Dynamic range models improve the near-term forecast for a marine species on the move

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Abstract

Population dynamic models are widely used to predict demography. However, they have rarely been extended to biogeographical applications despite widespread calls to do so. We developed a process-based dynamic range model (DRM) that estimated demographic rates and the effects of the environment on demographic rates to forecast species range shifts in response to temperature change. As a proof of concept, we fitted DRMs to historical observations of summer flounder (*Paralichthys dentatus*), a fish species in the Northwest Atlantic, and evaluated model skill at retrospective forecasting. The best DRMs outperformed a statistical species distribution model and a persistence forecast at predicting biogeographical dynamics across a decade. The DRM approach is general and can be applied to a wide range of species with historical observations across space and time. By explicitly modeling demographic processes and their relationship to climate, DRMs promise to substantially advance prediction of species on the move.

Introduction

Prediction has become a central goal of ecology (Mouquet et al., 2015). Predictive ecology often seeks to forecast human impacts on ecosystems. It supports biodiversity conservation, natural resource management, climate change mitigation and adaptation, and other applications (Urban et al., 2016). Near-term forecasting is a particularly pressing need so that the timescale of ecological information aligns with the often-short timescale of environmental decision-making (Dietze et al., 2018).

Species distributions have been a major emphasis of predictive ecology, particularly in the context of climate change (Pearson & Dawson, 2003). Species are shifting their ranges in response to climate change (Parmesan & Yohe, 2003), with cascading effects on communities, ecosystems, ecosystem services, and human welfare and well-being (Pecl et al., 2017). Early species distribution models (SDMs) projected species ranges and range shifts using correlations between species' presence (or sometimes abundance) and environmental variables (Elith & Leathwick, 2009). However, observed range shifts have been highly individualistic and are not well predicted by simple environmental variables (Davis et al., 1998; Rubenstein et al., 2023). SDMs have been critiqued in the context of near-term forecasting because they assume species are in equilibrium with the environment, may be trained on data that does not resemble future climates, and have demonstrated limited forecast skill to date (Jarnevich et al., 2015; Lee-Yaw et al., 2022). New approaches (e.g., hybrid and ensemble SDMs) are addressing some of these shortcomings, but still using fundamentally correlative approaches that do not explicitly model ecological mechanisms (Brodie et al., 2022; Ehrlén & Morris, 2015; Kearney & Porter, 2009; Zurell, 2017).

Mechanistic or "process-based" models are often presented as a way forward in forecasting range shifts and for predictive ecology in general (Dietze et al., 2018; Urban et al., 2016). These models can estimate assumed causal relationships, predict effects using those estimates, provide insight into fundamental ecological mechanisms, estimate parameters of interest, falsify ecological hypotheses, and incorporate processes over varying spatial and temporal scales (Cabral et al., 2017; Evans et al., 2016). Another advantage of mechanistic models is that (if implemented in a

hierarchical framework) they can model the underlying ecological processes separately from the data collection process, facilitating more accurate parameter estimation and error partitioning (Laubmeier et al., 2020). These are rare in biogeography, however, partly due to the heightened difficulty of parameter estimation and scale when mechanistic ecological models (e.g., population dynamic models) are made spatial (Briscoe et al., 2019).

One promising class of mechanistic models for range forecasting is dynamic range models (DRMs): spatially explicit population dynamic models that estimate demographic rates as a function of the environment (Pagel & Schurr, 2012). DRMs estimate key parameters from data on species' occurrences and abundances and can incorporate processes at multiple spatial and temporal scales, making them flexible tools that may be applied to a broad suite of ecological questions. However, this flexibility also makes them reliant on the availability of large datasets through time and space. Indeed, DRMs have mainly been fitted to simulated data for this reason (Zurell et al., 2016). DRMs have yielded useful results when applied to real data for parameter inference (Le Squin et al., 2021; Osada et al., 2019). However, DRMs have not been operationalized for range forecasting of real species—the main purpose for which they were designed (Briscoe et al., 2019; Pagel & Schurr, 2012).

An ideal system in which to operationalize DRMs for range forecasting is one where species have already shifted their ranges, where large-scale biodiversity surveys have been operating for some time, and where a strong theoretical understanding exists of the underlying population dynamics and how they relate to the environment. One such system is temperate marine continental shelf ecosystems. Range shifts have been particularly rapid and widespread in these systems because there are relatively few barriers to dispersal, species live close to their thermal limits, and spatial gradients in temperature are weaker in the oceans than they are on land (Pinsky et al., 2020). Marine systems are also relatively data-rich: we have records of historical fishing mortality, insights into the population dynamics of harvested marine species, and large-scale, long-term monitoring programs that have conducted scientific marine surveys for many decades (Maureaud et al., 2023).

Here, we built DRMs—mechanistic models that explicitly model demographic processes from

physiological to metapopulation scales—to forecast range dynamics in response to climate variability and change using more than four decades of biogeographical data. We implemented these DRMs as hierarchical Bayesian models fitted to historical data from 1972-2006 on summer flounder (*Paralichthys dentatus*), an important commercial and recreational fishery species on the east coast of the US. Harvest and management of summer flounder have been controversial in this region for decades (Terceiro, 2011), even before recent evidence that the stock has been shifting northward (Perretti & Thorson, 2019); thus, understanding patterns and trends in this species' spatiotemporal abundance in light of warming temperatures is also a priority for regional fishery managers and stakeholders. We then evaluated DRM performance with a retrospective forecast from 2007-2016. We modeled the data collection process separately from the underlying ecological dynamics and quantified both process and measurement error. We designed multiple DRMs representing different hypotheses about the underlying ecological processes; this allowed us to explore which vital rates were most strongly affected by changing temperatures and the value of incorporating additional ecological complexity (Briscoe et al., 2019; Zurell et al., 2016). Specifically, we compared DRMs with temperature-dependent recruitment, mortality, or movement. Out-of-sample DRM forecasts were more accurate and less biased than a statistical SDM or a persistence forecast at predicting range centroid and edge positions over a decade of testing.

1 Methods

We aimed to develop a DRM configuration that balanced broad applicability across species and ecosystems with relevance to our focal species. The DRM simulated age-structured, discrete-time population dynamics that are generally applicable to many species. For summer flounder, we then grouped the ages into three life stages (recruits, juveniles, and adults) to capture key ontogenetic differences in its life history (see Section 1.1.1) without estimating a large number of age-specific parameters for this relatively long-lived species. The number of stages and the relationship between age and stage structure could easily be changed in future applications of the DRM to other taxa and systems.

We discretized the spatial domain of the DRM into 10 habitat patches of 1° latitude along the

coastline (Fig. 2) such that each patch was adjacent to one or two neighboring patches (Fig. 1). We made this choice to introduce sufficient spatial structure that the model could reproduce changes in the species' range while not trying to fully resolve dispersal at such high resolutions over space and time that the model would be computationally intractable or contain non-identifiable parameters. We did not attempt to tailor the patch structure to summer flounder-specific biogeographic details and instead chose a generic spatial structure such as would be required for most species lacking such information. We also note that nothing about the DRM requires patches to be adjacent, and future applications of the DRM could add more complex patch structures and dispersal matrices to represent long-distance dispersal, oceanographic currents, or biogeographic breaks (Pappalardo et al., 2015; Watson et al., 2010). Summer flounder larvae disperse widely and without clear directionality despite prevailing southward ocean currents in the region (Hoey & Pinsky, 2018; Hoey et al., 2020) and adults are relatively mobile (Lux & Nichy, 1981). We therefore assumed that recruitment was a global process that did not vary over space (see Equation (1)) unless temperature effects were introduced (see Section 1.1.2); that juveniles could not move; and that adults moved between adjacent patches (see Equation (5)). These assumptions reflect a common scenario for marine animals: a well-mixed regional larval pool, low-mobility juveniles, and highly mobile adults. Each of these assumptions can be easily modified in future DRM implementations, including by adapting Equation (1) to estimate patch-specific recruitment or density dependence (e.g., Pagel & Schurr, 2012), or to allow movement at different ages.

Model parameters were estimated by fitting this process-based model to observations of species abundance density across space and time. We implemented a base model without temperature-dependent demographic rates and three models with temperature-dependent recruitment, mortality, or movement. We denote vectors, matrices, and arrays in bold. We used a hierarchical Bayesian approach to model observed numerical densities of all individuals regardless of age (**D**) as a function of the modeled latent age-structured population density ($N_{p,a,t}$) for each patch (p), age class (a), and time step (t). In our implementation, the units of both a and t were in years, i.e., one time step was one year. We incorporated observed presence (**P**) to help account for zero-density patches. Our methodology comprises a process model, which explicitly

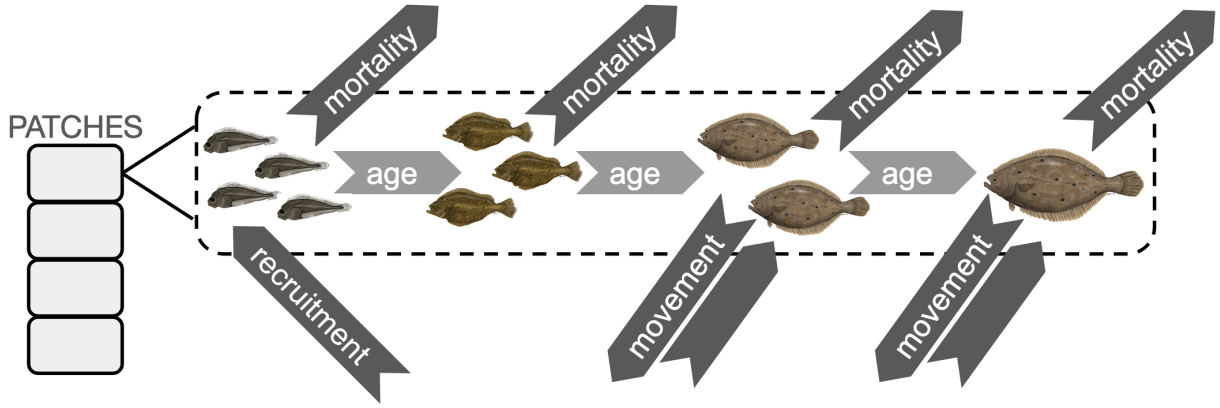

Figure 1: Schematic of the patch structure and temperature-dependent processes in the DRM design highlighting dynamics within an example patch. All patches contained distinct age classes and experienced stochastic recruitment. The three processes for which a temperature effect could be implemented are shown as dark grey arrows. Temperature-dependent recruitment affected the production of recruits by adults; temperature-dependent mortality affected all age classes; and temperature-dependent movement affected the dispersal of adults between adjacent patches.

models the underlying population dynamics, and an observation model, which relates these dynamics to observed data. We first describe the structure of the process model and its alternative configurations, followed by the observation model, which remained consistent across all process model configurations.

1.1 Process models

1.1.1 Base model

The base process model included age structure, adult dispersal, stochastic recruitment, and annual mortality for fifteen ages to match summer flounder life history in the northeast U.S. Application to shorter- or longer-lived organisms would consider fewer or additional age classes. The population dynamics driving $N_{p,a,t}$ were as follows. Recruitment (i.e., production of age 1 individuals) in each year and patch was calculated as a stochastic process (Johnson et al., 2016) around a long-term average:

$$N_{p,a=1,t} = \mu \times e^{r_t - \frac{\sigma^2_{\text{Proc}}}{2}} \quad (1)$$

where μ is the average density of recruitment per patch across all space and time, r_t represents recruitment stochasticity (through a first-order autoregressive process), and σ_{proc} is its conditional standard deviation. Equation (1) implies that recruitment in a given year is the same for all patches. Fertilized summer flounder larvae spend approximately a month in a pelagic phase during which they are broadly transported by currents (Keefe & Able, 1993). The species is considered to have a single, well-mixed population in the study region and has little relationship between adult biomass and annual recruitment (NEFSC, 2019), which motivated our representation of recruitment as a region-wide, density-independent process. Substantial larval dispersal and interannual variation in recruitment is common across marine fishes and invertebrates (Houde, 2008). Application to other kinds of species could modify this equation to instead consider local density dependence or eliminate the stochastic component (e.g., Pagel & Schurr, 2012).

The autoregressive term r_t was defined as

$$r_t = \alpha r_{t-1} + \sigma_{\text{proc}} z_t, \tag{2}$$

where z_t is an uncorrelated standard Normal error term and α is the temporal autocorrelation, namely the correlation between r_t and r_{t-1}.

We modeled adults and juveniles (the latter are older than recruits but not yet mobile or reproductive) separately. Summer flounder reach maturity around two years of age (NEFSC, 2019), so in our implementation, age class one represented recruits, age class two represented juveniles, and age classes three and older represented adults. Juvenile age classes were modeled as the fraction of the younger age class that survived to the following year in a given patch:

$$N_{p,a=2,t} = N_{p,a-1,t-1} \times s_{a-1,t-1} \tag{3}$$

where s represents annual survival fraction, which was constant across patches in the base model. Because summer flounder experience fishing mortality, we combined age- and year-specific fishing mortality $f_{a,t}$ with natural mortality m to calculate the annual survival fraction:

$$s_{a,t} = e^{-(f_{a,t}+m)}. \tag{4}$$

Both m and $f_{a,t}$ are instantaneous rates, so they can exceed 1. The fishing mortality term would be removed for species that are not harvested by humans. More complicated applications could consider adding predator or other sources of mortality in this equation.

Adult summer flounder are highly mobile predators that migrate offshore seasonally, so adults in the model differed from juveniles in that they could move among adjacent patches. In this base model, we calculated age-structured population density for adults with an isotropic dispersal fraction δ among adjacent patches:

$$\begin{aligned} N_{p,a,t} = (1-2\delta)N_{p,a-1,t-1} \times s_{a-1,t-1} \\ +\delta N_{p-1,a-1,t-1} \times s_{a-1,t-1} \\ +\delta N_{p+1,a-1,t-1} \times s_{a-1,t-1}, \text{ for } a > 2. \end{aligned} \tag{5}$$

Edges were treated as reflective for adults so that they did not disperse beyond the model domain, and dispersal rates were adjusted accordingly at the edges. Therefore, we specified $N_{p,a,t} = (1-\delta)N_{p,a-1,t-1} \times s_{a-1,t-1} + \delta N_{p-1,a-1,t-1} \times s_{a-1,t-1}$ in the northern-most patch, and $N_{p,a,t} = (1-\delta)N_{p,a-1,t-1} \times s_{a-1,t-1} + \delta N_{p+1,a-1,t-1} \times s_{a-1,t-1}$ in the southern-most patch, for $a > 2$. This assumption matches the active movement choices that adult summer flounder make. For species with dispersal at different ages or in different fashions, these decisions could be easily adapted.

1.1.2 Temperature effects

To incorporate the effects of temperature on demographic processes—and, consequently, on species distributions over space and time—we designed a series of alternative models for temperature dependence. These demographic impacts are not known for summer flounder, just as they remain unknown for most species on Earth, and so the DRM inferred which parameters best matched the spatiotemporal patterns of species abundance. These models represented different hypotheses describing how temperature may affect population dynamics. For example, adults

might move to track their preferred thermal conditions, and indeed, marine species ranges are highly correlated with their physiological thermal tolerances (Sunday et al., 2012). Adult movements in summer flounder are also seasonal (Packer et al., 1999), which could plausibly be linked to temperature. In addition, the distribution of recruits has shifted north faster than adults for some species, suggesting that temperature might instead affect recruitment (Perretti & Thorson, 2019). Lab studies and historical population dynamics in summer flounder are consistent with temperature effects on natural mortality (O'Leary et al., 2019; Packer et al., 1999), and temperature effects on mortality are quite general across species (Munch & Salinas, 2009). To explore these three hypotheses in the context of range shifts, we implemented alternative models that included temperature effects on (1) recruitment, (2) mortality, or (3) adult movement. To avoid parameter identifiability issues, we tested these temperature effects in separate models while acknowledging that all three could operate simultaneously to some extent. Climate effects on reproduction, survival, and movement are thought to be widespread (Scheffers et al., 2016), and so we expect that these models will be widely useful across other species as well.

In each case, we calculated a relative index of temperature suitability for each patch and year, $\mathbf{I}$. $\mathbf{I}$ was maximized at an optimal temperature, τ, which was estimated as part of model fitting. Although it always represented an optimal temperature in °C, the biological interpretation of τ depended on the model structure. In the recruitment model, τ was the temperature at which recruitment was highest. In the mortality model, it represented the temperature at which natural mortality was at its baseline level. In the movement model, τ represented the temperature toward which the greatest proportion of fish migrated from an adjacent patch. In all cases, $\mathbf{I}$ was calculated as a Gaussian function such that, as the actual temperature $\mathbf{T}$ deviated from τ, the temperature suitability index $\mathbf{I}$ declined at a rate inversely proportional to a width parameter ω that was also estimated,

$$I_{p,t} = e^{\left(-0.5(\frac{T_{p,t}-\tau}{\omega})^2\right)}. \quad (6)$$

The temperature-dependent recruitment model linked patch-specific temperature to recruitment by using $\mathbf{I}$ to rescale $N_{p,a=1,t}$, thus modifying Equation (1):

$$N_{p,a=1,t} = \mu \times e^{r_t - \frac{\sigma^2_{\text{proc}}}{2}} \times I_{p,t}. \tag{7}$$

In this case, μ becomes the average density of recruits under optimal environmental conditions, that is, when $T = \tau$. For application to other species, researchers could consider environmental factors other than temperature, or, where relevant, modify the equation so that recruitment is influenced by environmental conditions in a distant spawning or mating location, rather than where the offspring recruit.

To model temperature-dependent mortality, we modified Equation (4) to include the temperature effect **I**, which acted by reducing survival when the temperature was not at τ:

$$s_{p,a,t} = e^{-(f_{a,t} + m + \gamma(1 - I_{p,t}))}, \tag{8}$$

where γ scales the excess natural mortality due to temperature. Note that, unlike in Equation (4), s could now vary over p because the temperature effect led to distinct survival across patches. This formulation allowed mortality to increase at low or high temperatures, if such processes helped explain the spatiotemporal abundance data. More generally across species, mortality is often modeled as an increasing exponential function of temperature through a Boltzmann-Arrhenius function (McCoy & Gillooly, 2008).

The movement model required more complexity because we modeled both passive diffusion between patches and taxis—the directed movement by adults in response to environmental gradients. Such movement models are quite general and are widely used across animal ecology (J. R. Potts & Schlägel, 2020; Preisler et al., 2013), though even more complex movement models that consider individual decisions and biophysical interactions are also available (Morales et al., 2010; Swearer et al., 2019). We followed the diffusion-taxis methods in Thorson *et al.* (2021). Specifically, we log-transformed **I** and constructed a p-by-p taxis matrix **X** for each year by subtracting the **I** of adjacent patches and multiplying the difference (i.e., the habitat gradient) by β_{tax}, a parameter that defined how much taxis changed per unit of temperature. A p-by-p diffusion matrix, **Z**, simply included δ for adjacent patches (rescaled so that columns in the matrix

summed to 1 at the end) and zeros elsewhere. We then summed and matrix exponentiated $\mathbf{Z}$ and $\mathbf{X}$ in every year to yield the annual transition matrix $\mathbf{M} = e^{\mathbf{X}+\mathbf{Z}}$ containing annual movement fractions between each patch. Although $\mathbf{X} + \mathbf{Z}$ is only nonzero for adjacent patches (i.e., instantaneous taxis and diffusion only occurs locally), the annual transition matrix $\mathbf{M} = e^{\mathbf{X}+\mathbf{Z}}$ is dense (i.e., annualized movement can connect any two patches). Movement between non-adjacent cells is biologically plausible for mobile animals. Finally, we calculated abundance as

$$\mathbf{n}_{a,t}^T = \mathbf{n}_{a-1,t-1}^T \times s_{a-1,t-1}\mathbf{M}, \text{ for } a > 2 \tag{9}$$

where $\mathbf{n}_{a,t}^T$ is the row-vector of abundance $N_{p,a,t}$ across patches p, and this equation then replaced the previous Eq. 5.

1.2 Observation model

The observation model related the observed densities to the process model. We defined observed presence ($P_{p,t}$) from observed density ($D_{p,t}$) at patch p and time t as

$$P_{p,t} = \begin{cases} 1 & \text{if } D_{p,t} > 0 \\ 0 & \text{if } D_{p,t} = 0. \end{cases} \tag{10}$$

We assumed $P_{p,t}$ and $D_{p,t}$ were distributed as follows

$$P_{p,t} \sim \text{Bernoulli}(\theta_{p,t}) \tag{11}$$

$$(\log(D_{p,t}) \mid P_{p,t} = 1) \sim \mathcal{N}\left(\log(\lambda_{p,t}/\theta_{p,t}) - \frac{\sigma_{\text{obs}}^2}{2}, \sigma_{obs}\right), \tag{12}$$

where $\theta_{p,t}$ is the probability of encountering individuals in patch p and time t, $\mathcal{N}$ indicates a Normal distribution, σ_{obs} is the standard deviation of $\log(D_{p,t})$, and $\lambda_{p,t}$ is the latent density of individuals in each patch expected to be observed by the survey. Note that we divided $\lambda_{p,t}$ by $\theta_{p,t}$ in Equation (12) to ensure that product of encounter probability $\theta_{p,t}$ and expected positive catch $\mathbb{E}[D_{p,t}|P_{p,t} = 1]$ is equal to to predicted density $\lambda_{p,t}$, i.e., $\mathbb{E}[D_{p,t}] = \lambda_{p,t}$.

A logit-link was used to connect the probabilities of encounter $\theta_{p,t}$ to the predicted densities as follows

$$\text{logit}(\theta_{p,t}) = \beta_0 + \beta_1 \log(\lambda_{p,t}), \tag{13}$$

where β_0 and β_1 are slope and intercept parameters controlling how much the probability of the species being encountered increases with the latent density. Our formulation is similar to two-stage (or hurdle) models appropriate for many species observations across space and time that contain large numbers of zeros (J. M. Potts & Elith, 2006).

The ability of the survey (see Section 1.4) to observe summer flounder individuals depended on their size. To relate fish observations to the latent, age-structured densities in the DRM, we converted density-at-age to density-at-length using a length-at-age relationship. This relationship assumed that summer flounder, on average, grow according to a von Bertalanffy curve with log-normal deviations and a constant coefficient of variation of 20%. Using this relationship, we converted density of fish at a given age a to density of fish at length. From there, we assumed that the survey gear had a logistic selectivity curve, with the lengths at 50% and 95% selectivity estimated by the model. This selectivity curve converted the age-structured density of fish in the model ($N_{p,a,t}$) to the expected density of fish caught by the survey ($\lambda_{p,t}$):

$$\lambda_{p,t} = \sum_a \Phi(a) N_{p,a,t} \tag{14}$$

with the function $\Phi(a)$ encoding the probability of sampling an individual of age a. For application to other species or even the same species with other datasets, this part of the model would likely change to reflect different observation processes.

1.3 Model implementation

We wrote the DRM in Stan, a platform for Bayesian modeling (Stan Development Team, 2021), and used "cmdstanr" (Gabry et al., 2024) to produce the results in R (Supp. Tab. 1). We specified weakly informative priors for parameters α, β_0, β_1, σ_{obs}, and δ. We also bounded them to ecologically meaningful values: β_1 was restricted to positive numbers, and δ was restricted

to the interval $[0, 1/3]$.The prior for α was based on the recruitment autocorrelation estimated in previous studies (Johnson et al., 2016; Thorson et al., 2014). We also specified weakly informative priors for additional parameters in temperature-dependent models (Supp. Tab. 2). We specified fishing $f_{a,t}$ and natural mortality rate m as known values and informed priors, respectively (see Section 1.4).

For each model configuration, we obtained samples from the posterior from four parallel chains, each of which ran for 5,000 iterations, including 2,000 warm-up iterations. We considered a model to have converged if less than 5% of the transitions in the sampler after warm-up were reported as divergent. All statistical results from Bayesian models were reported with 95% Highest Posterior Density Intervals (HPDI) using the "coda" package in R (REF).

1.4 Data

To fit and evaluate the DRMs, we used data from National Oceanic and Atmospheric Administration (NOAA) bottom trawl surveys conducted in the northeast US since 1968 (Smith, 2002). These surveys have been conducted with standardized equipment and methods over time, and utilize a stratified random sampling design, making them ideal for climate biogeography applications (Fredston et al., 2021; Fredston-Hermann et al., 2020; Pinsky et al., 2013). We downloaded the 2020 release of OceanAdapt, a data portal that compiled North American bottom trawl survey records (Forrest et al., 2020). The NOAA Northeast survey operates in fall and spring; we used the fall survey that had more records of our focal species. To ensure that the years analyzed were sampled consistently throughout time, we used data from 1972-2016; this interval began when the surveys were standardized (Fredston et al., 2021; Fredston-Hermann et al., 2020; Pinsky et al., 2013) and ended before data gaps caused by recent disruptions to survey funding and operations, including the COVID-19 pandemic. These records encompassed the region from Cape Hatteras in North Carolina to the border between Canada and Maine (Fig. 2), from just north of 35°N to above 44°N.

The sampling unit for the survey is a single "haul", an event during which a fishing net is towed through the ocean for a fixed amount of time. Temperature is measured *in situ* for each

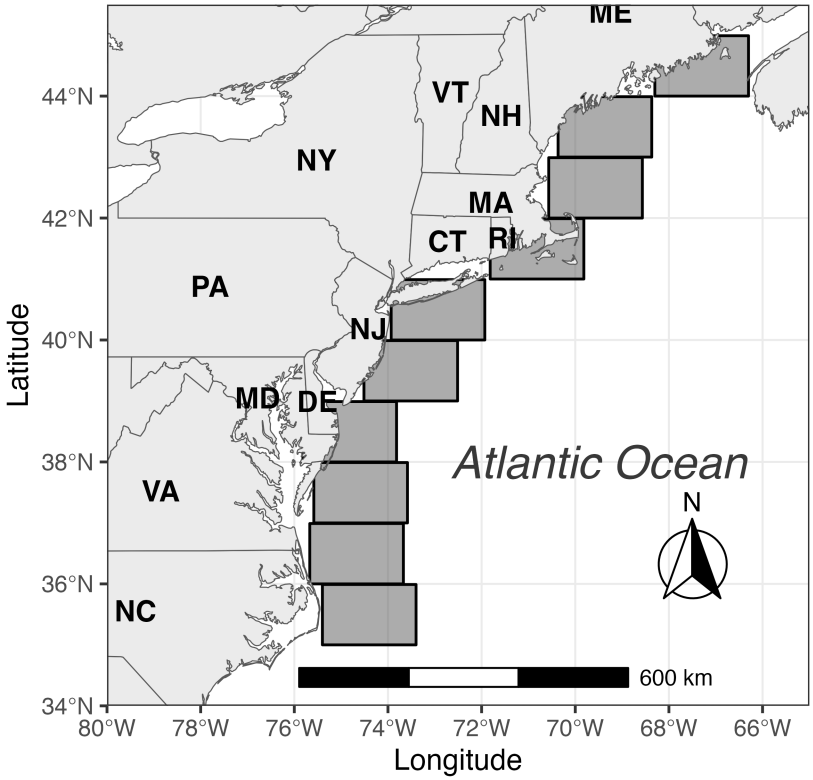

Figure 2: Map of the study region showing the modeled patches as grey boxes. Each patch was 1°latitude high. US states are labeled for reference.

haul at the seafloor. After each haul, scientists on board the survey vessel identify, count, weigh, and measure the catch in the net. We calculated $D_{p,t}$ as the average number of summer flounder per haul in patch p in year t. These observed density values—varying over space and time—were the main data input to the DRM.

We averaged bottom temperature data across hauls in every patch and year. *In situ* sea bottom temperature data was missing for some hauls, including all hauls south of 38°N in 2008. To fill this data gap, we fitted a Bayesian linear regression using Gaussian errors with latitude as a fixed effect, year as a group-level (random) effect with varying intercepts, and all available bottom temperature data as the response variable. We then used this fitted model to predict bottom temperature in patch-year combinations that were missing data.

Summer flounder are intensively fished (Terceiro, 2011), and so we leveraged existing sci-

entific information on their mortality caused by fishing and other factors (NEFSC, 2019). This component of the DRM could be simplified in future applications where (unlike for summer flounder) harvest is not important to population dynamics. Summer flounder have a stock assessment, which is a statistical analysis that integrates many regional surveys of both fish and fisheries catch, plus other information, to estimate fishery catch rates and other information that guides fisheries management (NEFSC, 2019). The assessment estimated instantaneous fishing mortality-at-age $f_{a,t}$, which varied across years t and age-classes a and ranged from 0.009 to 1.983 (NEFSC, 2019). We passed $f_{a,t}$ to the DRM as a parameter known without error. The assessment estimates of f began in 1982, so we imputed the 1982 values for our earliest years of summer flounder data (1972-1981). Based on summer flounder life history, the stock assessment assumed that $m = 0.25$; we used this value as an informative prior to model m in each DRM configuration (Supp. Tab. 2).

1.5 Species distribution model

To compare DRM performance to SDMs widely used in the range shift literature, we fitted a generalized additive model (GAM) SDM (Morley et al., 2018) with the "mgcv" package in R (Wood, 2017). The GAM SDM was a two-stage model; we fitted one GAM to presences and absences in the training data using a logistic regression (i.e., logit-link and Bernoulli family) and a second GAM to log-abundance conditioned on presence, assuming a Gaussian error distribution. Both were single intercept models with a spline on bottom temperature, the sole predictor. Unlike the DRMs, we fitted the GAM to the haul-level data (not aggregated to the patch scale). Bottom temperature records were missing from a number of hauls in 2008 (see Section 1.4). The interpolation method we used to fill these data gaps for the DRMs was not appropriate for the much higher spatial resolution of the GAMs, so we omitted 2008 data from the GAMs.

1.6 Model evaluation and comparison

We used a retrospective forecasting approach to assess model performance. The DRM and SDM were fitted to summer flounder data from 1972-2006 and then simulated for the final decade of

data (2007-2016). The DRM forecast was initialized with the final year of fishing mortality data passed to the model (2006) and then run forward by making draws from the posterior probability distribution of parameters estimated in the model fitting routine. Observed temperature data for 2007-2016 were used. We validated the forecasts against the held-out observations from 2007-2016, which we averaged into patches as we did for the input to the DRM (Section 1.4). The GAM SDM forecast used the bottom temperature records from 2007-2016. We then aggregated GAM predictions to the patch scale the same way we aggregated the raw data passed to the DRM (Section 1.4) to enable forecast comparisons. We also evaluated a persistence forecast, which was a continuation of the observations from the final year of the training interval (2006) into every subsequent year.

Forecast performance metrics included (1) the abundance-weighted latitudinal range center (i.e., range centroid) and (2) the cold and (3) the warm range edge positions. The edge positions were calculated as abundance-weighted 0.05 and 0.95 quantiles of latitude (Fredston et al., 2021; Fredston-Hermann et al., 2020). Note that because our study domain did not encompass the full geographic distribution of the focal species (which is found at lower densities in the southeast US as well), these represented population range metrics, not metrics for the full species range.

For each of these metrics, we calculated the residuals (forecasts minus observations) in each year. We then calculated bias (mean of residuals) and root mean square error (RMSE, square root of the mean of the squared residuals) for each metric. For the DRMs, we calculated the residuals for each of 12,000 posterior draws and then used the mean residual value for each posterior to calculate bias and RMSE.

2 Results

Summer flounder exhibited complex spatiotemporal dynamics during the study period, including a decline in density in the 1980s and an increase beginning in the 1990s (Fig. 3). Its geographic distribution was relatively stable from 1972-1990, then shifted north substantially through 2002 before another period of relative stability through 2016 (Fig. 3). During the northward shift (1990-2002), for example, the centroid shifted from the latitude of Virginia (37.7 °N) to that of

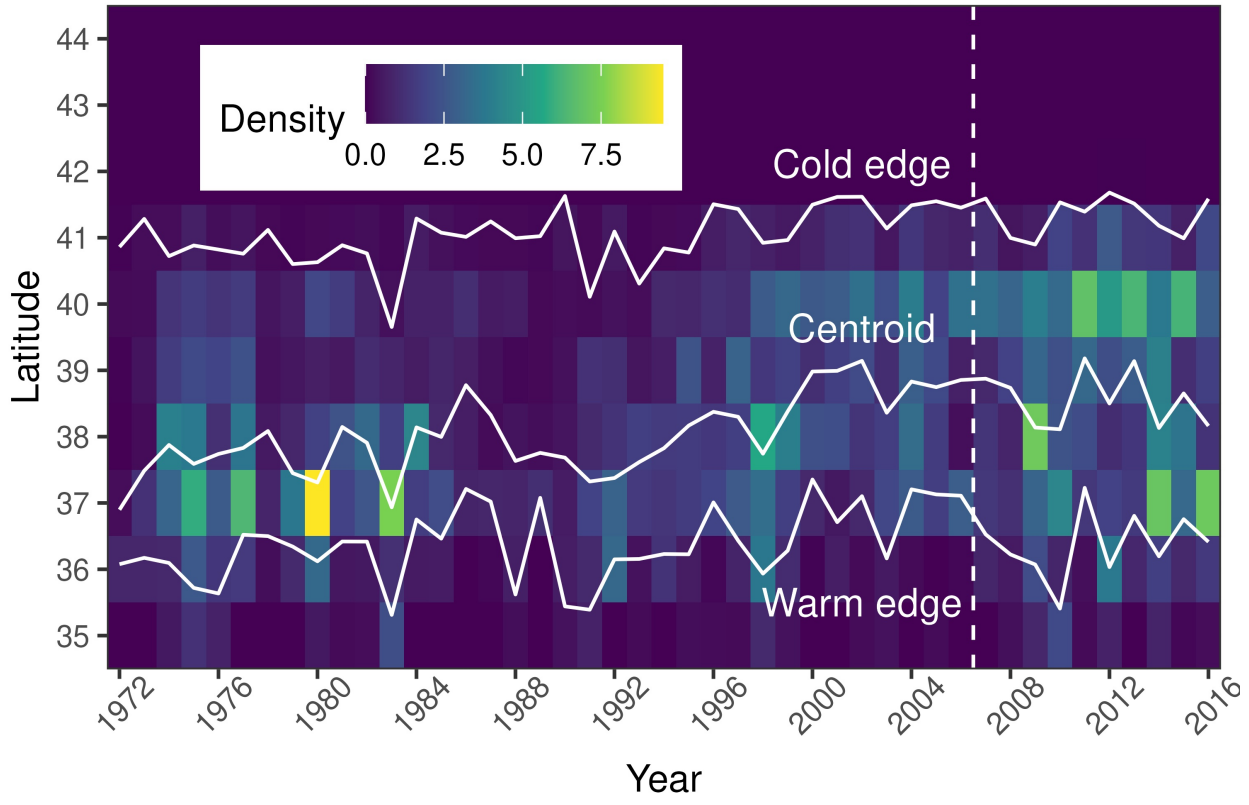

Figure 3: Observed summer flounder dynamics over space and time in the study region from 1972-2016. Cells are color-coded by mean density in the survey, and summary statistics used to evaluate and validate models (the position of the range centroid and warm and cold edges) are plotted.

New Jersey (39.1 °N), approximately 155 km (Fig. 2). These observed shifts occurred primarily during our model training interval. From 2007-2016 (our testing interval), summer flounder did not shift north significantly (Bayesian linear regression of latitude on time; 95% HPDI -0.15 – 0.09, -0.10 – 0.19, and -0.07 – 0.10 for the range centroid, warm edge, and cold edge, respectively; Fig. 3).

The *in situ* sea bottom temperature exhibited warming of 0.04 °C per year across the study region from 1972-2016 (median posterior value from Bayesian linear regression of temperature on year; 95% HPDI 0.04 – 0.05). This trend was spatially and temporally heterogeneous; warming was concentrated in the center of the study domain (Fig. 2) during the training period (Supp. Tab. 3), with a particularly intense period of warming from 1988-2000 (Fig. 4) that aligned with the strong northward shift observed in flounder (Fig. 3). During the testing decade, warming was concentrated in the northern half of the study domain, starting at 40 °N (Fig. 4, Supp. Tab. 4).

Observations were available for 14,025 individual summer flounder caught across 12,203 hauls from 1972-2016. As is common in marine fish surveys, the data were heavily zero-inflated; 81% of these hauls did not catch any summer flounder and 96.5% of hauls caught fewer than ten (Supp. Fig. 1). The number of hauls per year was generally between 225 and 325, although 1978 and 1979 had almost 500 (Supp. Fig. 2).

All four DRM configurations (no temperature effect, or temperature effect on recruitment, mortality, or movement) converged when fit to the data and produced density estimates consistent with observations (Supp. Fig. 3-6). The models generally reproduced the decline in density until 1990 and the increase afterwards, though the null model (no temperature effect) failed to re-create the lower abundances towards the northern and southern range edges and higher abundance in mid-latitudes (Supp. Fig. 3). The DRMs with temperature-dependent demography, and particularly recruitment or mortality, more effectively captured these spatial gradients (Supp. Fig. 4-6). In addition, their parameter estimates differed substantially (Supp. Fig. 7). Temperature-dependent recruitment had an optimum of 14.7 – 14.9 °C with a width of 1.49 – 1.60 °C (95% HPDI; see Eqn. 6), suggesting a narrow range of optimal temperatures for recruit-

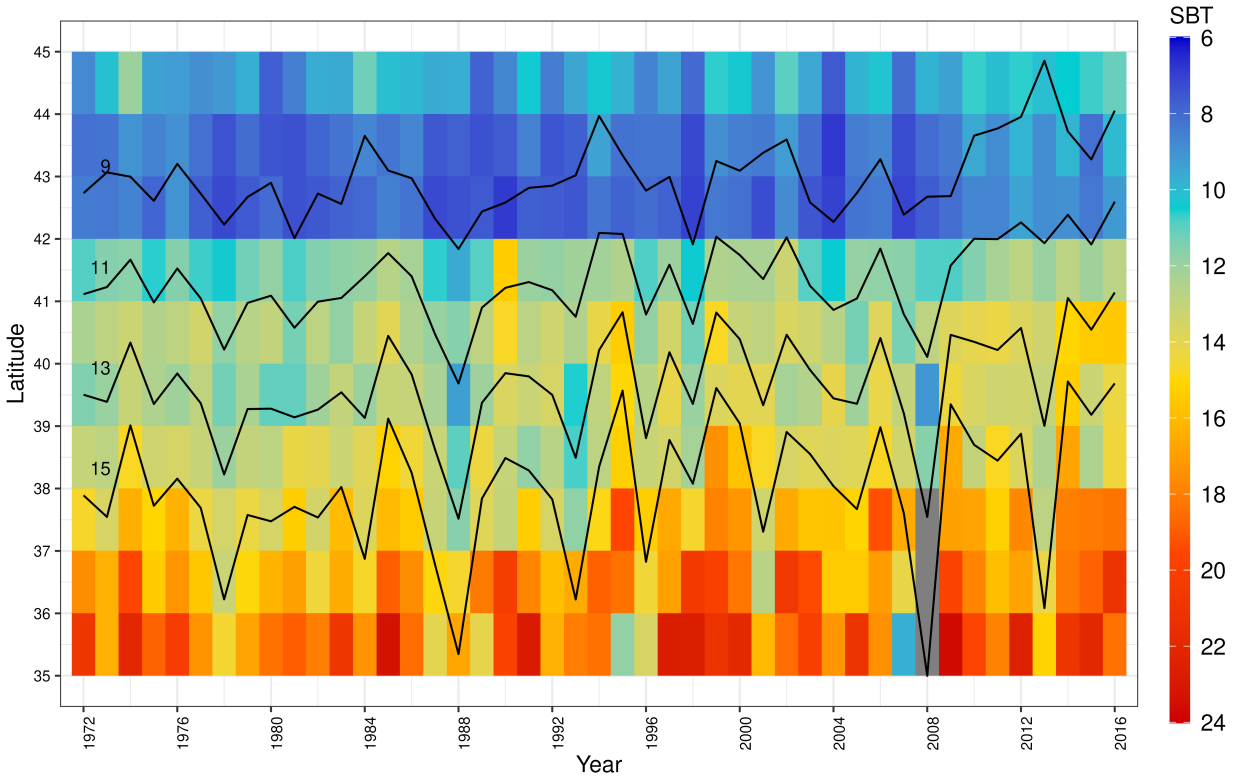

Figure 4: Sea bottom temperatures (SBT) recorded *in situ* by trawl surveys by patch and year, calculated as means of haul-level observations. Grey boxes indicate data gaps. Solid black lines represent isotherms. Their positions were calculated by fitting a Bayesian linear regression with Gaussian errors of temperature on latitude in each year and calculating the median estimated latitudinal position of each degree Celcius isotherm value.

ment of new offspring. Temperature-dependent mortality had a similar optimum (14.7 – 14.9 °C) but a greater width (4.23 – 5.73 °C) that implied substantially less sensitivity of mortality to differences in temperature. By contrast, movement had a higher optimal temperature (16.4 – 20.4 °C) and a narrow width (1.03 – 1.28 °C), suggesting adults moved towards warmer waters than were optimal for recruitment of offspring. The temperature-dependent mortality model and the null model estimated intermediate values for the between-patch diffusion rate (0.03 – 0.17 and 0.06 – 0.21); and the temperature-dependent recruitment model estimated a much lower adult diffusion rate (0.0006 – 0.02).

The temperature-dependent recruitment forecast, the temperature-dependent mortality forecast, and the persistence forecast most often had greater skill (lower RMSE) and less bias out-of-sample than the other models tested (Fig. 5, Supp. Fig. 8). Both of these DRMs notably out-performed the persistence forecast at the warm range edge, where the persistence forecast substantially over-predicted the edge latitude (Fig. 6). The GAM and other two DRM configurations (a temperature effect on movement, or no temperature effect) performed worse across the considered metrics, with less skill and greater bias. For the temperature-dependent recruitment DRM, every observed range metric fell within the 95% HPDI in every year (Fig. 6). By contrast, the GAM over-predicted the range size of summer flounder, estimating the warm edge further south and the cold edge much further north than they were found in the survey (Fig. 6). The observed spatiotemporal distribution of summer flounder in the survey from 2007-2016 was highly concentrated between 37-40°N, which was better captured by the persistence and DRM forecasts (Fig. 3).

3 Discussion

Integrating greater biological process and mechanism into forecasts of species responses to climate change and variation has long been a goal (Pagel & Schurr, 2012; Urban et al., 2016). Here, we showed that dynamic range models with climate-dependent demographic rates outperformed a statistical SDM and a persistence forecast in near-term forecasting of range dynamics during a 10-year interval of environmental variability. These results provided evidence that rates of pop-

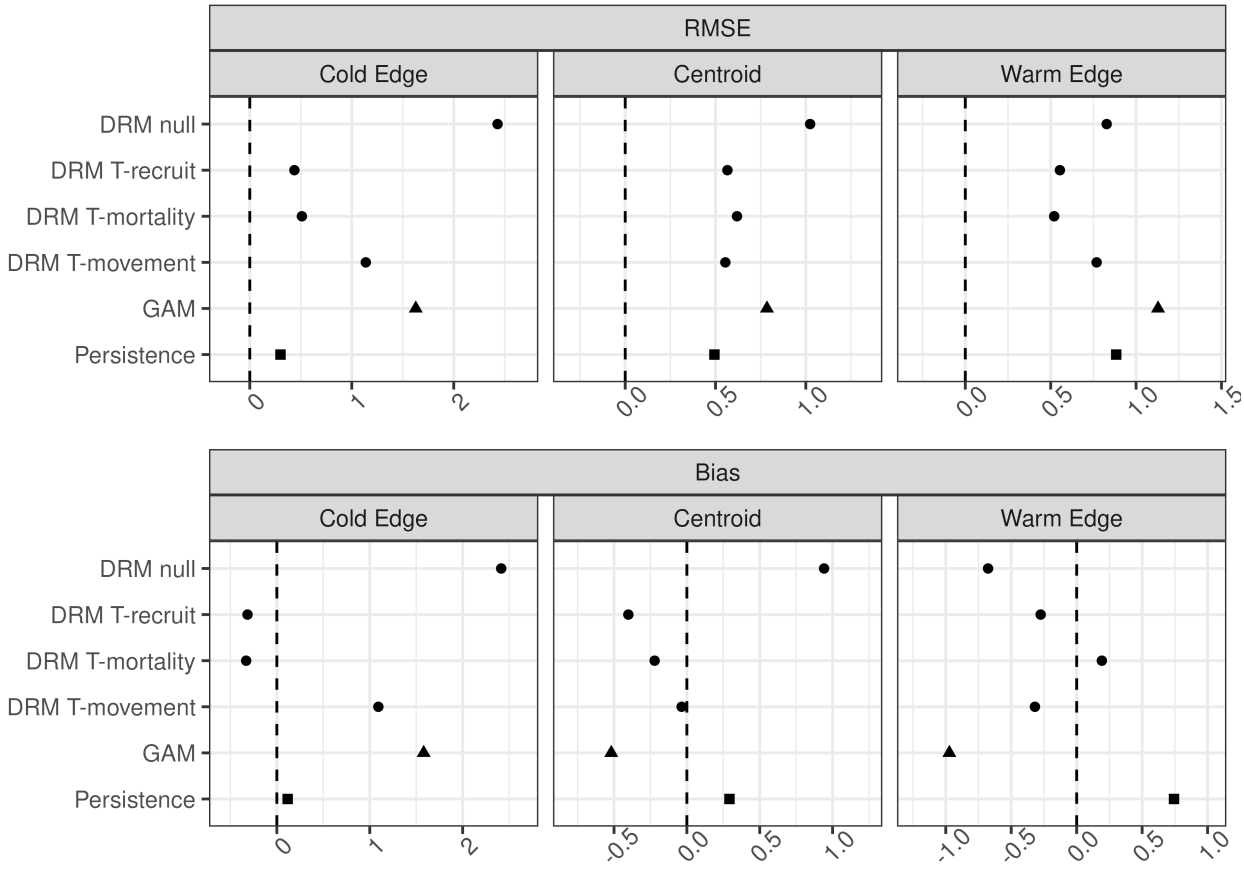

Figure 5: Skill of DRMs, GAM, and a persistence forecast at predicting summer flounder range dynamics out-of-sample from 2007-2016 measured as root mean square error (RMSE) and bias. The DRMs included no temperature effect (null) or a temperature effect on recruitment (T-recruit), mortality (T-mortality), or movement (T-movement). We measured ranged dynamics with three metrics: the warm and cold range edge positions and the centroid (abundance-weighted latitudinal average) every year. RMSE measures how close the predictions were to the observed values; lower RMSE values indicate greater accuracy. Bias measures whether the predictions were consistently too far north (positive bias) or too far south (negative bias); values closer to zero (indicated by the vertical dashed line) indicate less bias. Note that x-axis scales vary by panel.

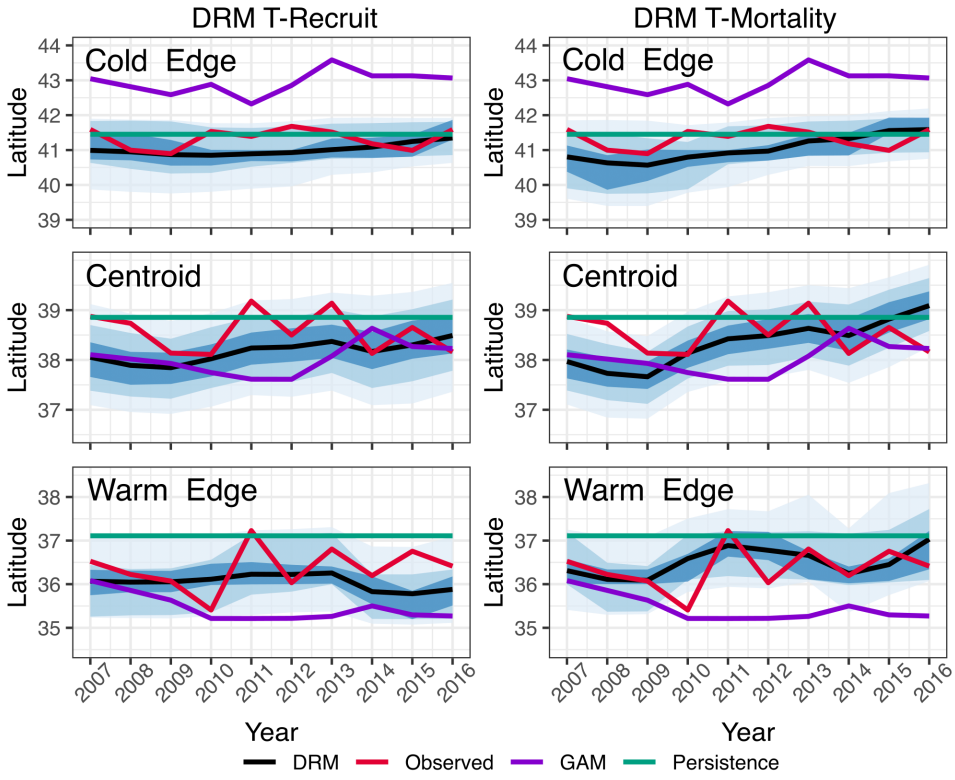

Figure 6: Observed range dynamics of summer flounder (red line) in the study domain (Fig. 2) during the testing decade (2007-2016) and range dynamics forecasted by the temperature-dependent recruitment (left) and temperature-dependent mortality (right) DRMs and by the GAM and persistence forecasts. Latitudinal positions of the cold edge (top row), range centroid (middle row), and warm edge of the population (bottom row) are shown. Shaded blue regions represent HPDIs (0.5, 0.8, and 0.95) of the DRM forecast.

ulation growth, dispersal, and reproduction are important for understanding species responses to a changing climate, especially in the common scenario where species are not in equilibrium with the climate (Guisan & Thuiller, 2005). Because of their Bayesian structure, the DRMs also allowed the quantification and communication of uncertainty around forecasted state variables like geographic position.

By testing alternative mechanistic models, our approach further provided evidence that range shifts in summer flounder can be explained by temperature-dependent recruitment or mortality. Temperature-dependent recruitment may drive northward shifts as habitats warm further north and become thermally suitable for larvae and small juveniles. Indeed, a more rapid northward shift in small juvenile summer flounder than in adults has been reported (Perretti & Thorson, 2019). Alternatively, increasing rates of survival at and beyond northern range edges can also drive a northern shift in the density of the species, as suggested by the temperature-dependent mortality model. Previous research suggested that summer flounder mortality is linked to oceanographic conditions, though that study did not try to explain the northward geographic shift in summer flounder distributions (O'Leary et al., 2019). In addition, our results lend support to the hypothesis that adult fish prefer and move towards higher temperatures than are optimal for larvae and juveniles. This ontogenetic difference is consistent with patterns across fishes suggesting that adult high temperature limits are higher than for larvae (Dahlke et al., 2020), though inconsistent with generally lower temperature preferences in larger than in smaller fishes (Lafrance et al., 2005). More broadly, our application of DRMs provides a model for moving research on geographic range shifts towards demographic and ecological mechanisms. The explicit demography in the DRMs allows them to be theoretically extended to include other mechanisms, including species interactions (Urban et al., 2016).

The persistence forecast—i.e., the prediction that future conditions will be identical to the final year of available data—performed relatively well in our analysis. This result arose because the geographic range of summer flounder was remarkably stable during the testing decade despite marked environmental variability, and was unexpected given widespread observations of temperature-related range shifts in marine fishes in this region (Fredston et al., 2021; Fredston-

Hermann et al., 2020; Mills et al., 2024; Pinsky et al., 2013). However, temporal autocorrelation in biological systems (often termed "ecological memory") is common and often used to inform statistical models of near-term change (Ogle et al., 2015; Wolkovich et al., 2014). Indeed, the time horizon of 1-10 years that we selected for its management relevance may be uniquely difficult to predict, being longer than the daily-to-annual lead times of most near-term forecasting programs (Dietze et al., 2018) but shorter than mid- and end-century projections that ignore transient population dynamics (Morley et al., 2018). Other studies at this time horizon have found that persistence forecasts performed similarly to, or even better than, mechanistic models (Harris et al., 2018; Ward et al., 2014). The time horizon chosen and the stable range dynamics exhibited by summer flounder during an interval of significant warming likely also influenced the relatively poor performance of the statistical SDM, though we note that extensive tuning and refinement of the SDM was beyond the scope of our study (Brodie et al., 2022; Davies et al., 2023).

The DRM estimated some parameters that are difficult to observe, such the diffusion rate between habitat patches. This fact is both a feature, in that difficult-to-observe population processes can be reconstructed, and a challenge, since these estimates are difficult to independently validate. We emphasize that the primary purpose of this model is predictive, not providing precise estimates of population parameters as would be done in a spatial stock assessment model (Punt, 2019). Indeed, as a consequence of designing a process-based model for prediction with multiple options for temperature effects, there are subtle differences in the interpretation of certain model parameters in the DRM (e.g., μ) depending on the model configuration (Equation (1) *versus* Equation (7)). This distinction matters because the performance of a primarily predictive model can only really be judged relative to a benchmark such as an alternative model, as we did here. In contrast, an inference-focused model must demonstrate reliable identification of individual estimated parameters, which we have not rigorously explored here (Tredennick et al., 2021). There is no guarantee that the model or parameter values that maximize predictive skill are the same as those with the greatest inferential power.

Dynamic range models that represent biological processes can be extended to a wide range of taxa and systems that are underrepresented in the literature on forecasting biodiversity responses

to global change (Urban et al., 2022; Zurell et al., 2022). One advantage of the DRM approach is that, like other mechanistic models, it can in theory capture any ecological process for which one can write down an equation hypothesizing its effect on a population parameter (Pagel & Schurr, 2012). Another advantage is that DRMs are conducive to best practices in informing environmental decision-making, such as mechanistic representation of causal linkages, selection of model structure for management relevance, measurement of forecast skill with decision-relevant metrics, and quantification of uncertainty (Bodner et al., 2021; Mason et al., 2023; Schmolke et al., 2010; Schuwirth et al., 2019). We tested mechanisms of temperature dependence and fishing for a single species as a case study. Future work can test the performance of models incorporating temperature effects on multiple life history processes; incorporate new processes such as species interactions, density dependence, or local adaptation; and test DRM approaches against more species with different life histories. Methodological investigations of dynamic range modeling are also needed, including the effect of spatial and temporal scale and extent on projections, and incorporating multiple observational data streams. Both kinds of research would be facilitated by easy-to-use computational and statistical tools for creating, fitting, and evaluating DRMs. In addition, for the summer flounder DRM to be operational as a future (rather than retrospective) forecasting system, additional work would be needed to incorporate future temperature projections (e.g., Koul et al., 2024). Given the limited use to date of mechanistic models that are both validated against historical observations and ready to forecast species on the move, we hope that the results here motivate further investment in this promising new field.

Data and Code Accessibility Statement

An de-identified version of the GitHub repository has been generated via Anonymous Github (https://anonymous.4open.science) and is available at: https://anonymous.4open.science/r/mid_atlantic_forecasts-318E/.

Acknowledgments

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Author Contribution Statement

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