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RESEARCH ARTICLE

Win, lose, or draw: Evaluating dynamic thermal niches of northeast Pacific groundfish

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Abstract

Understanding the dynamic relationship between marine species and their changing environments is critical for ecosystem based management, particularly as coastal ecosystems experience rapid change (e.g., general warming, marine heat waves). In this paper, we present a novel statistical approach to robustly estimate and track the thermal niches of 30 marine fishes along the west coast of North America. Leveraging three long-term fisheries-independent datasets, we use spatiotemporal modeling tools to capture spatiotemporal variation in species densities. Estimates from our models are then used to generate species-specific estimates of thermal niches through time at several scales: coastwide and for each of the three regions. By synthesizing data across regions and time scales, our modeling approach provides insights into how these marine species may be tracking or responding to changes in temperature. While we did not find evidence of consistent temperature-density relationships among regions, we are able to contrast differences across species: Dover sole

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and shortspine thornyhead have relatively broad thermal niche estimates that are static over time, whereas several semi-pelagic species (e.g., Pacific hake, walleye pollock) have niches that are both becoming warmer over time and simultaneously narrowing. This illustrates how several economically and ecologically valuable species are facing contrasting fates in a changing environment, with potential consequences for fisheries and ecosystems. Our modeling approach is flexible and can be easily extended to other species or ecosystems, as well as other environmental variables. Results from these models may be broadly useful to scientists, managers, and stakeholders—monitoring trends in the direction and variability of thermal niches may be useful in identifying species that are more susceptible to environmental change, and results of this work can form quantitative metrics that may be included in climate vulnerability assessments, estimation of dynamic essential fish habitat, and assessments of climate risk posed to fishing communities.

Introduction

The relationship between marine species and their environment is complex and dynamic, shaped by both biological interactions and physical factors. In recent years, the urgency to understand this relationship has intensified due to the rapid rate of climate change and its profound impact on marine ecosystems [1]. Tools to understand these effects of climate change have grown in response, including rapid advancements in both the complexity of statistical approaches for modeling the spatiotemporal variability of species [2–4] and methods used to quantify environmental drivers of distribution. Quantifying the tolerance of marine species to temperature or oxygen across their range is critical for prioritizing species that may be most at risk [5–7] or for making predictions in novel environments (e.g., unsampled areas in space or under future environmental conditions). These predictive efforts are grounded in the concept of the Grinnellian niche [8], which emphasizes the importance of the physical environment and the species' role within its ecosystem to their distribution patterns [9]. The Grinnellian niche concept (where a species may exist) is closely related to the concept of the realized environmental niche (where a species does exist). Understanding how species niches change in time or space allows for predicting more accurately how fish populations, and the fisheries that depend on them, may shift in response to climate change [10]; identifying species tolerance thresholds [11]; and understanding the dynamics of invasive species [12].

In marine environments experiencing long-term changes with respect to temperature, oxygen, or other dynamic ocean variables, species niches may be shaped by life-history characteristics, species interactions, ability to adapt to new environments, as well as temporal variability in the environment. For instance, as their natal environment changes, highly mobile species that are unconstrained by specific structural habitats or substrate types may be able to move to novel environments, and experience little to no change in their realized environmental niche. Variability in niche width may also be affected by a species' sensitivity to changes in the environment; species that are highly adapted or insensitive to change may have broader niche widths than more sensitive species (Fig 1). Finally, the upper and lower bounds of a species range may be affected by different processes; both lower and upper bounds may shift in a warming environment if cooler habitats disappear, while upper bounds may also be influenced by species-specific metabolic constraints [13].

The environmental niches of species can be estimated using a variety of methods, including laboratory experiments [14], field observations, and statistical modeling. As lab and field

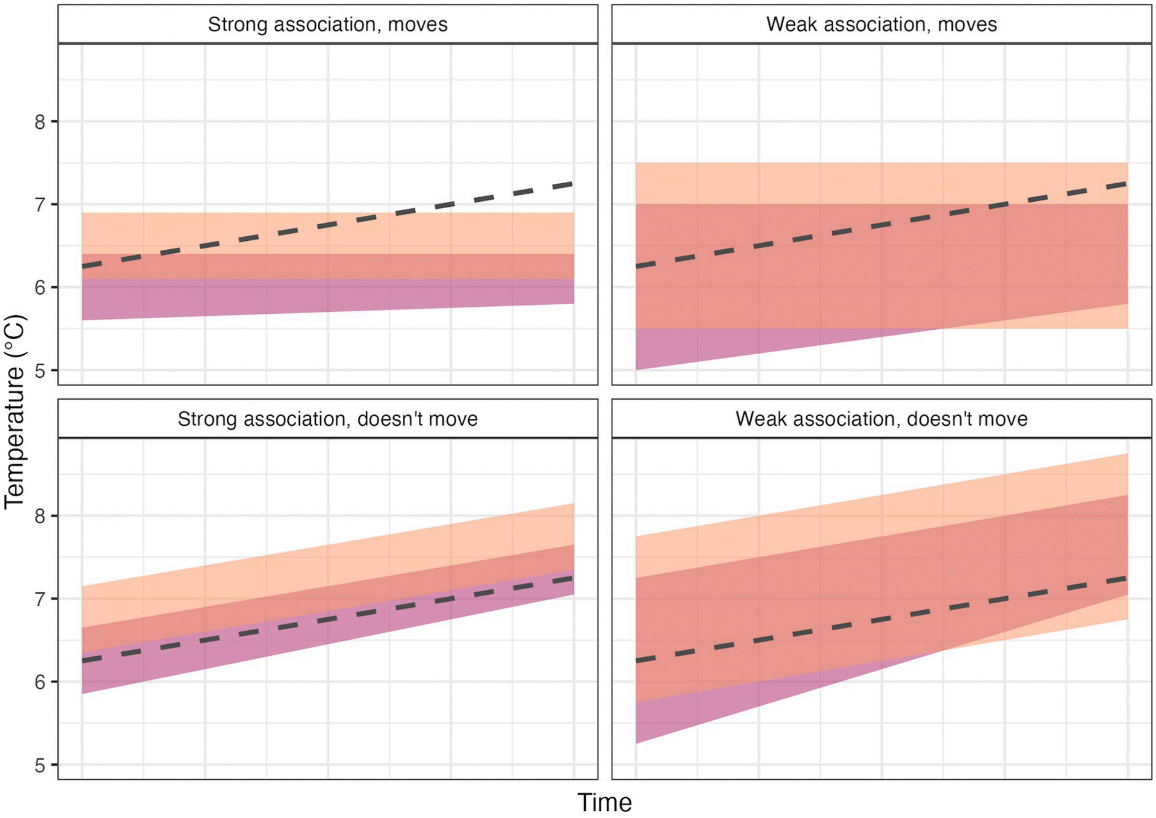

Fig 1. Illustration of potential changes in thermal niche widths in a warming environment (mean temperature represented with dashed line). In each plot, the realized thermal niche is indicated by the shaded regions, and each plot shows a different combination of thermal niche width (columns) and dispersal capacity (rows). Purple shading indicates realized niches shrinking when all habitats warm evenly while orange shading indicates how the niche is affected when cooler areas are available despite overall warming. Though not shown, upper bounds of thermal niches may be further constrained by metabolic limits.

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experiments can be prohibitively expensive on a large geographic scale, we focus on statistical modeling approaches for describing realized environmental niches from existing field observations. Common frameworks for statistical approaches include species distribution models (SDMs), environmental niche modeling (ENM), and habitat suitability models (HSMs). Though data inputs or interpretation may differ slightly between these approaches [15], a common thread across these techniques is making inferences about the breadth of distribution of environmental variables that an organism inhabits or could potentially inhabit (i.e., niche width). While the terminology around models and niche concepts may cause confusion, we follow recent applications of the Grinnellian niche to define the space that an organism may inhabit, constrained by multiple environmental variables [9].

There are several existing statistical approaches for quantifying niche width or ranges [16]. Some previous studies have taken a largely empirical approach, using the observed range of environmental conditions where species are found [9]. Model-based approaches have also been developed, generally with presence-only data (e.g., ecological niche factor analysis, MaxEnt), though assumptions about absences may be problematic in some settings [15]. More recently, model-based approaches have been used to estimate shifts in environmental niches using range edges [17]. Recognizing that no single approach will perform best for all species and ecosystems [18], we aim to develop a model-based approach to estimating Grinnellian niches, using georeferenced surveys of biological and abiotic conditions [19].

The objective of this paper is to extend existing spatiotemporal modeling tools to estimate the Grinnellian thermal niche for a novel dataset of 30 marine species on the West Coast of North America (USA, Canada) and gauge the sensitivity of species' thermal niches by quantifying changes in the locations and widths of species thermal niches through time. Using three long-term fisheries-independent datasets collected across a large-scale gradient of temperatures and depths, we (1) fit five SDMs to evaluate support for regional variation in density–depth and density–temperature relationships, and (2) generate time-varying estimates of temperature niches for each species. Using time-varying niches, we also evaluate which species niches are changing in direction (trending warmer / colder) or variability (increasing / decreasing niche widths) in response to warming. Thus, we infer which species have been climate 'winners' or 'losers' based on the historical change in thermal niche.

Methods

Data

Around the world, fishery-independent surveys of marine fishes are routinely conducted to support science and management; these surveys sample both commercially important species, as well as species of conservation concern. We used fisheries-independent trawl survey data from the following three regions in the Northeast Pacific Ocean (Fig 2): the West Coast of the United States (California-Oregon-Washington states, COW), British Columbia (BC), and the Gulf of Alaska (GOA). Data from the US West Coast bottom trawl survey have been collected annually by NOAA Fisheries since 2003 [20]. Surveys in British Columbia have been conducted by Fisheries and Oceans Canada, also annually since 2003. Surveys in British Columbia are stratified in four regions, with two regions usually sampled in odd years (Hecate Strait and Queen Charlotte Sound) and two in even years (West Coast Vancouver Island and West Coast Haida Gwaii) [21, 22]. Finally, we used data from the Gulf of Alaska bottom trawl survey on the continental shelf, which have been collected by NOAA Fisheries since 1984. The Gulf of Alaska survey region extends from the Islands of Four Mountains in the Aleutian Islands to Dixon Entrance in Southeast Alaska. The Gulf of Alaska survey was conducted every three years until 1999, when the survey became biennial. Because of changes in the sampling design and gear use in 2001 and earlier, and limited overlap with other surveys before 2003, we only included 2003–2021 Gulf of Alaska survey data. Surveys from all three regions use a similar stratified random sampling design, allowing for data to be combined and broad comparisons to be made. Across the three regions, we restricted our analysis to data-rich species, retaining only those with at least 50 observations in all survey years (n = 35 species from the US West Coast, n = 31 in British Columbia, n = 18 in Gulf of Alaska; S1 Text). Species were further filtered to only include those occurring in two or more survey regions, yielding a total of 30 species (S1 Table). All code and data to reproduce our analysis are in our public Github repository https://github.com/fate-spatialindicators/temperature-niche.

Models

Workflow. Our approach to estimating the distribution of species thermal niches through time involved separately fitting coastwide spatiotemporal models to species' densities (catch per unit effort) and bottom temperature, so that predictions from each may be projected onto a regularized grid within the domain of the surveyed regions, for each year (2003 to 2021). As an alternative to in situ bottom temperature, predicted temperature from regional oceanographic models could be used as a covariate. We then merge gridded predictions of density and temperature for each species—year combination to generate estimates (with uncertainty) of thermal niches.

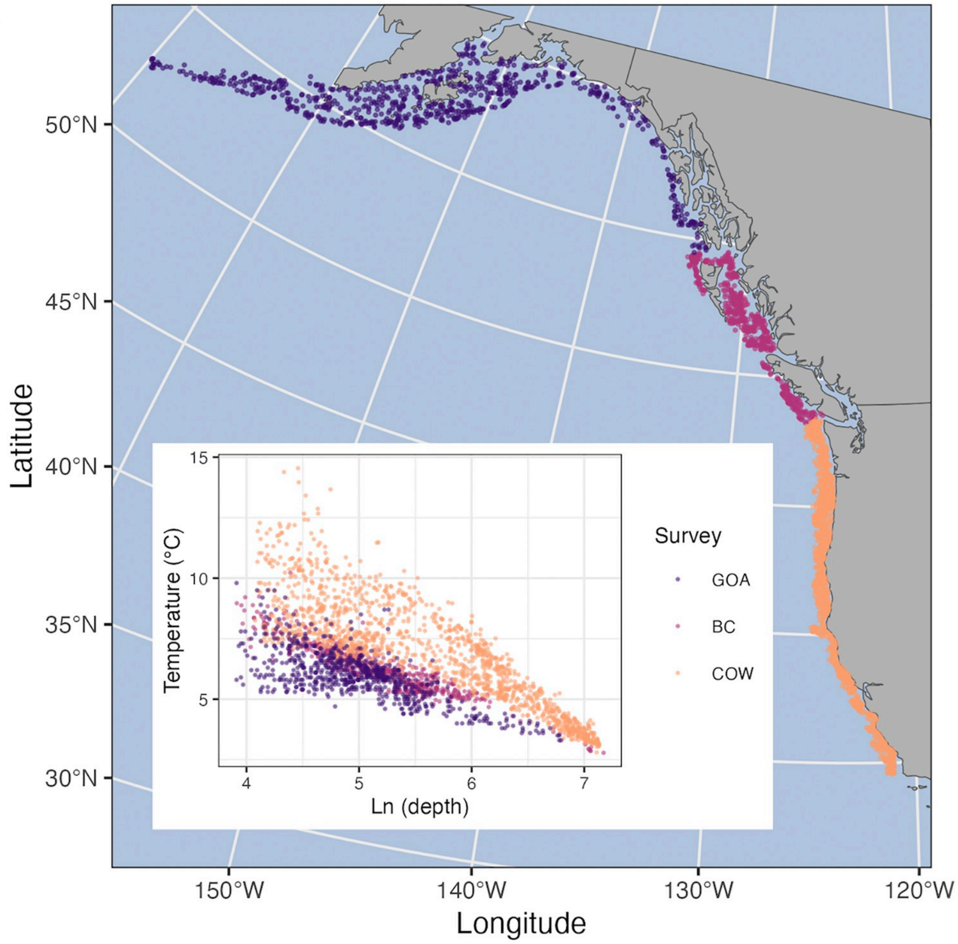

Fig 2. Map of study area in the Northeast Pacific Ocean, using fishery-independent data from the Gulf of Alaska (GOA), British Columbia (BC), and the West Coast of the USA (California, Oregon, Washington states = COW). Survey locations in 2015–2016 are shown to depict the spatial extent sampled in each region; the inset illustrates the correlation between the natural log of depth in meters and temperature in degrees Celsius for each region. Map data taken from [36].

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Constructing flexible species distribution models. To estimate the responses of groundfish density to temperature in a variable environment, we implemented spatiotemporal generalized linear mixed models (GLMMs), which have been widely used in fisheries to assess population status via index standardization [23], quantify range shifts [24, 25], and identify spatial areas with high recruitment [26]. These spatiotemporal GLMMs are flexible in that commonly used distribution families can be used to model the response. Variants of these methods used in species distribution modeling and fisheries applications have either modeled species presence–absence or total catches, or have used a hurdle (delta) framework to separately model occurrence and positive catch rates [27]. For each included species (S1 Table), we constructed spatiotemporal GLMMs using total catch rate as a Tweedie distributed response (log link; [23]) because these values are both zero inflated and positively skewed.

The general form of the spatiotemporal GLMM can be represented as

$$\boldsymbol{u}_t = f^{-1}(\mathbf{X}\mathbf{b} + \boldsymbol{\omega} + \epsilon_t)$$

where $\boldsymbol{u_t}$ represents a vector of predicted occurrences across all locations at time t,$f^{-1}()$ is the inverse link function, $\mathbf{X}$ represents a matrix of main fixed-effects coefficients (such as year effects, region, depth, or environmental covariates) with estimated coefficients $\mathbf{b}$. We separate the spatial variation $\boldsymbol{\omega} \sim \mathrm{MVN}(\mathbf{0},\Sigma_{\omega})$ from the year-to-year spatiotemporal variation $\epsilon_{\boldsymbol{t}}$, where the spatial component represents a spatial intercept (treated as a Gaussian Markov random field) and the spatiotemporal component represents temporal deviations from $\boldsymbol{\omega}$. As the BC and GOA regions in our dataset do not have consistent sampling in each year, we modeled spatiotemporal variation as a random walk process $\epsilon_{\boldsymbol{t}} \sim \mathrm{MVN}(\epsilon_{\boldsymbol{t-1}},\Sigma_{\epsilon})$ to allow for flexibility in estimating the spatial and temporal processes in years without data [28]. Latent spatial and spatiotemporal random fields were approximated using a triangulated mesh [29] with 1322 vertices (with a minimum distance between vertices of 50km) calculated with the INLA R package [30]. For simplicity, we assumed a shared range parameter between the spatial and spatiotemporal fields, though we allowed each field to have a unique variance. Additional details of the mesh construction are given in the SI (S1 Text).

A challenge in estimating the effects of a changing environment on fish populations is that environmental variables such as temperature or oxygen are often correlated with depth. These effects are present in our datasets, though the relationship varies across regions (Fig 2). Such correlations are not unique to the marine environment; many terrestrial datasets also include similar correlations with altitude [31]. As correlated variables may be problematic for some SDMs [32, 33], we fit five models to data from each species (S1 Table), allowing for a range of assumptions about depth and temperature effects varying by region. All models included quadratic effects of depth (log-transformed, then standardized to have zero mean and unit variance) but differed with respect to the inclusion of quadratic effects of standardized bottom temperature and interactions between region, depth, and temperature (S2 Table). We restricted the effects of temperature to be quadratic, following on theory and previous work relating temperature variability to species distributions [14, 34, 35].

We found the maximum marginal log likelihood using Template Model Builder (TMB; [37]), which implements the Laplace approximation to integrate out random effects. Specifically, we fit all models in R 4.1.0 [38] using the sdmTMB package [39] which interfaces automatic differentiation in TMB with INLA [30]. Models that successfully converged (positive-definite Hessian matrix, and a maximum absolute log likelihood gradient < 0.001) were then compared using the marginal Akaike's Information Criterion (AIC; [40]) to evaluate the data support for alternative relationships between depth or temperature by region. For each species, we used the model with the lowest AIC score to estimate the historical trend and variability of the thermal niche through time. This approach is flexible, allowing for variability in both the environment and distribution in space and time.

Estimating thermal niches. First, we generated predictions of gridded bottom temperature data using observations from the trawl surveys in our analysis. We fit *in situ* bottom temperature measurements from each of the trawl surveys as the response variable with penalized regression splines on depth and calendar day and spatiotemporal variability (spatiotemporal fields allow mean bottom temperature to be slightly different in each year and to vary in a non-linear pattern over time). Spatiotemporal fields were modeled as an autoregressive AR(1) process, allowing warm and cool locations to persist across time steps. A single model was fit to data from all three regions, and predictions were made using prediction grids for each region (cell size differed slightly by region with most cells being 13.72 km^2 in the GOA, 4 km^2 in BC, and 10.29 km^2 in COW; [20]). Using 1 July as a standardized date, we used the fitted model to predict bottom temperature to the grid from each region. To better understand the temporal variability across regions, we calculated a spatially weighted average of gridded predictions to generate a standardized temperature index that accounts for year-to-year variability in sampled locations, depths, and temperatures.

Second, we used the fitted SDMs for species-specific catch rates described above to make predictions of gridded densities by year (using the same prediction grid as used in generating gridded bottom temperature). Model-based estimates of thermal niche means and ranges were generated for each species–year combination by using the projected species' densities in each grid cell as weights, $p_{i,t} = \frac{E[y_{i,t}]}{\sum_{i=1}^{n} E[y_{i,t}]}$, where $\mathrm{E}[y_{i,t}]$ is the model predicted density of a given species in cell *i* and time *t*. Gridded bottom temperature cells in each year were then sampled with replacement, using the density weights to assign higher probabilities to cells with higher densities (this procedure was repeated independently for each of the 30 species). To better understand potential drivers of change within each region, we repeated this resampling procedure by only using the data from each region; the distribution of these temperature values in each year represents the estimated thermal niche. To quantify the ability of each species to track changes in the environment, we calculated the correlation between the mean thermal niche for each species and the average temperature across its range (following work quantifying essential fish habitat, we used grid cells representing 95% of total density; [41]).

Changes in thermal niches in response to recent warming. In addition to changes in the direction of the realized niche over time, the range of thermal niches may be expanding or contracting in response to warming conditions [9, 42, 43]. To evaluate support for these hypotheses, we defined the niche width (Δw) as the difference between the 90% and 10% prediction intervals, and modeled inter-annual variability in Δw as the response, with the year-over-year change in temperature (ΔC) as the predictor,

$$\Delta \mathrm{w}_{i,t} = \Delta \mathrm{C}_{i,t} b_i + \delta_{i,t}$$

where species-specific (i) slopes are estimated as random effects, $b_i \sim N(\mu,\gamma)$, and residual error for species i at time t is $\delta_{i,t} \sim N(0,\sigma)$. So that we could make probabilistic statements about the densities of individual (b_i) and hierarchical parameters (μ,γ), models were fit using Bayesian linear mixed models with the R package brms [44] interfacing with Stan via rstan [45, 46]. Modeling changes in differenced temperature and niche widths accounts for non-stationary patterns, such as trends over time, and because the expectation is zero, no intercept is needed. We implemented this regression model using four Markov chain Monte Carlo chains, each with a burn-in period of 2000 iterations (followed by 2000 samples). Half Student-t (3, 0, 2.5) priors were used on both standard deviations (γ,σ), and a flat uniform prior was placed on the global mean, μ. Convergence was assessed using R-hat diagnostics (< 1.05) and the absence of divergent transitions.

To evaluate support for spatial homogeneity in bottom temperature trends within each region (e.g. all habitat warming similarly, Fig 1), we de-meaned the predicted gridded bottom temperature for grid cell, and then calculated the standard deviation across all spatial grid cells within each region, by year. Annual time series of standard deviations from each region were then normalized to the 2003 values. To evaluate support for biomass being redistributed in warmer years (as a result of movement or other factors), we calculated anomalies with respect to temperature and species densities for each grid cell (de-meaning the time series of each independently). We then calculated the correlation and associated uncertainty between temperature anomalies and density anomalies for each species-–year combination.

Results

Changes in bottom temperature

Our coastwide model of bottom temperature demonstrates differences in the magnitude and variability of sampled temperatures across the Northeast Pacific. Over the past two decades, on average, bottom temperatures in BC were warmer than other regions, and temperatures in the GOA were coolest (Fig 3). Similarly, the aggregate bottom temperature index for the GOA exhibited relatively high variability compared to other regions (Fig 3). As the sampling in each of the three regions is spatially random within strata, differences in mean temperature and the variability of temperature partially reflects differences in bathymetry (e.g., samples in the GOA were generally taken in depths shallower than 250 m, while approximately one third of samples in COW waters were deeper than 500 m, S3 Fig).

Sensitivity of groundfish to changes in temperature

We found strong support for the temperature and depth effects on species' densities to vary spatially (27 of 30 species, S3 Table). For the majority of species in our analysis, the marginal effects of temperature supported a concave relationship between density and temperature

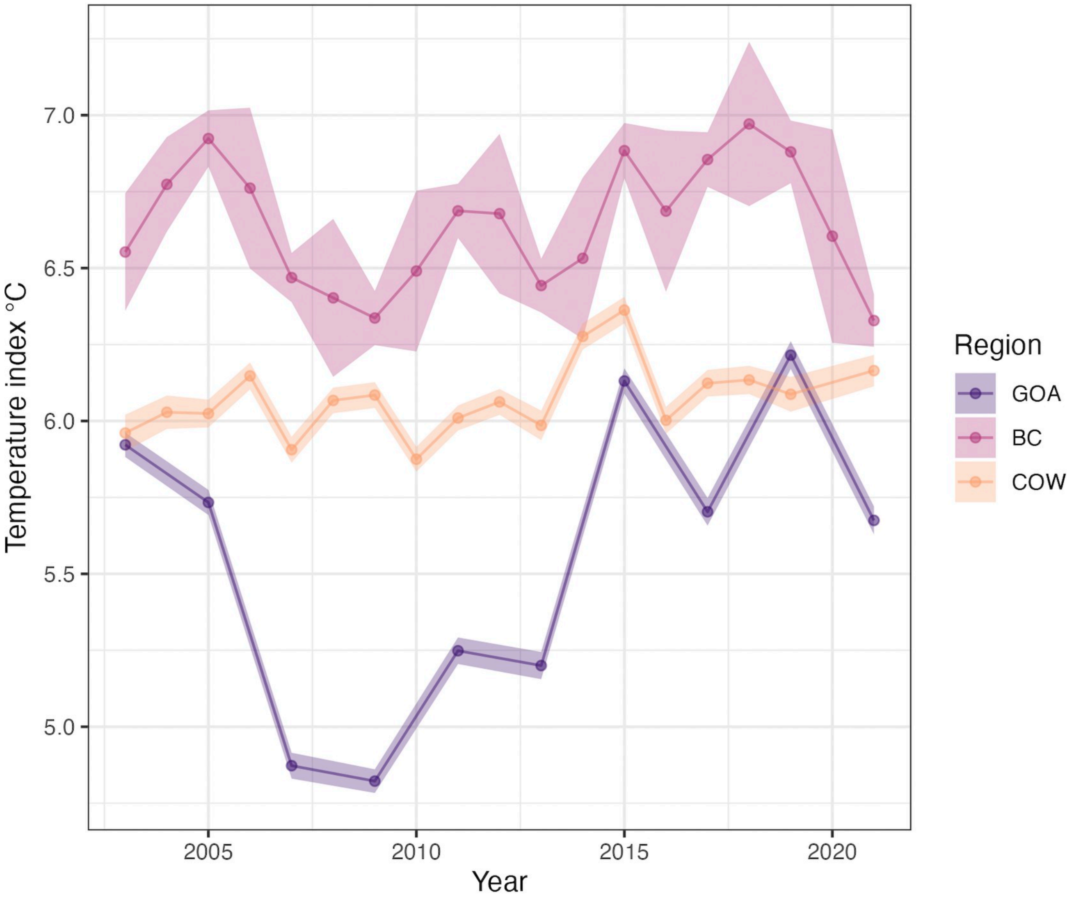

Fig 3. Estimated annual bottom temperature index from each of the regions (Gulf of Alaska, GOA; British Columbia, BC; California-Oregon-Washington, COW) in our analysis (projected to July 1). Points and solid lines represent means; ribbons represent 95% confidence intervals. Similar indices by depth bin are given in S3 Fig.

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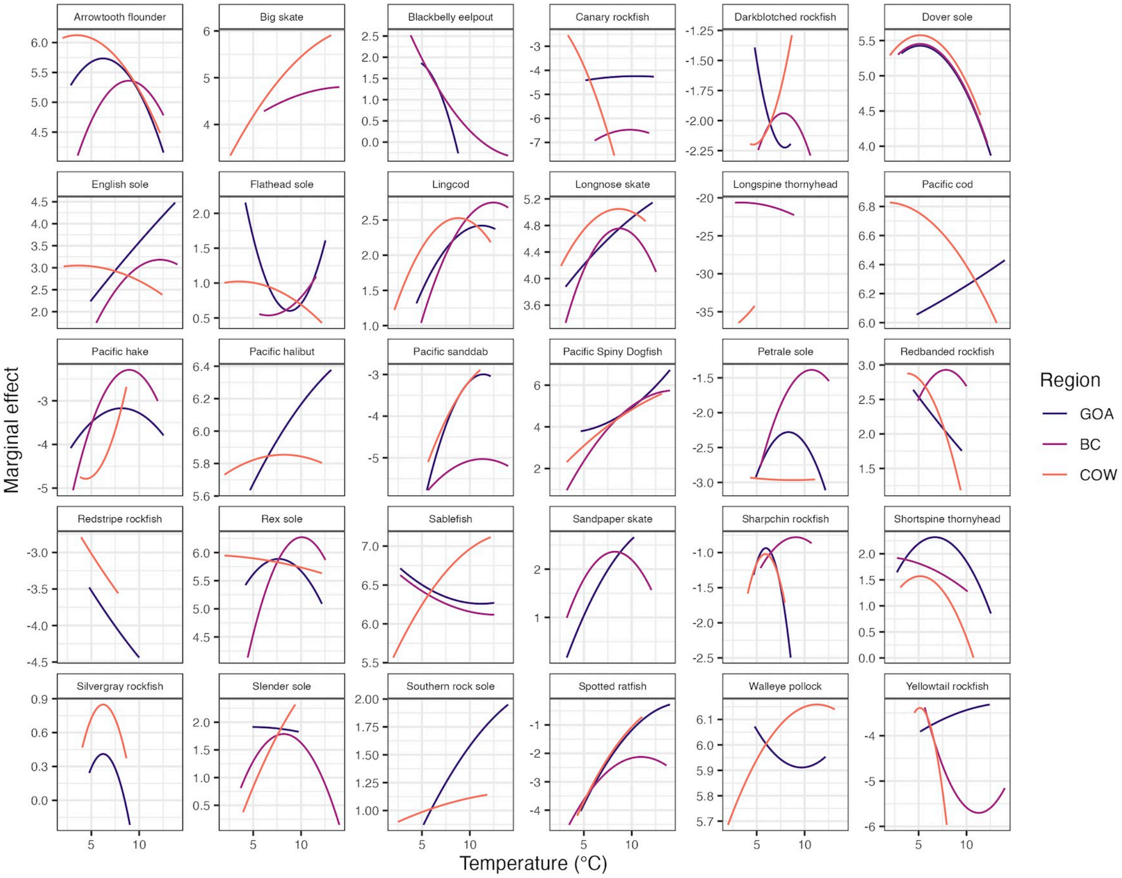

Fig 4. Estimated conditional effects of temperature, by region, for each of the 30 species in our analysis. Marginal effects are not shown for species–region combinations that lack enough data to be included in our models (S1 Table). For some species (Dover sole, etc.) the most supported model does not include region-specific temperature effects, and a similar curve is applied to all regions (slight differences remain because of small differences in the spatial fields between regions). For each species-region combination, the marginal temperature effect is only shown over the range of empirical data (temperatures where the species is present). All other variables (spatial random effects, depth) are held at 0.

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(Fig 4; exceptions included blackbelly eelpout and yellowtail rockfish). The marginal effects of temperature in our SDMs do not support consistent temperature-density relationships among regions, and do not support consistent differences across regions (such as stronger temperature gradients at lower latitudes).

Model based estimates of thermal niches

The estimated thermal niches for the species in our analysis appear to be species specific—depending on depth patterns, for example—but not associating with other identifying features (Fig 5 and S4 Fig). We found that species inhabiting southern areas of the California Current region, and those associated with shallow habitats, had the warmest thermal niches (e.g., rockfishes, big skate, lingcod; Fig 5; S5 Fig) while species found at deeper depths had the coolest thermal niches (e.g., sablefish; Fig 5). Seven species had estimated niches whose mean temperatures indicated significant change through time; these included Walleye pollock (1.33˚C / decade), sharpchin rockfish (0.37˚C / decade), Pacific hake (0.27˚C / decade), sablefish (0.20˚C / decade), longnose skate (0.15˚C / decade), Pacific ocean perch (0.14˚C / decade), and spotted ratfish (-0.14˚C / decade). Across regions, we found the highest associations between bottom temperature and estimated niche midpoints to occur in the Gulf of Alaska (S4 Fig).

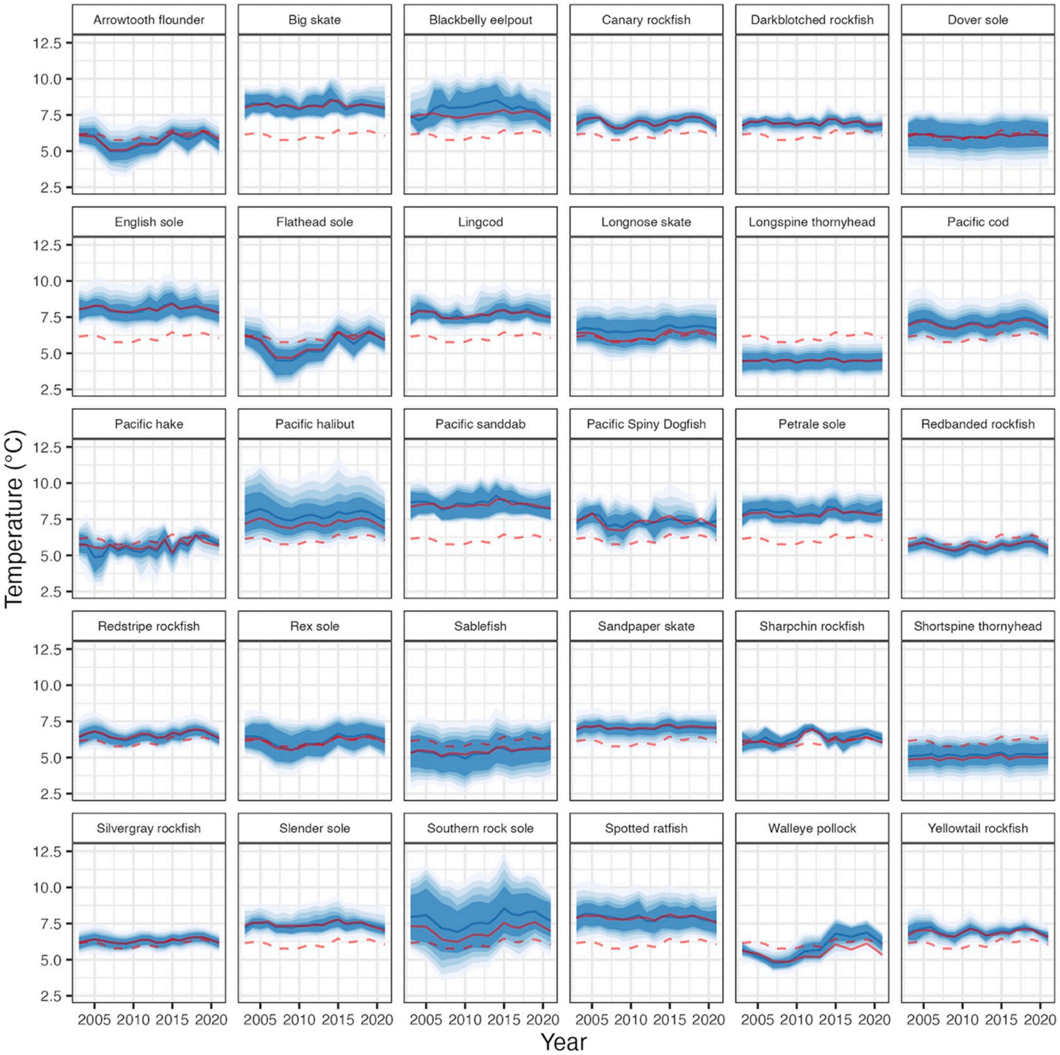

Fig 5. Estimated coastwide, realized thermal niches for 30 species. Dark blue lines indicate mean estimates and ribbons represent 50%, 60%, 70%, 80%, and 90% predictive intervals. Red solid lines represent the species-specific empirical mean temperature in the core range (where 95% of the density was found over the entire time period) while red dashed lines represent the average temperature across the three regions in our analysis and are the same across plots.

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Changes in thermal niche widths in response to warming

Our regression model relating changing thermal niche widths to changing temperatures estimated a near-zero global slope (-0.02, 95% CIs = -0.25, 0.22) but with considerable species-specific variation around that (Fig 6). Species whose niches were estimated to narrow with increases in temperature included Pacific spiny dogfish, arrowtooth flounder, canary rockfish, three species of sole, and lingcod (Fig 6). In contrast, the thermal niche widths of halibut, sablefish, and yellowtail rockfish were estimated to broaden with increasing temperature suggesting that an increase in temperature is associated with increases in the variability of thermal environments these species are found in.

Across the three regions in our study, bottom temperatures in British Columbia exhibited the largest trend in spatial variability (declining variability, indicating more homogeneous conditions within the survey area; S6 Fig), though these trends were generally small in

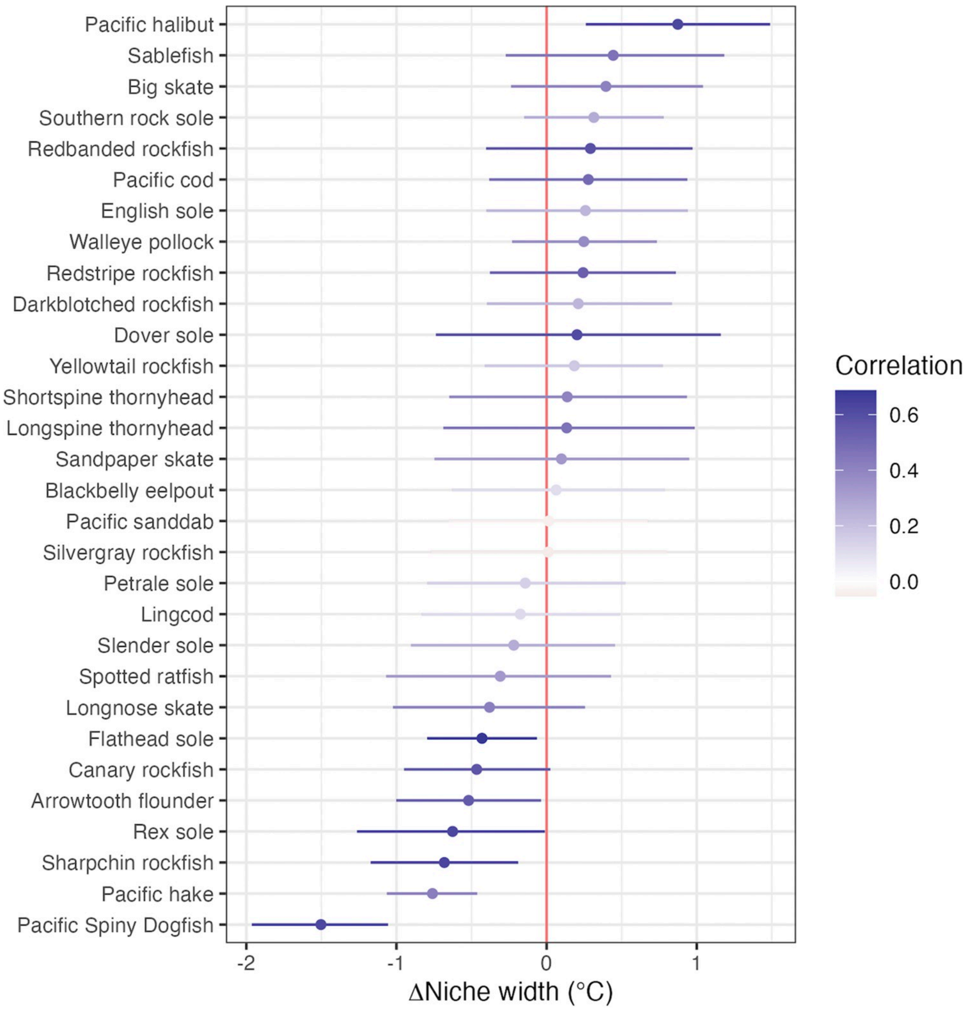

Fig 6. Estimated change in the thermal niche range (difference between the 90% and 10% intervals, with units in degrees Celsius) of 30 species resulting from a change in 1 degree of temperature. Points represent the posterior means, horizontal lines represent the 95% credible intervals, and colors correspond to the correlation between observed and predicted changes in niche widths for each species. The horizontal red line at zero represents no change.

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magnitude. There appeared to be little evidence of the redistribution of biomass from warmer to cooler spatial regions (S7 Fig), though several species had consistent negative relationships between density and warming (longspine thornyhead, Pacific cod, silvergrey rockfish). In contrast, Pacific spiny dogfish and longnose skate demonstrated positive correlations with temperature (higher density in warmer areas).

Discussion

The effects of climate change and warming oceans have been evident in a wide range of species around the world; these effects include shifts in distribution and changes in abundance [47], recruitment [48], metabolism [49], and reproduction or growth (including phenology; [50, 51]). As the effects of warming conditions are expected to vary among species and over space and time, the thermal niches that species inhabit are expected to shift in direction or expand/contract in response to warming conditions [7, 9, 42, 52]. Understanding the sensitivities of species to change and how well species are able to track changes in the environment is critical for sustainably managing fisheries, prioritizing resources for future data collection and protecting species at risk [53]. While previous approaches in the Northeast Pacific have used more qualitative approaches to prioritize climate vulnerability [54], our modeling represents a powerful quantitative approach using *in situ* measurements from fishery-independent observations across a large continuous geographic area.

Using three long-running fishery-independent datasets collected across the shelf of the Northeast Pacific, we applied novel spatiotemporal modeling techniques to (1) develop coastwide models relating species densities to depth and temperature, and (2) use predictions from SDMs to generate dynamic estimates of species realized thermal niches. Our results highlight a spatial contrast between the cooler and shallower waters of Alaska (where temperatures on average are more variable) with the warmer and deeper waters off the West Coast of the USA (Fig 3 and S3 Fig); for species occupying a wide range of depths (e.g., sablefish), deeper waters with less variable temperatures may offer a refuge as future temperatures increase at other depths and in other regions, provided that other conditions in deep waters along the West Coast remain ecologically suitable. Though historical variability may not be indicative of future change, multi-decadal scale forecasts suggest that over the next 75 years, sablefish and other groundfishes will shift to deeper waters in the California Current, reducing their availability to fisheries [55]. These projected shifts may not change the niche width for species like sablefish that do not have additional habitat requirements, but for structure-associated species such as rockfish that typically found near boulders and rock formations, niche widths may narrow since such structure is less common farther from shore. Several ecological hypotheses, including the climate variability hypothesis and Rapoport's Rule, have been proposed to suggest why the environmental niches of species inhabiting higher latitudes are wider than those inhabiting tropical regions [56]. Results from our study do not support strong latitudinal gradients across regions, and these findings complement recent physiology—distribution models, which have also contradicted these hypotheses [57].

Several species in the Northeast Pacific groundfish community indicated either directional change in thermal niches or a narrowing of the niche width in response to changing conditions. Our analysis provided evidence of warming thermal niches for two pelagic species (walleye pollock in Alaska, Pacific hake in BC/COW, Fig 4) and several demersal species (including sablefish and Pacific Ocean perch)–however our analysis did not support a narrowing of niche widths in response to temperature for these species. Species whose niche widths did appear to narrow over time in association with warming included Pacific spiny dogfish, canary rockfish, and arrowtooth flounder (Fig 5). As there have not been large redistributions of biomass for most species across survey regions over the last 20 years, these directional changes in niches and narrowing of niches in response to warming are more likely driven by local relationships between temperature and density (within survey regions). Using arrowtooth flounder and walleye pollock as examples, the increased warming of the thermal niches for these species since the mid-2000s (Fig 5) is largely driven by the directional change in temperatures in the Gulf of Alaska over this period, where the majority of biomass for these species is concentrated (Fig 3 and S5 Fig). These distinctions between species tracking climate with a constant or broadening niche width and species whose niche width is narrowing can help define climate winners and losers. Taken together, changes in spatial distribution and niche width provide insight into how climate is influencing marine community structure.

Interpreting changes in environmental niches

There are a number of potentially confounding processes that make interpreting changes in the direction or variability of environmental niche widths complicated, and changes in the mean or variance may not always be associated with distribution shifts. For example, estimated thermal niches may warm more rapidly if a species' distribution shifts to warmer waters but also if their distribution remains static and surrounding ocean conditions warm at a similar rate. Changes in thermal niches may also occur if the depth distribution of a species shifts or if external pressures that are not spatially random (e.g., fisheries harvests) remove large portions of a population. Similarly, changes in the thermal niche width of a species may not be independent of a change in distribution; niches may narrow as a result of a species' shifting its distribution to a less variable environment but also may occur if temperatures across the range become more uniform. Finally, apparent changes in the direction or width of an environmental niche may also be driven by changes in population age structure; if older individuals are much more resilient to a broader range of environmental conditions than younger individuals, a large cohort pulse through the population may lead to inference that the environmental niche is shifting or contracting over time. Furthermore, many species demonstrate ontogenetic shifts in habitat that could complicate inference (either gradual shifts in depth along seafloor, or vertical distribution changes due to the presence of pelagic and demersal life stages). Future work extending our approach to include multiple stage- or age-classes may help refine our understanding of thermal niches for these species.

Links to management

Our analysis represents an application of statistical models to quantify environmental tolerances to marine fishes throughout their range. Tracking changes in the direction or breadth of thermal niches may be useful for management; these approaches may help in prioritizing species for more frequent stock assessments and identifying species that may be most at risk to future change. In each of the study regions, efforts are already underway to include ecosystem/environmental information within the fisheries management process. For example, Ecological and Socio-Economic Profiles (ESP) have been developed for priority stocks in the Alaska groundfish fishery management plans. The ESP is a standardized methodology and framework to identify critical processes that may impact the survival of a given stock and to integrate this information within the stock assessment process (ESPs, 52). Risk tables, a tool to address ecosystem/environment and population dynamic concerns external to stock assessments and inform harvest recommendations [58], have also been developed for Alaska groundfish stocks and are gaining traction in U.S. west coast fisheries management as well. Changes in species habitat, distribution, and thermal niches are key considerations for ESPs and for assessing current and future risk posed to marine species, fisheries, and fishing communities in the face of a rapidly changing climate.

Additional modeling *to* tease apart intraspecific variation in responses may make *our* outputs *or those from similar analyses* even more valuable for management efforts. Some of the species in our analysis are relatively long lived (lifespans > 50 years) and may have differential vulnerability to changes in the environment across multiple life stages [59–61]. Understanding stage-specific impacts of changes in the environment may help managers better anticipate potential impacts of environmental change; for example, the ability to predict changes in population recruitment may help set precautionary harvest levels and forecast future population sizes in age structured population models. There are also potential linkages to transboundary management. For example, Pacific hake represents a commercially important species whose distribution is both linked to temperature and is highly variable year to year across the USA–Canada border [62]. Similarly, dogfish appear to have narrowing niches in warmer years, indicating a greater coastwide vulnerability to bycatch. Results from our modeling may be combined with global or regional climate models and applied to additional species to identify future hotspots of density or areas of elevated bycatch risk.

Conclusion

Our approach represents an advance in the development of model-based approaches for estimating environmental niches from spatial fishery-independent data. The species distribution models used represent correlative approaches, and a number of additional extensions could be made to increase understanding of the impacts of climate change on marine fishes [63]. One potential advance is to further integrate different kinds of data, such as data from experimental approaches or lab studies [64], to better understand metabolic processes or thresholds. Acknowledging the potential for observed distribution or abundance shifts to be affected by external factors (e.g., fisheries), intrinsic dynamics (e.g., changing age- or sex-structure), as well as impacts of climate, may help disentangle the effects of these various factors on empirical changes in niche distribution. Finally, effects of warming are expected to be non-linear and interact with other abiotic drivers (e.g., oxygen, habitat); our univariate approach focused on temperature may be easily extended to include additional dimensions to explore these more complicated interactions.

Supporting information

S1 Text. Supplemental information describing data collection for surveys in each of the three regions in our analysis, and details describing the construction of spatial meshes used in our estimation models.
(DOCX)

S1 Table. Summary of the 30 species included in our analyses; each is encountered in fishery-independent trawl surveys in at least two of the three Northeast Pacific regions (GOA = Gulf of Alaska, BC = British Columbia, COW = California-Oregon-Washington on the US West Coast).
(XLSX)

S2 Table. Table of candidate models included in our sensitivity analysis of estimating environmental niche. Columns with ':' represent models with estimated interactions between variables. For models with interactions, interaction terms are estimated for both the linear and quadratic coefficients.
(XLSX)

S3 Table. Table of marginal delta-AIC model selection values; smallest values (0, in bold) represent the most parsimonious models. Cells with missing values represent models that did not appear to converge (non-positive-definite Hessian matrix, or large final maximum gradients).
(XLSX)

S1 Fig. Estimated thermal midpoint (and range, as lines) for groundfish species from the Gulf of Alaska (GOA), British Columbia (BC), and California-Oregon-Washington (COW). Estimates are compared with and without a depth effect included, and the red line represents the 1:1 line.
(TIFF)

S2 Fig. Estimates of the range and midpoint of the quadratic effects of bottom temperature on groundfishes in the NE Pacific by region (color; the Gulf of Alaska, GOA; British Columbia, BC; California-Oregon-Washington, COW). All models are fit to unstandardized data, so both axes are in units of degrees Celsius.
(TIFF)

S3 Fig. Estimated temperature index (˚C) from fishery-independent trawl surveys by region (the Gulf of Alaska, GOA; British Columbia, BC; and California-Oregon-Washington, COW), stratified by depth bins. Shaded regions represent 95% confidence intervals, and solid lines (and points) represent index means. The proportion of samples in each depth bin varies across regions. The shallow depth bin represents 87% of the tows in the GOA, 76% of tows in BC, and 48% of tows in COW; the middle 250–500 m depth bin represents 11% of tows in the GOA, 22% of tows in BC, and 20% of tows in COW.
(TIFF)

S4 Fig. Correlations (Corr) between the estimated thermal niche and temperature within the range of each species, stratified by region (the Gulf of Alaska, GOA; British Columbia, BC; and California-Oregon-Washington, COW). This can be calculated as the correlation between the solid red and blue lines in Fig 5.
(TIFF)

S5 Fig. Estimated realized thermal niches by region, for 30 species. Ribbons indicate 80% predictive intervals (colored by region) and solid lines represent the mean. Regions include the Gulf of Alaska (GOA), British Columbia (BC), and California-Oregon-Washington (COW).
(TIFF)

S6 Fig. Spatial standard deviation of predicted gridded bottom temperature data for each of the three regions in our analysis (GOA = Gulf of Alaska, BC = British Columbia, COW = California—Oregon—Washington states). The standard deviation time series across all cells in a region is represented (normalized by the estimate for that time series in 2003, so that all series start at 1). The dark grey line represents the spatial standard deviation across the entire survey domain (for years when survey data were collected in all regions).
(TIFF)

S7 Fig. Estimated correlations between de-meaned gridded predictions of temperature and de-meaned gridded predictions of species densities (95% CIs are shown with error bars). Positive correlations indicate species-year combinations where warmer cells are associated with higher densities; negative correlations indicate species-year combinations where density declines as temperature increases spatially.
(TIFF)

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