# Changes in body size with age do not follow the temperature-size rule

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**Abstract**

**Aim**: The temperature-size rule is often described as a reduction in ectothermic asymptotic or maximum body size with warming. Although this coincides with the expectation that faster growth under warming would lead to larger sizes early in life but smaller sizes later in life, there remain few tests of changes in size across ontogeny. Here, we use > 99,000 observations of weight-at-age of commercially important fishes over 25 years to ask whether changes in size across ontogeny can be explained by temperature. We also examine whether oxygen, a key part of a proposed mechanism behind the temperature-size rule, explains patterns of weight-at-age better than temperature. Understanding how temperature and oxygen affect size across age offers a test of macroecological theory and can inform the future productivity of fisheries.

**Location**: Bering Sea, largest subarctic system (Latitude: 52° N – 66° N, Longitude: 160° E – 170° W)

**Time period**: 1987-2023

**Major taxa studied**: commercially important fishes

**Methods**: We coupled fisheries-independent survey data and climate model output with spatiotemporal generalized linear mixed models, a novel framework for testing the temperature-size rule. These models account for uneven sampling across space and time to assess long-term trends, as well as the effects of temperature and oxygen on size across age. We additionally explore the effect of model structure on our results by comparing the functional form and how spatial and/or spatiotemporal random effects are included.

**Results**: Weight-at-age was variable over time for all species with no long-term trend. Temperature better explained this variability than oxygen, but effects were small and not age-specific, counter to the temperature-size rule. Our results were sensitive to model structure as models with shared spatial effects across ages appeared to support temperature-size rule predictions, but this support reflected spatial autocorrelation in size rather than age-specific

temperature responses. Collectively, this work shows that support for the temperature-size rule in these fishes was an artifact of spatial patterns in size and growth.

**Main conclusions:** Our work tests macroecological theory using nearly complete body size trajectories to understand not only changes in adult stages but how size changes across age. We highlight that relationships among size, growth, temperature, and oxygen are not as straightforward as theory suggests and illustrate that modeling decisions can have a large effect on tests of ecological theory, and more broadly, our ability to understand biological responses to climate change.

Keywords: growth, size, life-history theory, spatiotemporal modeling, tinyVAST, sdmTMB

## Introduction

Changes in body size are one of the three biological responses to global change that are thought to be universal across species (Daufresne et al., 2009; Gardner et al., 2011; Sheridan & Bickford, 2011). Such shifts are evident in both endothermic and ectothermic animals, plants, and bacteria, and species in both terrestrial and aquatic systems (Forster et al., 2012; Gardner et al., 2011; Martins et al., 2023). Both increases and decreases in size have been documented; most organisms, and ultimately, populations, assemblages, and species, are getting smaller (Audzijonyte et al., 2020; Martins et al., 2023; Ohlberger, 2013). As body size is a central trait that influences many aspects of biology, reductions have countless implications for species and the systems in which they live (Andersen et al., 2016; Peters, 1986; Thorson et al., 2015). These implications span diverse biological and socioeconomic axes including ecosystem dynamics such as trophic relationships and other species interactions, as well as fisheries productivity (Audzijonyte et al., 2013; Baudron et al., 2014; Oke et al., 2020).

Increasing temperature is thought to be a major driver of declines in body size, particularly for ectotherms (Atkinson, 1994; Daufresne et al., 2009; Sheridan & Bickford, 2011). The negative relationship between ectothermic body size and temperature is so widespread that it is formalized as the temperature-size rule. This pattern was originally described based on laboratory experiments in which individuals reared under warmer conditions grew faster to a smaller size-at-maturity but has since become much broader in scope (Atkinson, 1994; Audzijonyte et al., 2019, 2025). It is now commonly used to describe changes in size and growth with temperature in natural populations both within and across species, and is the subject of ecological theory concerned with global change (Audzijonyte et al., 2019, 2025; Verberk et al., 2021). For example, the temperature-size rule intersects life-history theory and body size optimization, metabolic theory, and theories of physiological performance including oxygen limitation (Brown et al., 2004; Essington et al., 2001; Marshall & White, 2019; Pörtner, 2010).

One proposed mechanism underlying the temperature-size rule that has received much attention is oxygen limitation, or the mismatch between oxygen supply and demand (Atkinson et al., 2006; Forster et al., 2012). This mismatch stems from the faster increase in oxygen demand (i.e., metabolic rate) compared to oxygen supply as temperature increases, which is thought to be exacerbated for larger organisms (Audzijonyte et al., 2019; Rubalcaba et al., 2020). Additionally, the magnitude of decline in body size is greater in aquatic versus terrestrial ectotherms and coupled with the added challenges of extracting oxygen from water, supports the role of oxygen limitation behind the temperature-size rule (Forster et al., 2012; Rollinson & Rowe, 2018). More broadly, oxygen has been used in several mechanistic and phenomenological models to explain and predict widespread declines in maximum/asymptotic body size with warming (Bigman et al., 2023a; Cheung et al., 2013; Rubalcaba et al., 2020). However, the role of oxygen in the temperature-size rule remains debated and it is unclear whether oxygen availability can explain and predict changes in size and growth across levels of biological organization (Atkinson et al., 2022; Audzijonyte et al., 2019; Bigman et al., 2023b).

Many studies examining the temperature-size rule in natural systems, at least for fishes, often focus on whether the mean, maximum, or asymptotic body sizes of populations or species are smaller with warming and/or reduced oxygen availability (e.g., Baudron et al., 2014; Cheung et al., 2013; Van Rijn et al., 2017). There is less research addressing how size and growth vary along the ontogenetic trajectory to give rise to the pattern of faster growth to a smaller maturation size, and presumably, smaller maximum or asymptotic size. Size-at-age, or the size of individuals at a given age, is a metric that has been used to examine both growth and body size in tandem in natural populations (Pilipaitytė et al. 2025; Neuheimer & Grønkjær, 2012). The temperature-size rule predicts that faster growth under warming leads to smaller size-at-maturity; thus, younger fish are predicted to be larger-at-age and have positive size-temperature relationships and older fish are predicted to be smaller-at-age and have negative size-temperature relationships (Figure

1) (Atkinson 1994; Angilletta and Dunham, 2003; Forster et al., 2012). Prior studies using size-at-age to test these expectations have largely found that younger age classes are larger under warming but older age classes are smaller, matching theoretical predictions (Ikpewe et al., 2021; Neuheimer & Grønkjær, 2012; Ohlberger et al., 2018; Oke et al., 2022). Understanding how body size and growth vary over the lifetime of a fish is particularly critical for commercially important species as individuals are recruited to the fishery (able to be caught) at body sizes much smaller than maximum/asymptotic size (and sometimes smaller than size-at-maturity). Thus, changes in fisheries productivity (e.g., population biomass, maximum sustainable yield, yield-per-recruit) will result not just from reductions in maximum/asymptotic size but also changes in size along the ontogenetic trajectory (Baudron et al., 2014; Free et al., 2019; Oke et al., 2022).

Commercially important fish species are generally data-rich, but working with these and other geo-referenced data comes with added complexities (Cressie & Wikle, 2011; Thorson & Kristensen, 2024). Such data are often collected via monitoring surveys, where observations are collected at a specific location, often repeatedly over time. Such a sampling scheme results in observations being more similar to each other if collected closer in space and time, and this autocorrelation must be accounted for when modeling ecological processes using these data (Cressie & Wikle, 2011; Indivero et al., 2023; Thorson & Kristensen, 2024). Another layer of complexity is added when assessing patterns across age (or any other grouping structure), such as those predicted by the temperature-size rule. For example, the geographic distribution of individuals in different age classes varies spatially and temporally, particularly for fishes. Coupled with the uneven sampling of fish in space over time, it is likely that the degree of autocorrelation of observations in space and time differs across ages. Recent efforts to make spatiotemporal modeling frameworks more accessible, including those that allow random effects such as the spatial and spatiotemporal fields to be independent by age (or other grouping structure), have resulted in a rapid increase in the use of spatiotemporal modeling (Thorson, 2019; Thorson et al.,

2024, Anderson et al., 2025). However, the structure of these complex models, including how spatial and spatiotemporal fields are specified, can bias results or lead to spurious conclusions and thus careful consideration of model structure is important (Commander et al., 2022; Dormann et al., 2007).

Here, we aim to understand how size varies by age with temperature and oxygen, and whether seemingly simple relationships stemming from theory can further our understanding of how processes underlying fisheries productivity may respond to environmental change. We focus on weight-at-age – which ultimately affects total biomass available to the fishery – of four ecologically and commercially important groundfish species in the eastern Bering Sea, a region that is rapidly changing yet supports some of the most valuable fisheries in the world. Specifically, we ask two questions: (i) does size-at-age vary over time and (ii) is variability in size-at-age explained by temperature or oxygen as expected from the temperature-size rule, where size of younger age classes is positively related to temperature or oxygen and size of older age classes is negatively related (Figure 1). To answer these questions, we fit spatiotemporal generalized linear mixed models, which allow us to account for spatial autocorrelation through random effects implemented as Gaussian Markov random fields. Spatial fields account for the autocorrelation of observations collected in space and spatiotemporal fields account for the autocorrelation of observations collected in space and time and are estimated for each time step (here, year; Figure 2) (Cressie & Wikle, 2011; Thorson & Kristensen, 2024). We explored different parameterizations of these random fields to assess the sensitivity of support for the temperature-size rule to spatial structure in the data. Specifically, we examined whether spatial and spatiotemporal autocorrelation varies by age, which is likely given ontogenetic shifts in habitat use, distribution, depth, and the resulting unevenness of sampling in space across age (Figure 2). Specifically, we examined and compared models with (a) a spatial field that is shared across ages (‘shared spatial field’), (b) one spatial field and spatiotemporal fields for each year that are shared across ages (‘shared spatial and

spatiotemporal fields"), and (c) fully independent spatial and spatiotemporal fields by age (i.e., a spatial field estimated for each age class and a spatiotemporal field estimated for each age class for each year, "age-specific fields"). Understanding how size across ontogeny is affected by temperature and oxygen, and how to account for spatial patterns in size and growth, will inform both ecological theory and fisheries management, and more broadly, help us predict biological responses to global change.

## Materials and methods

### *Survey data*

We collated weight and age data for individuals of four groundfish species: arrowtooth flounder (*Atheresthes stomias*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Gadus chalcogrammus*), and yellowfin sole (*Limanda aspera*). These four species were chosen based on data availability and for comparison with other studies examining demographic trends (e.g., Holsman et al. 2020, Oke et al. 2022). Specimens were collected in fishery-independent bottom trawl surveys in the eastern and northern Bering Sea and aged by the National Oceanic and Atmospheric Administration's Alaska Fisheries Science Center (AFSC) using standardized procedures (Matta & Kimura 2012, Markowitz et al., 2024). Briefly, sagittal otoliths are extracted, cleaned, and preserved in glycerin-thymol solution at sea for later age determination in the laboratory. Otoliths are aged by surface examination or are sectioned and burned to enhance contrast between growth zones, depending on species and size. Ages are estimated by counting annual growth bands (paired opaque and translucent zones) along defined axes using a stereomicroscope. For more information on AFSC's ageing methodology, refer to Matta & Kimura (2012). The bottom trawl survey has historically focused on the eastern Bering Sea with periodic extensions to the northern Bering Sea, which have become more common in recent years

(Markowitz et al., 2024). The survey also evolved over time in terms of the species and number of specimens collected for ageing, resulting in a different collection of years sampled for each species (Table S1).

We followed AFSC's protocol to remove outliers from the age and weight dataset using a Bonferroni outlier test applied to the length-weight data (Rohan & O'Leary, 2024).

*Environmental variables*

For temperature and oxygen, we obtained weekly averaged, spatially resolved values of bottom temperature and bottom oxygen (defined as the mean temperature or oxygen over the bottom [deepest] 5 meters of the water column at each horizontal [latitude-longitude] location) from the hindcast of the Bering10K Regional Ocean Modeling System (hereafter, 'Bering10K'; Kearney et al., 2020). This reanalysis-forced simulation spans the period of 1970–present (through 2024 at the time of this paper), and its domain covers the Bering Sea and northern Gulf of Alaska using a 10-km horizontal resolution and 30 terrain-following depth levels. It has demonstrated high skill in reproducing key biophysical dynamics of the Bering Sea, including the seasonal extent of sea ice, formation of the cold pool, and general circulation and stratification patterns across the shelf (Hermann et al., 2016; Kearney et al., 2020; Pilcher et al., 2019). We chose to use modeled temperature and oxygen as we wanted a temporally averaged and spatially resolved time series, and *in situ* measurements are only available during certain times of the year (i.e., during the bottom trawl survey) for a sparse selection of years. For each week of each year, we matched the location of each survey station to the closest grid cell from the Bering10K using nearest neighbor matching (as implemented in the RANN package, Arya et al., 2019). We then averaged the temperature and oxygen values for the year preceding the survey (July of one year to June of the next year). We also calculated spatially resolved time series where temperature and oxygen were averaged over a shorter time span (three months prior to the survey, following Oke et al.,

2022) to ensure our results were not sensitive to the temporal scale at which we averaged our covariates. We found that annual estimates of temperature and oxygen were highly similar over space and time regardless of temporal span (Figures S1-S3). As size is a cumulative rather than short-term process, we choose to present the results using the covariates averaged over the longest time span possible (year before survey, as we have age-1 fish).

*Does weight-at-age change over time?*

To assess whether weight-at-age changed over time, we fit spatiotemporal generalized linear mixed-effects models, with $\log_{10}$-transformed individual weight as the response variable and year as the (factor) predictor variable. Fitting one model per species (with age class as a fixed effect) rarely converged due to the low sample size of some factor levels (i.e., few samples of a given age class in a given year) and so we fit separate models for each age class of each species and removed those species/age combinations resulting in failed model convergence. All models accounted for spatial and spatiotemporal random fields using the stochastic partial differential equation (SPDE) approximation to Gaussian random fields with Gaussian Markov random fields (Lindgren et al., 2011). These models were fitted using the R package *sdmTMB* (versions 0.3-0.4.1), which interfaces matrices necessary to implement the SPDE approach from the R package *fmesher* with Template Model Builder (TMB) to calculate the marginal likelihood, in R versions 4.3.0-4.3.3 (Kristensen et al., 2016; Lindgren, 2024, Anderson et al., 2025; R core team 2025).

*Does temperature or oxygen explain changes in size-at-age?*

To determine whether changes in weight-at-age over time can be explained by temperature or oxygen, as suggested by the temperature-size rule, we fit and compared three types of models. The first type of model did not include an environmental covariate (i.e., temperature or oxygen). The second type of model included a 'global' effect of temperature or oxygen, where the effect of temperature and oxygen on weight is the same for all ages. The third type of model included an

age-specific effect of temperature or oxygen on weight (i.e., an interaction between age and temperature or oxygen), where the effect of temperature or oxygen on weight is allowed to vary by age class. Because physiological and ecological relationships are complex, we explored three functional forms that may describe the relationship between weight and temperature/oxygen - linear, second order polynomial, and third order polynomial. All models had a fixed effect of age class to estimate age-specific intercepts. Weight was log10-transformed and temperature and oxygen were standardized (centered by the mean and scaled by the standard deviation) prior to analyses.

To explore how specification of spatial and spatiotemporal fields affected our understanding of changes in weight-at-age with temperature and oxygen, we fit all models described above with three different random effect structures. First, we fit multivariate models where spatial and spatiotemporal fields (by year) were estimated for each age class, and each age class had its own residual variance (models with 'age-specific fields'). These models are essentially equivalent to fitting a separate model for each age class. Second, we fit models with a shared spatial field and shared residual variance across ages, but with no spatiotemporal field (models with a 'shared spatial field'). Finally, we fit models where age classes shared a spatial field, spatiotemporal fields for each year, and residual variance (models with 'shared spatial and spatiotemporal fields'). To do so, we used the R package *tinyVAST* (version 0.7.1), which offers the flexibility to specify multivariate spatiotemporal models, and thus, random effect structures and error distributions by grouping structure (e.g., age, size, species; Thorson et al., 2024; Thorson & Barnett, 2017). The shared spatial field models are similar to fitting a generalized additive model (GAM) or generalized linear model (GLM) with an interaction (e.g., tensor product) of latitude and longitude to account for space, an approach used to ask similar questions (e.g., Oke et al., 2022).

We first fitted all models described above using restricted maximum likelihood (REML) estimation and then used (marginal) Akaike Information Criteria (AIC) to identify the most supported random effect structure. We then re-fit models with the most supported random effect structure with maximum likelihood (ML) estimation to test temperature-size predictions. In total, we fit 312 spatiotemporal models combined for the four fish species to test the effects of temperature and oxygen on weight-at-age (see Table S2, which reports all models fitted using one likelihood estimation [REML] for one species). Specifically, for each species, we fit:

(i) models without an environmental covariate ("no covariate model") with three different spatial and spatiotemporal random effect structures (shared spatial fields, shared spatial and spatiotemporal fields, and age-specific fields) both using ML (facilitates comparison of fixed effects) and REML (facilitates comparison of random effects) estimation (n = 6 models for each species, 24 models total),

(ii) models with a global effect of *temperature* on weight as a linear, second order polynomial, and third order polynomial effect, each with three spatial and spatiotemporal random effect structures and with both ML and REML estimation (n = 18 models for each species, 72 models total),

(iii) models with an age-specific effect of *temperature* on weight as a linear, second order polynomial, and third order polynomial effect, each with three spatial and spatiotemporal random effect structures and with both ML and REML estimation (n = 18 models for each species, 72 models total),

(iv) models with a global effect of *oxygen* on weight as a linear, 2nd order polynomial, or 3rd order polynomial effect, each with three spatial and spatiotemporal random effect

structures and with both ML and REML estimation (n = 18 models for each species, 72 models total), and

(v) models with an age-specific effect of *oxygen* on weight as a linear, 2nd order polynomial, or 3rd order polynomial effect, each with three spatial and spatiotemporal random effect structures and with both ML and REML estimation (n = 18 models for each species, 72 models total).

A change in Pacific cod otolith age determination criteria has been documented wherein ages prior to 2008 were generally overestimated (Barbeaux et al., 2018). To ensure this did not affect our model results for Pacific cod specifically, we refit all models with environmental covariates (temperature and oxygen) to data from years 2008 and forward for Pacific cod. We then compared the top model with the full dataset to that of the dataset 2008 and forward.

Please see the supplementary methods for all statistical formulations of all models. All data and code are available at (https://github.com/jennybigman/size-at-age).

## Results

Overall, for all four species, we found variability in size-at-age from year to year, a small, nonlinear, non-age specific effect of temperature on weight, and more support for temperature explaining variation in weight compared to oxygen availability. We also found that model structure, specifically how spatial autocorrelation is included in the model, greatly affects our tests of temperature-size predictions. We detail these findings below.

### *Changes in weight-at-age over time*

Predicted weight-at-age was highly variable over time for all four species (Figure 3). While many ages had enough data per year to assess a change in weight over time, some did not. We could assess whether weight-at-age changed for ages 2 - 6 and 8 for arrowtooth flounder, ages 1 - 7 of Pacific cod, ages 1 - 14 for walleye pollock, and ages 3 - 11 and 28 for yellowfin sole. Although no significant positive or negative trend in weight-at-age over time existed for any species or age over the span of the survey period (Figure S4), weight for many ages of arrowtooth flounder, Pacific cod, and yellowfin sole may be increasing in recent years. For walleye pollock, weight-at-age is more variable and may be increasing for younger (2, 3) and older (8+) fish, but decreasing or not changing otherwise (Figure 3).

*Does temperature or oxygen explain changes in weight-at-age over time?*

Counter to the temperature-size rule, which suggests stronger positive correlations with temperature and size at younger ages, the relationships between weight and temperature were not age-specific for any of the four species, meaning that the most supported models did not have an interaction between age and temperature (Figure 4, Figures S5-S7; Tables S3-S6).

While no age-specific temperature-size relationships existed, temperature was a better predictor of weight compared to oxygen (Tables S3-S6). This was especially true for arrowtooth flounder and walleye pollock, where models with temperature were clearly supported over models with oxygen (Tables S3, S5). The most supported models for Pacific cod (whose results did not differ between the top model fitted to the full dataset [all years] and a trimmed dataset [2008 and forward]; Figure S8) and yellowfin sole also included temperature, but out of all models within two AIC units, one model included oxygen (Table S4, S6). For Pacific cod, four models were within two AIC units from the most supported model and of the five total models, four included temperature and not oxygen. Likewise, three models were within two units of AIC of the top model for yellowfin sole and of the four total, three included temperature and not oxygen. Although

models with temperature were more supported than models without, the effect size of temperature on weight was small and a nonlinear functional form was supported for all species (Figures 4, S2-S4; refer to the 'Supplementary Results' section of the Supplementary Material for detailed results on functional form comparisons).

*How did model structure affect our results?*

For all four species, models with age-specific fields — those that allowed independent spatial and spatiotemporal random fields by age class (and age-specific residual variances) were strongly supported over models with shared fields (Tables S2, S7-9). When mapping residuals, there were clear patterns in space and time for any model with shared spatial and/or spatiotemporal fields (Figure 5, Figures S9-S12). For models with a shared spatial field, the residuals clustered in space and time such that certain areas and years had larger than expected weights and certain areas and years had smaller than expected weights. These patterns were also true for models with shared spatial and spatiotemporal fields, although with some improvement. Yet when examining residuals spatially and temporally for the models with age-specific fields, much of the patterning in residuals in space and time that was evident in the other models was reduced (Figure 5, Figures S9-S12). Overall, our results suggest that models with age-specific fields — those with spatial and spatiotemporal fields that are allowed to vary by age class — are strongly supported over models that share the spatial or spatial and spatiotemporal fields across ages.

There were two notable differences between models with age-specific fields and those with shared fields that are important to consider in the context of understanding whether temperature or oxygen can explain variation in size-at-age. First, the models with shared fields (the shared spatial field models and the shared spatial and spatiotemporal fields models) suggested that the relationship between weight and temperature and weight and oxygen differed by age class (Figures 4, S5-S7). This was not the case for the most supported models overall — those with

age-specific fields — as these models all found support for an additive effect of temperature, or one that is the same for all ages (Figure 4, Tables S3-S6). Second, the most supported models with shared spatial fields and the shared spatial and spatiotemporal fields suggested that the relationship between weight and temperature followed expectations from the temperature-size rule, where younger ages prior to maturity had generally positive relationships between weight and temperature and older ages after maturity had generally negative relationships (Figure 4, S5-S7). Again, this result was not found in the most supported models overall — those with age-specific fields, which did not find support for age-specific relationships between weight and temperature and weight and oxygen (Figure 4; Tables S3-S9).

## Discussion

Our work suggests that although temperature explains changes in size and growth over time, this effect is small and not age-specific. Accordingly, we did not find support for temperature-size rule predictions that warming leads to faster growth and larger sizes for younger age classes but smaller sizes for older age classes. Inference was strongly influenced by model structure: models with spatial and/or spatiotemporal random fields shared across ages supported temperature-size rule predictions, but this support reflected spatial autocorrelation in size and growth rather than age-specific temperature responses. Once spatial and spatiotemporal autocorrelation was accounted for separately by age, model fit improved for all four species and revealed no age-specific temperature relationships – and, thus, no support for the temperature-size rule. Collectively, our results indicate that the effect of temperature and oxygen on size and growth may not be as simple as suggested by ecological theory and highlight the complexities of modeling such relationships from fisheries data.

We found that although small, the effect of temperature generally had more support than oxygen in explaining historical patterns of weight-at-age. This result suggests that oxygen is unlikely to be a universal driver of changes in size and growth and contrasts with explanations that focus on oxygen's central role behind the temperature-size rule (Atkinson et al., 2006; Forster et al., 2012; Pörtner, 2010). Despite the body of literature suggesting oxygen may be behind the temperature-size rule, oxygen-related explanations have generally received mixed support when tested (Audzijonyte et al., 2019; Verberk et al., 2021), as found here. While we do not attempt to disentangle the many proposed mechanisms to explain the temperature-size rule (e.g., prey availability, life history theory, cell size, etc. [Angilletta et al., 2004; Audzijonyte et al., 2019; Verberk et al., 2021]) our work indicates that oxygen is unlikely to invariably explain changes in size and growth with temperature and that other explanations are likely important.

The effect of temperature on weight was consistently small across ages for all four species and not age-specific and, thus, we did not find support for temperature-size rule predictions. Despite mounting evidence for temperature-size responses in controlled laboratory settings, responses in natural populations remain mixed (Audzijonyte et al., 2020; Forster et al., 2012; Verberk et al., 2021). Studies on natural populations often examine population- or species-level metrics of size and growth, metrics that are both observed (e.g., maximum size) and modeled (e.g., von Bertalanffy growth coefficient and asymptotic size), many of which naturally differ from laboratory-measured size and growth (Audzijonyte et al., 2025; Verberk et al., 2021). For example, Audzijonyte et al. (2020) found increases, decreases, and no change in body size when examining trends in size across spatial (latitudinal) and temporal changes in temperature in 335 unexploited coastal reef fishes, with responses related to maximum body size such that smaller-bodied species were more likely to become smaller in warmer waters. Complicating studies in natural populations, size and growth data often come from individuals that have survived size-dependent fishing and natural mortality, forming a biased sample. When assessing the effect of

418 temperature on size and growth, it is therefore important to consider what the expected
419 relationship with temperature (or other predictors) may be in a particular setting or at a particular
420 biological level (individual, population, species), as we have done here. While we extended tests
421 of the temperature–size rule by examining size across age, size-at-age remains an imperfect
422 metric of growth as it reflects multiple processes beyond growth (e.g., fishing and natural
423 mortality), highlighting ongoing challenges in detecting temperature-driven size responses in
424 natural populations (for a detailed review, see Audzijonyte et al., 2025).
425
426 Our inference of how size and growth vary with temperature (or oxygen) across age was sensitive
427 to the assumption of similarity in spatial processes. Models with shared spatial and/or
428 spatiotemporal random effects (assuming autocorrelation is the same for all ages) supported
429 temperature-size predictions, but this support likely reflects spatial autocorrelation in size rather
430 than age-specific temperature responses. These models did not fit the data as well as those with
431 age-specific effects (assuming autocorrelation varies by age), which did not support temperature-
432 size predictions. The importance of age-specific spatial and spatiotemporal random effects is
433 unsurprising as ecology and physiology (e.g., distribution, thermal limits) are known to change
434 across ontogeny, likely exacerbating the unevenness in sampling in space and space through
435 time. The task of modeling these complex spatial dynamics is an area of active research (Hodges
436 & Reich, 2010; Thorson et al., 2023; Ward et al., 2022). Commander et al. (2022) highlighted that
437 predictions of biomass and center of gravity (i.e., the biomass-weighted mean latitude and
438 longitude) for sablefish off the West Coast of the United States differed depending on how spatial
439 or spatiotemporal random effects were included. Spatial confounding — where spatially structured
440 covariates of interest (e.g., temperature or oxygen) are correlated with spatial or spatiotemporal
441 random effects — may have influenced our results by making it difficult to disentangle variation
442 attributable to fixed effects vs. latent spatial structure (Hodges & Reich, 2010). Future work should
443 explicitly investigate this possibility and consider approaches such as restricted spatial regression

(Hodges & Reich, 2010), particularly for forecasting future responses (Ruiz Diaz and Thorson *in review*). Given the growing use of spatiotemporal models in marine resource management, it is crucial to evaluate model structure and assumptions before drawing conclusions and translating model output to fisheries management.

Although our work advances understanding of shifts in size and growth with temperature in natural populations, many challenges remain. First, disentangling the dynamics among size, growth, and temperature is difficult for numerous reasons, many of which are interrelated. A general consensus regarding the temperature-size rule or a consistent pattern across species, systems, and settings is lacking, complicating the identification of the underlying mechanism by which temperature affects size and growth (Audzijonyte et al. 2025). In turn, the lack of a mechanistic understanding hinders our ability to predict how future warming will affect size and growth of fishes. Second, it may be that other abiotic or biotic factors (e.g., food availability, demography) more strongly affect size and growth compared to temperature. Finally, it is important to consider how temperature (or any other predictor) is summarized temporally and spatially for modeling. While size-temperature responses are evident at both coarse and fine spatial and temporal scales (suggesting that these relationships may be robust to the different ways temperature is spatially and temporally summarized; Cheung et al., 2013; Lindmark et al., 2025), future work could identify best practices for summarizing time series of environmental variables that vary over space and time in relation to the biological response being studied. Relatedly, future work could explore how to best detect changes in size and growth with temperature – what metrics to use, what spatial and temporal scale is appropriate, etc. A first step in this direction would be to outline best practices for designing experiments and statistical models that aim to detect the effects of temperature on size and growth, as illustrated here with spatial and spatiotemporal random effect structure.

Commercially important fish species pose both opportunities and obstacles to studying responses to climate change (e.g., Hobday and Evans 2013). Such species are generally data-rich compared to unharvested taxa and, thus, changes in size across the ontogenetic growth trajectory with temperature can be examined as done here. Yet, identifying and understanding responses to environmental change in harvested taxa remains challenging. In addition to the complexity of modeling these types of data, accounting for the effect of fishing, which is known to truncate age- and size-structure, and act synergistically with temperature, is a central challenge when working with data from exploited populations (Waples & Audzijonyte, 2016, Wootton et al., 2021, Sadler et al., 2024). Another central challenge is not just understanding how species will respond to environmental change, but predicting how they will change. Our work is a step in this direction as we identify that while temperature (and oxygen) does relate to changes in size, this relationship is not consistent across species nor likely strong enough to be useful for generating predictions of size-at-age from temperature. Future work in this area could include other processes not explored here (e.g. cohort and sex effects, Cheng et al., 2023; Stawitz et al., 2015), with the goal of identifying how best to predict size-at-age in addition to testing an explicit theoretical prediction, as done here. As fisheries globally face an uncertain future due to continued and projected changing environmental conditions, it is critical to ensure the stability of future fisheries, as well as the livelihoods and economies they support. Doing so will require continued exploration into how climate change is affecting commercially important fish populations, ideally with the goal of predicting how distributions, biomass, and abundance will change in the future.

## Supporting Information

Additional supporting information can be found inline in the Supporting Information section. The Supporting Information includes Supplementary Methods, Supplementary Results, Supplementary Tables, Supplementary Figures, and Supplementary References. **Table S1**: Number of samples (individuals) and range of collection years per species. **Table S2:** Models

with age-specific random fields are more supported than models with shared spatial and spatiotemporal fields across ages for arrowtooth flounder. **Table S3:** Models with temperature and no interaction between temperature and age are the most supported models explaining changes in weight-at-age over time for arrowtooth flounder. **Table S4:** Same as Table S3 but for Pacific cod. **Table S5:** Same as Table S3 but for walleye pollock. **Table S6:** Same as Table S3 but for yellowfin sole. **Table S7:** Same as Table S2 but for Pacific Cod. **Table S8:** Same as Table S2 but for walleye pollock. **Table S9:** Same as Table S2 but for yellowfin sole. **Figure S1:** Time series of temperature and oxygen averaged over a shorter (three months prior to the survey) and longer (averaged year before survey) time span for (a) arrowtooth flounder, (b) Pacific cod, (c) walleye pollock, and (d) yellowfin sole. **Figure S2:** Comparison of temperature averaged over a shorter (three months prior to the survey) and longer (averaged year before survey) time span for each grid cell for each year (broken up across three panels for to ensure readability). **Figure S3:** Comparison of oxygen averaged over a shorter (three months prior to the survey) and longer (averaged year before survey) time span for each grid cell for each year (broken up across three panels for to ensure readability). **Figure S4:** There was no long-term change in weight-at-age over time for any of the four species examined in this study. **Figure S5:** Predictions of weight from temperature from three spatiotemporal models: (1) age-specific spatial and spatiotemporal fields (blue lines), (2) shared spatial field and spatiotemporal fields across ages (purple lines), and (3) shared spatial field across ages with no spatiotemporal fields (orange lines) for arrowtooth flounder. **Figure S6:** Same as Figure S5 but for walleye pollock. **Figure S7:** Same as Figure S5 but for yellowfin sole. **Figure S8:** Same as Figure 4 but with data from 2008 and forward. **Figure S9:** Comparison of residuals over space and time for arrowtooth flounder among models with the same fixed effect structure but the three different random effect structures (see text): age-specific fields (first figure), shared spatial and spatiotemporal fields (second figure), and shared spatial fields (third figure). **Figure S10:** Same

as Figure S9 but for Pacific Cod. **Figure S11:** Same as Figure S9 but for walleye pollock.

**Figure S12:** Same as Figure S9 but for yellowfin sole.

## Data and code availability statement

All data and code are freely available. Data is available from the surveyjoin R package (https://dfo-noaa-pacific.github.io/surveyjoin/) and all code is available at (https://github.com/jennybigman/size-at-age).

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## Conflict of interest disclosure

The authors declare no conflicts of interest.

## Ethics approval statement

NA

## Patient consent statement

NA

## Permission to reproduce material from other sources

NA

## Clinical trial registration

NA

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Author contributions

JSB: conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, software, visualization, writing – original draft, writing – review and editing; LAKB: data curation, investigation, methodology, writing – review & editing; JTT: methodology, writing – review & editing; SCA: methodology, writing – review & editing; KO: writing – review & editing; KK: data curation, investigation, writing – review & editing; DP: data curation, investigation, writing – review & editing; WC: data curation, investigation, writing – review & editing; EG: investigation, writing – review & editing; MEM: investigation, writing – review & editing, KKH: data curation, writing – review & editing; LAR: methodology, supervision, writing – review & editing.

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Figures

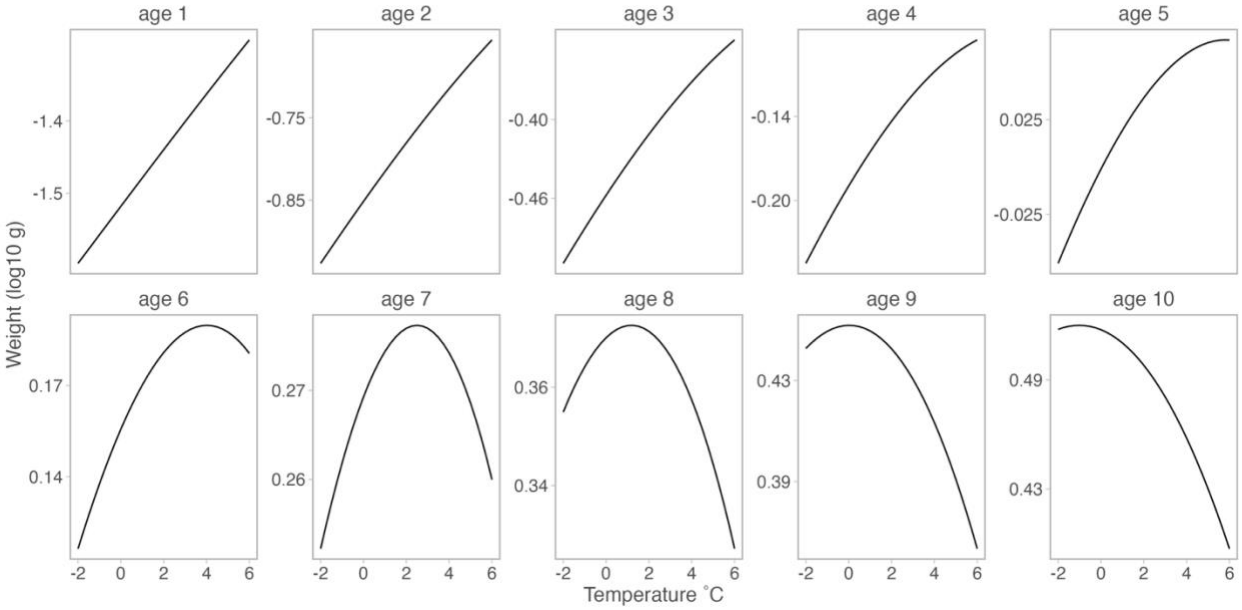



**Figure 1**. A conceptual figure illustrating the predictions of the temperature-size rule tested in this study: warming leads to faster growth of younger fish to smaller size-at-maturity, resulting in positive relationships between size and temperature for younger age classes and negative relationships in size and temperature for older age classes. We show weight-at-age arising from the von Bertalanffy growth function (which models growth as the balance between anabolism and catabolism; see Essington et al., 2001 for more discussion), $(W_{t+1}) = W_t + \alpha(T)W_t^{\frac{2}{3}} - \beta(T)W_t$, where the rate of anabolism, $\alpha(T), = \frac{0.2}{3}\mathrm{e}^{0.05T}$ and the rate of catabolism, $\beta(T)$, $= \frac{0.1}{3}\mathrm{e}^{0.1T}$ given temperature $T$, i.e., showing that the temperature-size rule is predicted to emerge when the temperature-sensitivity of catabolism is greater than that for anabolism (e.g., Morita et al., 2010).

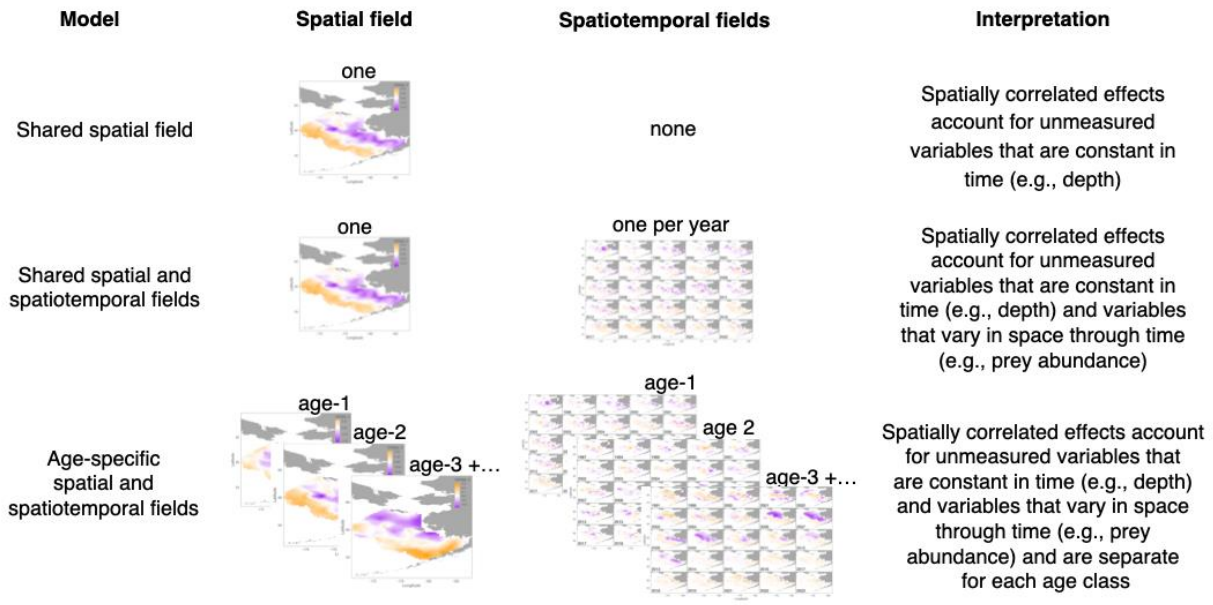
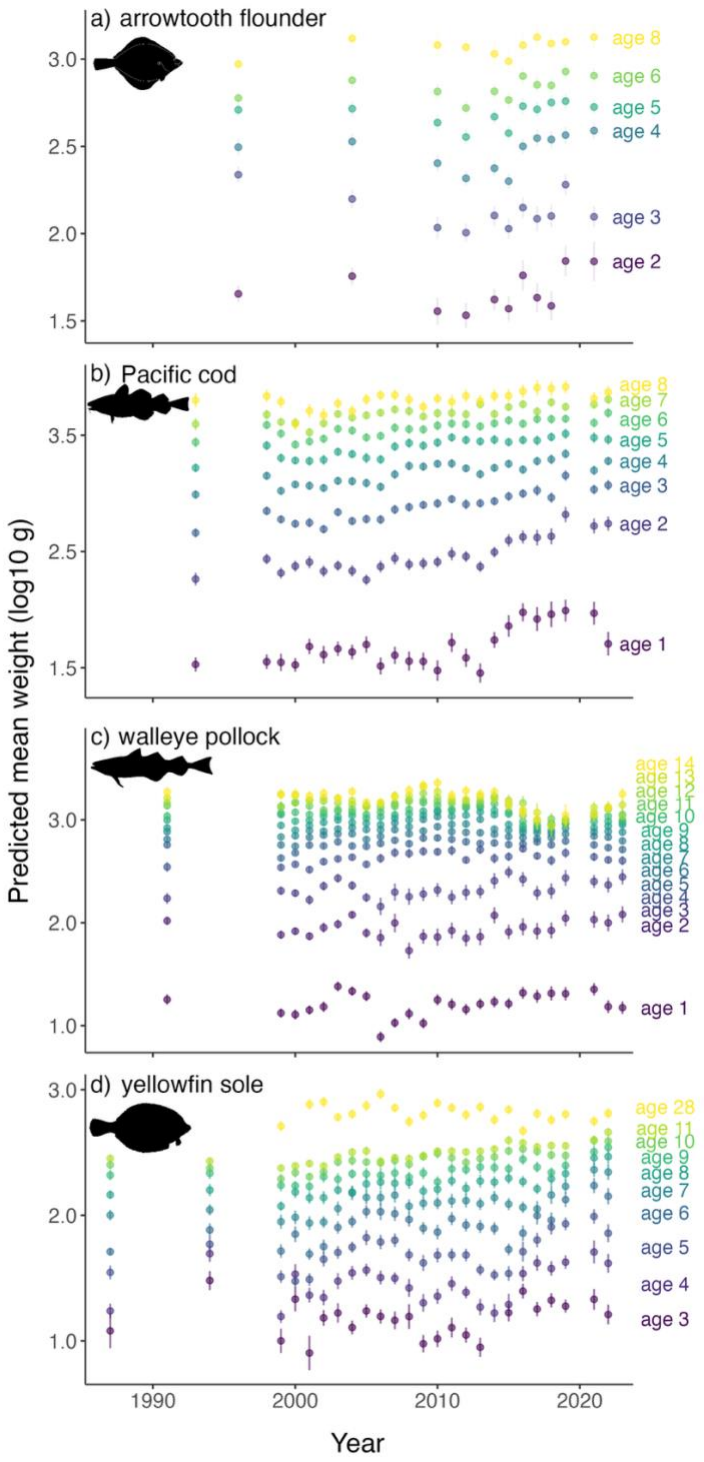
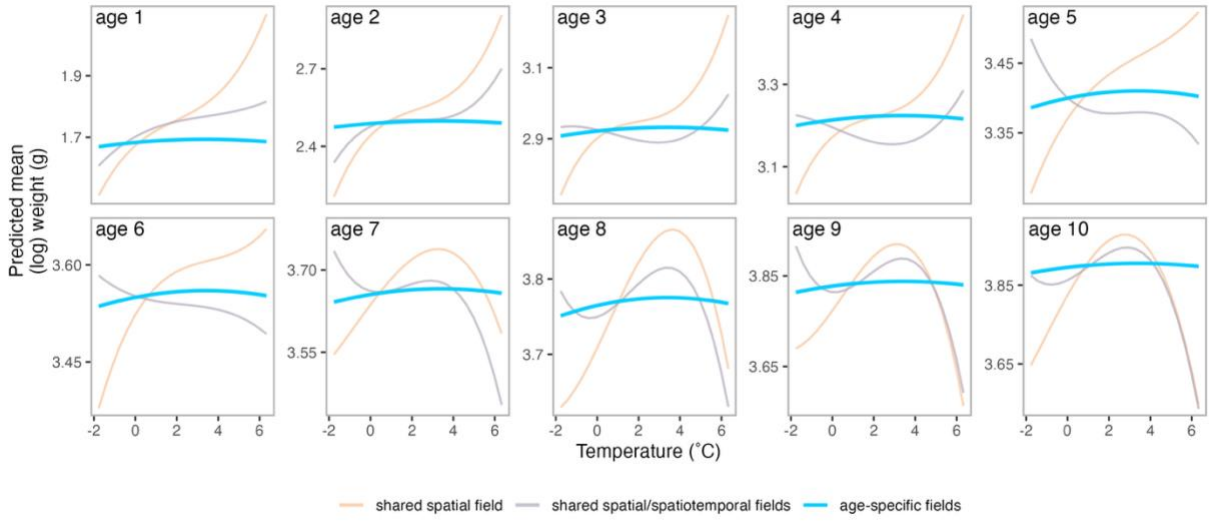



**Figure 2**. Illustration of the structure of whether and how spatial and spatiotemporal autocorrelation is accounted for in each model type and its interpretation. 'Shared spatial field' models (row 1) have one spatial random effect shared across all ages and no spatiotemporal fields. 'Shared spatial field and spatiotemporal fields models' (row 2) have one spatial random effect shared across all ages and a spatiotemporal random effect for each year that is shared across all ages (each panel is a separate year). 'Age-specific fields' models (row 3) have a separate spatial random effect for each age class, and a spatiotemporal random effect for each year for each age class.




874

875 **Figure 3. Weight-at-age was variable over time for all four species**. Change in mean
876 weight-at-age over time for arrowtooth flounder (top left), Pacific cod (top right), walleye pollock
877 (bottom left), and yellowfin sole (bottom right). Colored circles are the mean predicted weight-at-
878 age and error bars are one standard error around the mean (see text). Color indicates age with
879 labels insetted in each panel. Note the y-axis (the predicted mean weight [log10 g]) differs for
880 each panel.




881

882 **Figure 4. Model structure affected our understanding of how temperature affects weight-**
883 **at-age: models with shared spatial and spatiotemporal fields provide spurious support**
884 **for the temperature-size rule**. Predictions of weight based on temperature from three
885 spatiotemporal models with different random effect structures: (1) age-specific spatial and
886 spatiotemporal fields (blue lines), (2) shared spatial field and spatiotemporal fields across ages
887 (purple lines), and (3) shared spatial field across ages with no spatiotemporal fields (orange
888 lines) for Pacific cod (other three species in Supplementary Material, Figures S6-S8). Each
889 panel corresponds to a separate age class (labeled in the upper left-hand side of the panel).
890 Predictions were generated from the most supported model for each random effect structure
891 (i.e., most supported models for each random effect structure in Table S3). Note the y-axis (the
892 predicted mean weight [log10 g]) differs for each panel.
893

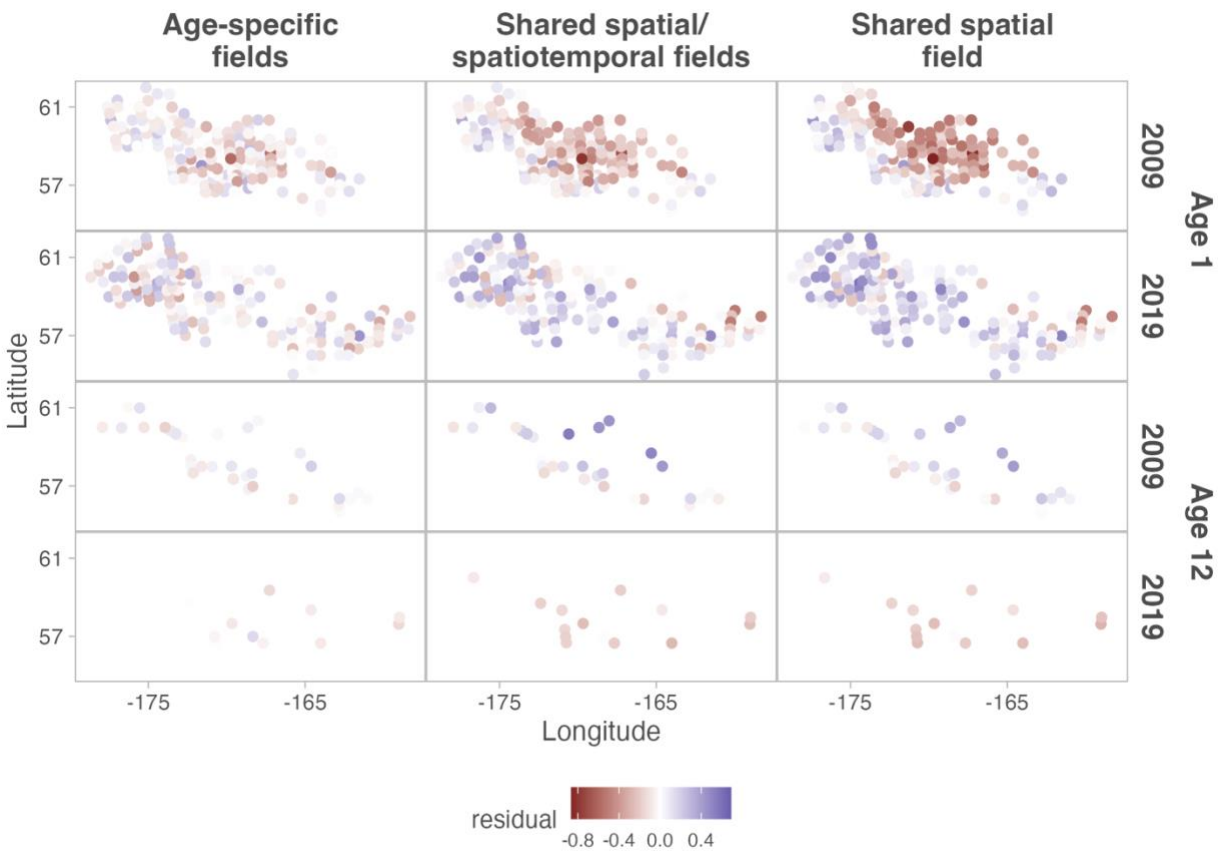



**Figure 5. Models with age-specific spatial and spatiotemporal fields by age class have less residual structure over space and time compared to models with shared effects**. Comparison of residuals over space and time for two distant age classes (1 and 12, rows) for two distant years (2009, 2019, rows) among models with the same fixed effects and functional form but different specification of the random fields: age-specific spatial and spatiotemporal random fields across ages (first column), shared spatial and spatiotemporal effects across ages (middle column), and shared spatial effects across ages with no spatiotemporal effect (right column). Residuals shown here are for walleye pollock and calculated from a model fitted to weight with a fixed effect of age class as a factor, an effect of temperature, and an interaction between age class and temperature, where the effect of temperature on weight is a second order polynomial (i.e., the most supported model structure for walleye pollock; see Table S3). Figures S9-S12 show maps of residuals for all age classes for all years for all species.