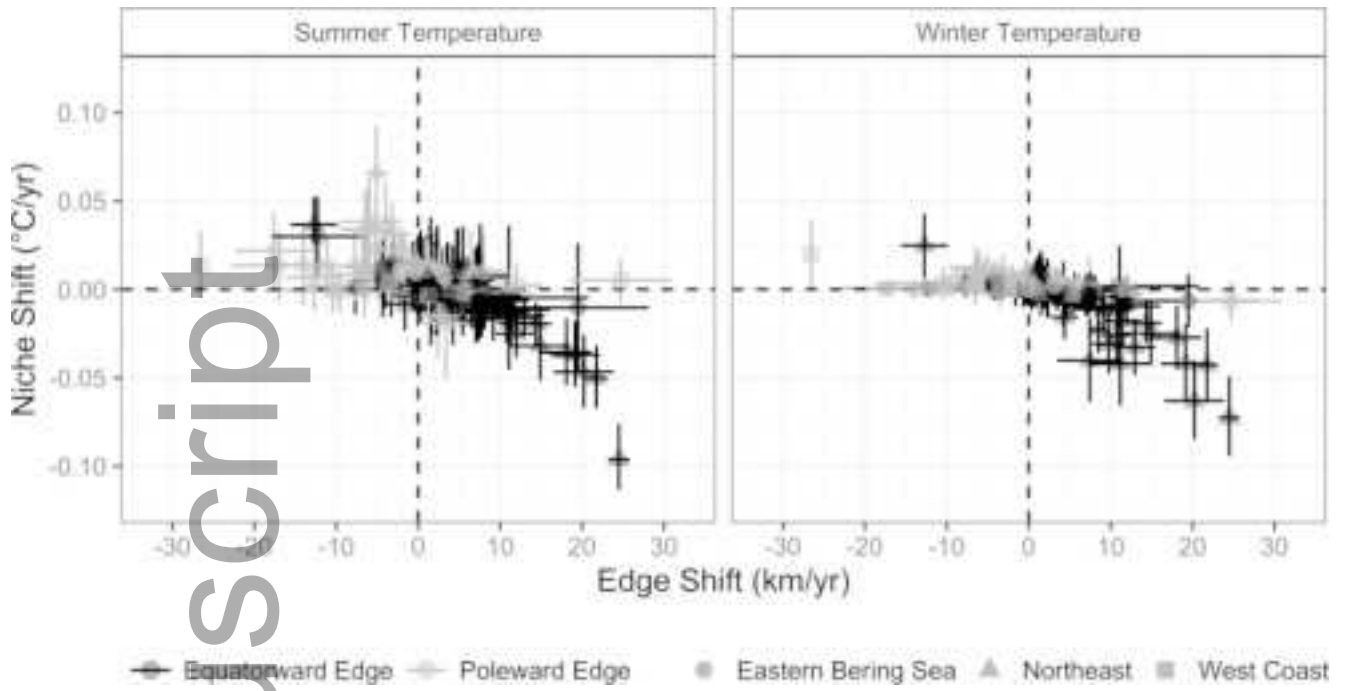
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788 **Figure 4.** Distribution of range edge shifts over time (x-axis) grouped by whether the edge  
789 thermal niche was conserved over time (y-axis) in the Northeast (A), the West Coast (B), and the  
790 Eastern Bering Sea (C). Each point corresponds to a single range edge. Positive x-axis values  
791 represent poleward shifts (i.e., northward) and negative values represent equatorward shifts (i.e.,  
792 southward). Range edges could track cold (blue), warm (red), both (purple), or neither (grey)  
793 temperature extremes. The thickness of each horizontal band represents a relative weighting of  
794 point densities along the x-axis. Outlier species (shifts with an absolute value greater than 15  
795 km/year) are labeled. Images by Armelle Ansart, Timothy J. Bartley, Maxime Dahirel, Ellen  
796 Edmonson, Harold N. Eyster, T. Michael Keeseey, Ekaterina Kopeykina, and others via  
797 phylopic.org (<https://creativecommons.org/licenses/by-nc-sa/3.0/>).



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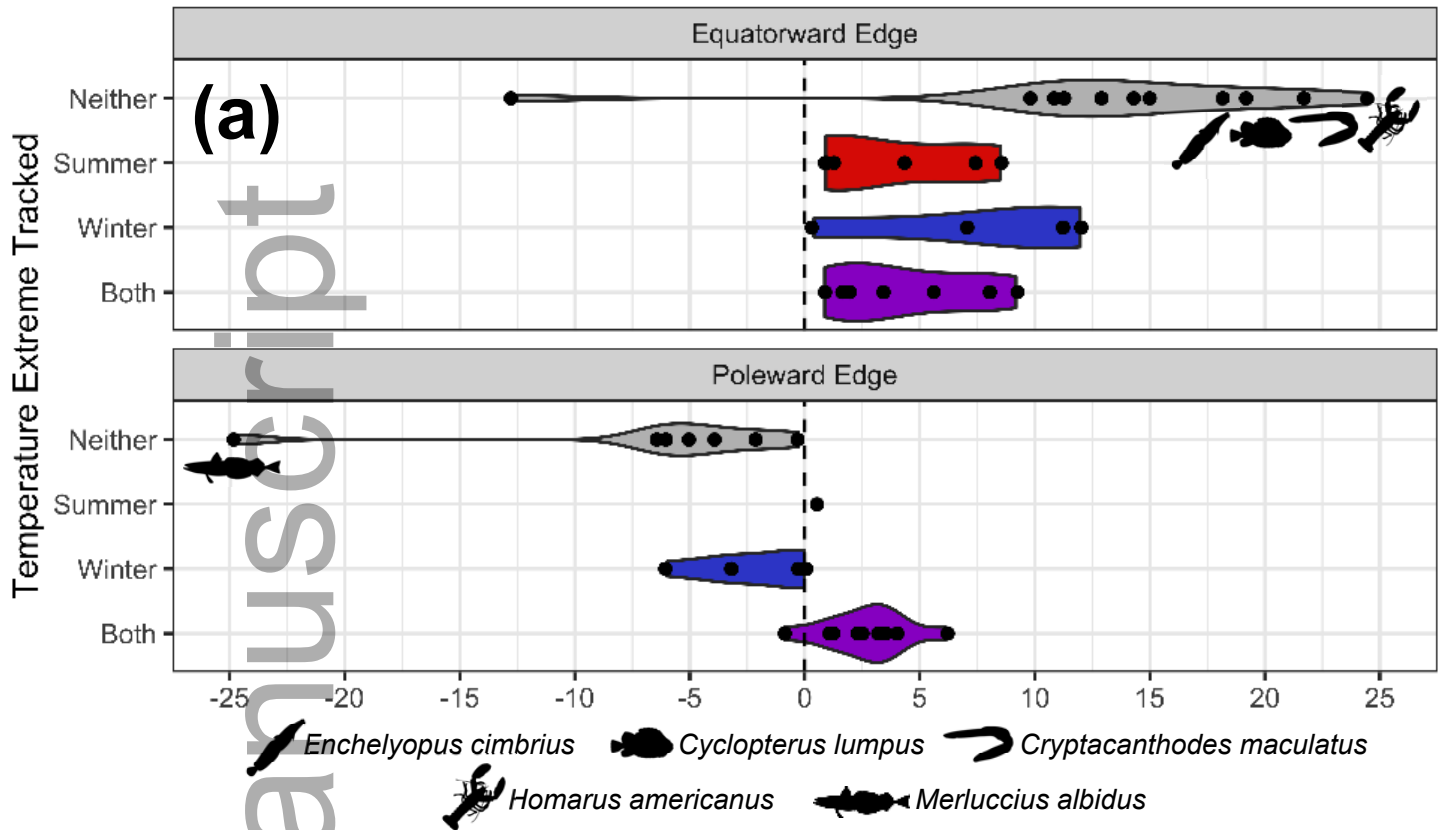
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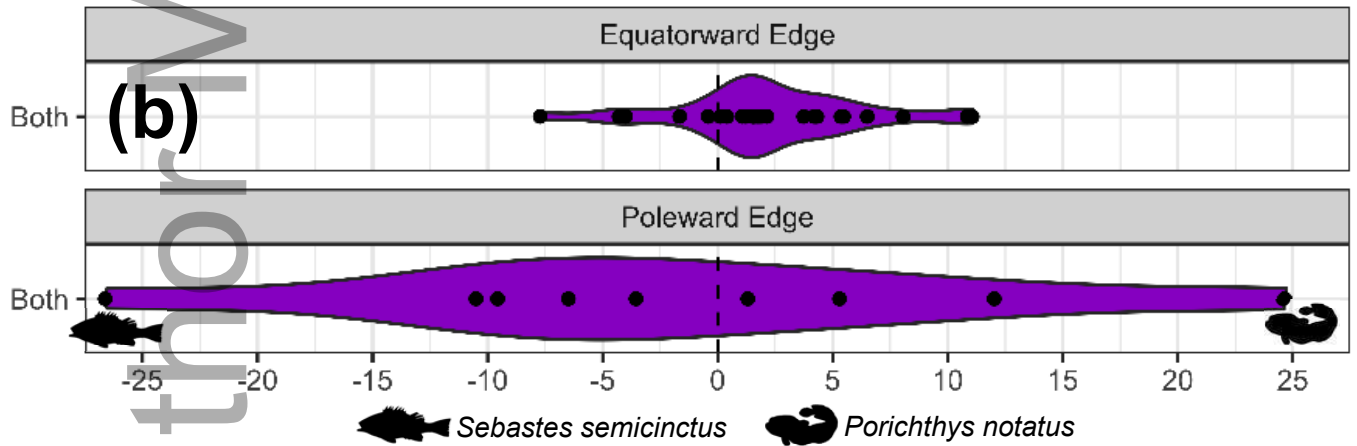
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## Northeast



## West Coast



## Eastern Bering Sea

