

Contrasting climate velocity impacts in warm and cool locations show that effects of marine warming are worse in already warmer temperate waters

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Warming worse in already warmer temperate waters: a meta-analysis of the impact of climate trends and velocities on 38 species of demersal marine fishes

Impacts of climate velocity on demersal fish biomass depend on initial climate conditions: a meta-analysis across 38 species in the northeast Pacific

Running head: Contrasting climate velocity impacts

Abstract

2 Species responses to climate change are often measured at broad spatiotemporal scales, which can
miss fine-scale changes that are relevant to conservation and fisheries management. We develop
4 a scale-able geostatistical approach to assess how juvenile and adult fish distributions have been
shaped by changes in bottom temperature and dissolved oxygen over a recent decade of warming
6 in the northeast Pacific. Across 38 demersal fishes, biomass trends were associated negatively with
warming and positively with dissolved oxygen, but when trends in both biomass and climate were
8 converted to velocities—the speed and direction an organism would have to move to maintain
consistent conditions—the effect of temperature change differed depending on local conditions. In
10 the warmest locations, warming velocities were associated with negative biotic velocities for 19
of 69 species-maturity combinations, and yet were almost always associated with stable or posi-
12 tive biotic velocities in the coolest locations (64 of 69). These spatially consistent biomass declines
(negative biotic velocities) in the warmest locations and increases in cooler locations suggest a
14 redistribution of species with the potential for new ecological and fisheries interactions. After
controlling for temperature, the more spatially consistent effects of dissolved oxygen were often
16 negative, suggesting a mechanism other than hypoxia avoidance—potentially changes in primary
production. Our approach identifies the species and locations that are most sensitive to observed
18 changes in the environment at any scale, thus facilitating future vulnerability assessments.

20 Keywords: biotic velocity, climate change, context dependence, dissolved oxygen, groundfish,
spatiotemporal distribution models

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Introduction

44 Managing the impacts of a rapidly changing climate on ecological communities, particularly those
that provide food for humans, is a critical challenge facing society (e.g., [Doney *et al.* 2012](#)). An in-
46 crease in atmospheric CO₂ is not only causing increases in both mean ocean temperature and the
frequency of extreme heat waves ([Frölicher *et al.* 2018](#)), but is also affecting patterns of circulation,
48 productivity, and marine chemistry ([Pörtner *et al.* 2019](#)). Combined, these environmental changes
can impact the distribution and abundance of many ecologically and commercially important fish
50 species, leading to local loss of some species, colonizations, and changes in species interactions
and bycatch composition (e.g., [Pinsky and Fogarty 2012](#), [García Molinos *et al.* 2016](#), [Morley *et al.*](#)
52 [2018](#)). Furthermore, such changes can lead to temporary climate-induced hyperstability—catch
rates that remain high despite population declines—if organisms move towards preferred habitat
54 during population decline, or if population density increases faster than range expansion during
population growth (the basin model of density-dependent habitat selection theory; [MacCall 1990](#),
56 [Thorson *et al.* 2016b](#)). Because traditional stock assessment methods, fisheries regulations, and
choices regarding habitat protection generally assume stationary species distributions, new meth-
58 ods that anticipate and incorporate the effects of climate change on species distributions will be
crucial for successful resource management in the future ([Hare *et al.* 2010](#), [Bell *et al.* 2020](#)).

60 Species responses to climate change are often studied along range edges ([Parmesan and Yohe](#)
[2003](#), [Sunday *et al.* 2015](#), [Fredston *et al.* 2020](#), [Fredston-Hermann *et al.* 2020](#)) or as aggregate in-
62 dices (e.g., at species or region levels; [Pinsky *et al.* 2013](#), [Thorson *et al.* 2016a](#), [Morley *et al.* 2018](#)).
The centre of gravity is perhaps the most commonly used measure of changes in distribution for
64 marine fishes (e.g., [Perry *et al.* 2005](#), [Rindorf and Lewy 2006](#), [Dulvy *et al.* 2008](#), [Nye *et al.* 2009](#),
[Adams *et al.* 2018](#), [Rooper *et al.* 2020](#)). However, these approaches can overlook fine-scale spatial
66 variation that may be important for understanding species responses ([Oldfather *et al.* 2020](#)) and
distribution shifts may take longer to manifest at aggregate scales. Aggregate measures such as
68 the centre of gravity are also challenging to interpret and apply in cases where both surveys and
management actions are constrained by geographic or political boundaries that partition the dis-
70 tribution of a species. Indeed, laboratory experiments have demonstrated that thermal tolerances
and optimums can differ sub-regionally (e.g., [Pörtner *et al.* 2008](#)) and there is evidence that warm
72 range edges have shifted further north than expected and cold range edges contracted southward

(in the northern hemisphere), which suggest roles for competition, depredation, and/or density
74 dependent habitat selection (Fredston *et al.* 2020). Despite this, projections of future species' dis-
tributions often assume that responses to climate variables are consistent across space and time
76 (e.g., Morley *et al.* 2018). While coarse-scale changes can be informative for long-term planning,
changes in local abundances at finer spatial scales will likely occur more quickly due to the shorter
78 dispersal distances involved and may be more informative in steering local conservation actions.

Local velocities are commonly used to quantify changes at finer spatial scales than captured
80 in population-wide indices (e.g., Brito-Morales *et al.* 2018). A local climate velocity represents the
movement of an isocline—a boundary along which a climate metric is constant. More intuitively,
82 a climate velocity gives the speed and direction an individual must move to maintain a constant
climate condition (e.g., temperature) (Loarie *et al.* 2009). Gradient-based estimates of climate ve-
84 locity are calculated as a trend in a climate metric through time (e.g., temperature trend), which
can be positive or negative, divided by the local gradient in space comprised of a magnitude and
86 direction (see Methods Eq. 12; Table 1; Burrows *et al.* 2011). These velocities scale local climate
trends to emphasize locations where climate is relatively consistent across a neighbourhood of
88 cells. Alternatively, analog-based velocities are estimated using search algorithms that identify
nearest climate matches within a user-defined threshold of change from the reference cell con-
90 ditions (Hamann *et al.* 2015). While analog-based velocity estimates can be more geographically
precise, the choice of thresholds and other statistical properties (e.g., clumpiness) make them less
92 useful than gradient-based local velocities for meta-analysis (Ordonez and Williams 2013).

Changes in abundance, density, or probability of species occurrence can also be expressed as
94 velocities (e.g. Serra-Diaz *et al.* 2014, Comte and Grenouillet 2015, Alabia *et al.* 2018). When applied
to species distribution models, these are referred to as biotic velocities and can be thought of as the
96 minimum distance one would have to move to maintain an equivalent degree of habitat suitability
(Carroll *et al.* 2015, Comte and Grenouillet 2015). Similarly to climate velocity, a positive local
98 biotic velocity is associated with an increase in habitat suitability at the focal location and a nega-
tive value represents a decline in suitability. The magnitude of the velocity estimates the distance
100 to the nearest location that is predicted to match the original probability of occurrence or abun-
dance. Because changes in climate may cause shifts in fish population density before range shifts

102 based on presence-absence are clearly detectable, abundance and biomass-based models of species
distributions are potentially more sensitive to local change than simple occupancy estimates.

104 Bottom-trawl fisheries tend to capture a taxonomically and ecologically diverse suite of fishes.
For example, the groundfish bottom-trawl fishery in Canadian Pacific waters encounters >100
106 species (Anderson *et al.* 2019), many of which are managed via an individual transferable quota
system with 100% at-sea and dockside monitoring (Turris 2000, Wallace *et al.* 2015, DFO 2019).
108 Random depth-stratified fishery-independent bottom trawl surveys have been fitted with conduc-
tivity, temperature, depth (CTD), and dissolved oxygen (DO) sensors since 2008. In addition to
110 estimates of biomass density for each species captured in the surveys, data on size distributions
and reproductive maturity are collected for many species (Anderson *et al.* 2019). Collectively, these
112 species occupy a large range of depths, especially along the shelf edge where short movements
can result in large environmental changes, and vary in their potential for behavioural responses
114 to climate. For example, some species are migratory or highly mobile (e.g., Sablefish, *Anoplopoma*
fimbria, many flatfish species), while others are relatively sedentary (e.g., many species of rockfish,
116 *Sebastes* spp.).

Here, we explore the extent to which groundfish distributions in the northeast Pacific have
118 been shaped by local temperature and DO trends and velocities over a decade spanning a rela-
tively cool period through a recent marine heat wave (Okey *et al.* 2014, Frölicher and Laufkötter
120 2018). We do this by quantifying broad patterns and species-level relationships between climatic
and biotic change in order to answer the following questions: (1) Are local changes in bottom
122 temperature or DO correlated with changes in local groundfish densities, and are these effects
stronger in already warm or low-oxygen regions? For example, has local warming had a larger
124 effect in locations that are already at the warm-extreme of a species' local distribution? (2) How
do these relationships differ between the spatial contexts captured by gradient-based velocities vs.
126 their component trends? (3) How do these effects vary between species and are they correlated
with life-history characteristics such as age and growth rate; or ecological traits such as depth
128 range, latitude, trophic level, foraging zone, or sociality? We address these questions by using
spatiotemporal models applied to a decade of survey-derived climate and species density data,
130 and then assess relationships between velocities of biotic and climatic change for 38 commonly

encountered species using a geostatistically explicit hierarchical analysis that controls for change
132 in both temperature and DO.

Methods

134 Survey data

We analyzed biomass density distributions and morphometric data for 38 species of groundfish that
136 were regularly encountered by fisheries-independent bottom-trawl surveys and are widely dis-
tributed within Canadian Pacific waters (DFO 2020, Table S1). The surveys were stratified within
138 four regions, two of which were surveyed in odd years (Hecate Strait and Queen Charlotte Sound)
and two in even years (West Coast Vancouver Island and West Coast Haida Gwaii) since at least
140 2005. Each region was sampled over the same month-long period between late May and early
August in each survey year. Combined, these surveys covered most of the upper continental slope
142 and shelf in Pacific Canada and shared similar random depth-stratified designs, fishing gear, and
fishing protocols (Sinclair *et al.* 2003). We only included tows of > 15 minutes duration and con-
144 verted total biomass of each species to a biomass density based on the speed, distance covered,
and net opening (e.g., Williams *et al.* 2018, Anderson *et al.* 2019). Biological sampling protocols
146 varied among species, depending on size of catch and commercial importance. In general, catches
of between 10–50 fish were sexed, weighed and measured individually, while larger catches were
148 subsampled and, for commercially important species, maturity data and otoliths for aging were
collected.

150 Estimating spatiotemporal variation in maturity-specific biomass density

Because ontogenetic shifts in habitat, particularly depth, are well documented for groundfish
152 species (e.g., Mindel *et al.* 2016, Barbeaux and Hollowed 2018, Li *et al.* 2019), we estimated biomass
densities separately for mature and immature size classes whenever possible. Maturity was not
154 assessed for certain Chondrichthyans, or when catches were particularly low. To do this, we first
estimated length at 50% maturity as defined by gonadal development stages using ogives fit as
156 sex-specific logistic regressions to individual specimens (see Supplementary Methods). To split
the estimated biomass density per tow into mature and immature components, we calculated the

158 summed biomass of all measured fish that were above (for mature) or below (for immature) the
length-at-50% maturity threshold, divided by the total biomass of all measured fish, and multiplied
160 this ratio by the estimated biomass density for each tow. For each tow that resulted in too small
a catch for detailed measurements to have been taken, we applied the mean ratio from all mea-
162 sured tows to estimate mature biomass (applied to a median of 9% [range 1–40%] of each species’
total sampled biomass). For species without any maturity data, we assumed that the total biomass
164 estimate represented the mature population, because mature individuals are larger, and therefore
likely to be numerically dominant (* in Table S1). However, it is possible that biomass sampled
166 in some areas was actually dominated by immature individuals, particularly for the skate species,
whose mean lengths fall close to the sizes at maturity found in [Love \(2011\)](#).

168 We modelled spatiotemporal biomass density separately for mature and immature fish of each
species using spatial GLMMs. Environmental variables, such as temperature, may be included in
170 these models explicitly and can be used to assess the vulnerability or tolerance of a given species
to change ([Godefroid et al. 2019](#)). However, such approaches require strong assumptions (e.g.,
172 that effects are constant through both time and space). Instead, we use a climate-agnostic ver-
sion of a species distribution model with a spatiotemporal random effect structure to estimate
174 local variability in biomass density change. Our models relied on spatial random effects to cap-
ture unmeasured components of habitat suitability and allow suitability to change through time
176 without making assumptions about the shape of species-specific responses to possible climatic
and geographic covariates (e.g., [Shelton et al. 2014](#), [Ward et al. 2015](#), [Thorson et al. 2015b, 2017](#)). We
178 modelled each species and maturity class separately because, although these density patterns are
correlated, explicitly modelling those relationships among groundfish species has not been shown
180 to dramatically improve precision of overall estimates ([Thorson and Barnett 2017](#)), and maintaining
independent estimates should make identification of shared climate responses more conservative.

182 We modelled biomass density with a Tweedie distribution and a log link because densities
contain both zeros and positive continuous values ([Tweedie 1984](#), [Dunn and Smyth 2005](#), [Anderson](#)
184 [et al. 2019](#)):

$$Y_{s,t} \sim \text{Tweedie}(\mu_{s,t}, p, \phi), \quad 1 < p < 2, \quad (1)$$

$$\mu_{s,t} = \exp(\alpha_t + \gamma_{1,t}D_{s,t} + \gamma_{2,t}D_{s,t}^2 + \omega_s + \epsilon_{s,t}), \quad (2)$$

$$\gamma_{1,t} \sim \text{Normal}(\gamma_{1,t-1}, \sigma_{\gamma_1}^2), \quad (3)$$

$$\gamma_{2,t} \sim \text{Normal}(\gamma_{2,t-1}, \sigma_{\gamma_2}^2), \quad (4)$$

$$\omega \sim \text{MVNormal}(\mathbf{0}, \Sigma_\omega), \quad (5)$$

$$\epsilon_t \sim \text{MVNormal}(\mathbf{0}, \Sigma_\epsilon), \quad (6)$$

186 where $Y_{s,t}$ represents the biomass density at point in space s and time t , μ represents the mean
 biomass density, p represents the Tweedie power parameter, and ϕ represents the Tweedie dis-
 188 persion parameter. The parameter α_t represents the mean effect for each year, and $\gamma_{1,t}$ and $\gamma_{2,t}$
 represent time-varying coefficients associated with depth (D) and depth-squared covariates (D^2),
 190 respectively, which both follow a random walk constrained by $\sigma_{\gamma_1}^2$ and $\sigma_{\gamma_2}^2$. The initial values $\gamma_{1,t}$
 and $\gamma_{2,t}$ at $t = 1$ share an implied Uniform($-\infty, \infty$) prior. We considered alternative covariates not
 192 described here (Supporting Methods) The parameters ω_s and $\epsilon_{s,t}$ represent spatial and spatiotem-
 poral random effects that were assumed drawn from Gaussian Markov random fields (e.g., [Latimer](#)
 194 [et al. 2009](#), [Cressie and Wikle 2011](#), [Lindgren et al. 2011](#)) with covariance matrices Σ_ω and Σ_ϵ that
 were constrained by Matérn covariance functions ([Cressie and Wikle 2011](#)). The covariance matri-
 196 ces for a given maturity-species combination shared a common κ parameter that controls the rate
 of decay of spatial correlation with distance ([Cressie and Wikle 2011](#)).

198 We modelled the spatial components as random fields using a triangulated mesh with vertices
 selected using a k-means algorithm (via the k-means function in R; e.g., [Shelton et al. 2014](#)) at
 200 a specified number of locations, known as knots, used to approximate the spatial variability in
 observations. We used 500 knots for mature density, 400 for immature density, and 300 for less
 202 well-sampled species (Bocaccio *Sebastes paucispinis*, Shortraker *Sebastes borealis*, and immature
 Redstripe Rockfish *Sebastes proriger*). Based on estimated values of the spatial surface at these
 204 knot locations, we used bilinear interpolation to approximate a continuous spatial field ([Rue et al.](#)
[2009](#), [Lindgren et al. 2011](#)).

206 We fit our models in R version 3.6.1 ([R Core Team 2019](#)) with the R package sdmTMB ([Anderson](#)
[et al. 2019, 2020](#)), which interfaces automatic differentiation and the Laplace approximation in the

208 TMB (Template Model Builder) R package (Kristensen *et al.* 2016) with the SPDE (Stochastic Partial
 Differential Equation) approximation to Gaussian Markov fields from the INLA (Integrated Nested
 210 Laplace Approximation) R package (Rue *et al.* 2009) to find the value of the fixed effects that min-
 imizes the the marginal negative log likelihood. We confirmed that the non-linear optimizer had
 212 converged by checking that the Hessian matrix was positive definite and the maximum absolute
 gradient across fixed effects was < 0.005 .

214 Climate trends and velocities

Bottom temperature and dissolved oxygen (DO) levels have been collected on most tows during
 216 the synoptic bottom trawl surveys since 2008, using Seabird Electronics SBE 19 profilers. From
 these measurements, we predicted seafloor climate using an approach similar to the one described
 218 above for biomass density except we used a Gaussian observation model, 800 knots, and allowed
 the spatiotemporal random fields to follow an autoregressive (AR1) process:

$$C_{s,t} \sim \text{Normal}(\mu_{s,t}, \sigma^2), \quad (7)$$

$$\mu_{s,t} = \mathbf{X}_{s,t}\boldsymbol{\beta} + \omega_s + x_{s,t}, \quad (8)$$

$$\boldsymbol{\omega} \sim \text{MVNormal}(\mathbf{0}, \boldsymbol{\Sigma}_\omega), \quad (9)$$

$$\mathbf{x}_{t=1} \sim \text{MVNormal}(\mathbf{0}, \boldsymbol{\Sigma}_\epsilon), \quad (10)$$

$$\mathbf{x}_{t>1} = \rho\mathbf{x}_{t-1} + \sqrt{1 - \rho^2}\boldsymbol{\epsilon}_t, \quad \boldsymbol{\epsilon}_t \sim \text{MVNormal}(\mathbf{0}, \boldsymbol{\Sigma}_\epsilon). \quad (11)$$

220 Here $C_{s,t}$ represents the climate variable (bottom temperature or log DO) in space s and time t , μ
 represents the mean, and σ represents the observation error standard deviation. The symbol $\mathbf{X}_{s,t}$
 222 represents a vector of predictors (described below) and $\boldsymbol{\beta}$ represents a vector of corresponding
 parameters. The spatial random effects ω_s were defined as in Eq. 5 whereas the spatiotemporal
 224 random effects were structured to follow a stationary AR1 process with first-order correlation
 ρ . Because DO is known to be influenced by both water temperature and seasonal biological
 226 processes, we included a quadratic effect for temperature and a linear effect for day of year along
 with estimated means for each year. Although not shown above for simplicity, we again allowed
 228 the quadratic depth covariates to follow a random walk through time as in Eq. 3. Our bottom
 temperature model fixed effects included only depth and estimated means for each year, because

230 including day of year did not improve model fit based on AIC (Akaike Information Criterion).
Because bottom temperature data (but not DO) have been collected in synoptic surveys since 2003,
232 we included these earlier data in the temperature model to provide more information for estimating
the fixed spatial random field ω_s .

234 For all climate and biomass models, we then projected the model predictions onto a 4×4 km
grid (UTM 9 projection) representing the survey domain. We excluded all cells with predicted
236 conditions outside the range of conditions observed during sampling (99% quantiles of 3.07 to
11.3 °C and 0.28 to 7.06 ml/L DO). We then calculated gradient-based velocities of change and
238 constituent local trends and spatial gradients for each cell. Gradient velocities (V) were calculated
as a ratio of the temporal trend (linear regression slope of each cell's climate time series) divided
240 by gradient in space g of variable A

$$V_s = (\Delta A_s / \Delta t) / g_s, \quad (12)$$

where A is any temporally varying feature of focal cell s . Depending on the portion of the survey
242 grid considered, we calculated the trend through time for biennial time-steps between 2008 and
2018 (6 surveys across 10 years) or 2009 and 2017 (5 surveys across 8 years), but reported values for
244 all cells as a rate of change, or trend, per decade (Table 1). The spatial gradient g_s was calculated as
the vector sum of the mean north-south and east-west gradients based on a 3×3 cell neighbourhood
246 (Burrows *et al.* 2011); however, the values of A from which a spatial gradient is calculated can be
based on any particular subset of times t , or the mean of all Δt .

248 The magnitudes of gradients g_s strongly influence the distribution of velocities V . Most prior
applications of gradient-based velocities have used g_s calculated from the mean cell conditions of
250 the entire period analyzed (e.g., Burrows *et al.* 2011, Molinos *et al.* 2019). Estimated velocities will
tend to be larger (as $g_s \rightarrow 0$, $V_s \rightarrow \infty$) when more estimates (in this case sample years) are averaged
252 for the cells included in the g_s calculation, because a larger sample reduces the variability between
the mean values of adjacent cells. Furthermore, the gradients most relevant to the actual distance
254 an organism would need to travel are those present after changes have begun to occur. Given that
samples were collected only once every two years and that there is variability among species in
256 terms of when dispersal occurs and how long it takes, we used the last two sample periods in our

estimates of spatial gradients (2015–2018). This time period begins the first survey season following
 258 the onset of the 2014–2016 marine heat wave in the north-eastern Pacific (Peterson *et al.* 2015) and
 is approximately the end point of the transition to warmer conditions in the Bering sea (Alabia
 260 *et al.* 2018). We calculated spatial gradients using the vocc R package (Brown and Schoeman 2020)
 and collapsed extreme velocity estimates to their 0.005 and 0.995 quantiles to reduce the impact
 262 of outliers from the resulting heavy-tailed distributions.

Linking biotic changes with climate

264 To explore the relationship between change in estimated local climate and percent changes in
 estimated biomass densities for each 4×4 km grid cell, we used similar spatial GLMMs to control
 266 for spatial autocorrelation among cells. Our models estimated the rate of change in biomass (Y)
 of each maturity class of each species as a function of local climate change (temperature and DO)
 268 and an interaction between the mean climate of each cell and its local rate of change:

$$\Delta Y_{k[s]} \sim \text{Normal}(\mu_{k[s]}, \sigma^2), \quad (13)$$

$$\mu_{k[s]} = \beta_{0,k[s]} + \beta_{1,k[s]}\bar{T}_s + \beta_{2,k[s]}\Delta T_s + \beta_{3,k[s]}\bar{T}_s\Delta T_s + \quad (14)$$

$$\beta_{4,k[s]}\bar{O}_s + \beta_{5,k[s]}\Delta O_s + \beta_{6,k[s]}\bar{O}_s\Delta O_s + \beta_{7,k[s]}\bar{Y}_{k[s]} + \omega_{k[s]},$$

$$\omega_k \sim \text{MVNormal}(\mathbf{0}, \Sigma_\omega), \text{ for } k = 1, \dots, K, \quad (15)$$

$$\beta_{r,k} \sim \text{Normal}\left(\eta_{r,k}, \sigma_{\beta_r}^2\right), \text{ for } k = 1, \dots, K \text{ and } r = 0, \dots, 7, \quad (16)$$

where \bar{T}_s and ΔT_s represent the mean temperature and decadal trend in temperature for spatial
 270 location s . A row of data represents a given spatial grid cell s and species-maturity k combination.
 The symbols \bar{O}_s and ΔO_s represent mean dissolved oxygen and decadal trend in dissolved oxygen,
 272 and the symbol $\bar{Y}_{k[s]}$ represents log biomass density for species-maturity k . Parameters β_0 through
 β_7 (indexed by r) represent coefficients that are allowed to vary as random effects across species
 274 with means $\eta_{r,k}$ and variances $\sigma_{\beta_r}^2$. We accounted for spatial autocorrelation through the spatial
 random effects $\omega_{k[s]}$, which follow a Matérn Gaussian Markov random field as described above.

276 We fit model configurations where both biomass and climate were calculated as either raw
 temporal trends or gradient-based velocities. The trend-based models assessed whether biomass
 278 changes were correlated with changes in climate at the 4×4 km grid cell scale. The velocity-

based models assessed whether changes in biomass, especially those with low local variability
280 in biomass, were correlated with the predicted speed of climate isoclines within the 12×12 km
neighbourhood of cells. We did not include both trends and velocities in the same model because
282 both the units and spatial scales captured are different.

For each maturity class of each species, we included all grid cells that encompassed 95% of
284 the mean total biomass across all sample years and the mean log biomass density of each cell as
a covariate to reduce the influence of changes occurring only at either the highest or lowest den-
286 sities for a particular species. These models used a 600 knot mesh, Gaussian observation errors
when estimating trends, and Student-t observation errors (with a degrees of freedom fixed at 7)
288 to account for heavy-tailed residuals when estimating velocities. We scaled all covariates by their
standard deviations. We centered local average temperature, DO, and log biomass density by their
290 overall means, but kept temperature and DO trend variables uncentered to maintain interpretabil-
ity. We tested additional covariates, including local changes in fishing intensity, but we have not
292 included them in the final models because they did not change our conclusions (see Supplementary
Methods).

294 **Simulation study**

We conducted a simulation study to assess: (1) the ability of the geostatistical models to cope with
296 the high levels of spatial covariance inherent in spatial grid-based climate and biomass estimates,
and (2) to what extent similarities in climate and biotic spatial gradients were responsible for the
298 observed patterns in the velocity-based models. We simulated biomass trends for each species
as random fields using the true variance and spatial correlation parameters estimated for each
300 species. Next, we assessed how well our trend-based model accounted for spatial autocorrelation
among grid-based estimates by re-fitting the trend-based model using four unique iterations of the
302 simulated data and contrasting the effect sizes and number of species that showed a significant re-
lationship with climate trends in the observed vs. simulated models. If the spatial random effects
304 were effective in preventing type I errors, the trend-based models using simulated data should
not show a significant effect of climate more than expected by chance. In the case of velocities,
306 we used the ratio of the simulated biomass trends to the observed spatial gradients in biomass
to simulate biotic velocities (henceforth, 'time-null' velocities). This approach maintains the rela-

308 tionships between spatial gradients in biomass and climate that are likely to occur because both
species abundances and climate on the seafloor are correlated with depth. Rather than being a test
310 of spatial autocorrelation, these time-null velocities were used to test how important the gradient
component was to the results of the fitted velocity model.

312 Null models based on simulated biotic trends and observed climate trends showed fewer sig-
nificant relationships at the species level than would be expected by chance (Figures S1, S2, and
314 S3), confirming that the spatial random effects in our models (e.g., Figure S4) successfully con-
trolled for the spatial autocorrelation. In contrast, models predicting time-null biotic velocities did
316 produce more significant effects than would be expected by chance (Figures S5, S6, and S7 vs. S8).
These associations were likely due to the simulated velocities being based on the observed spatial
318 gradients (Figure S9); however, comparisons between the velocity model and time-null models
suggest that some patterns cannot be accounted for by similarities in the spatial gradients and can
320 be reliably attributed to variation in temporal trends (differences between areas encompassed in
black vs. grey violins for interaction terms in Figure 2b). This is in contrast to the complete overlap
322 in black and grey violins for DO velocity in Figure 2b, which indicates that any set of species with
identical overall distributions and population variability, but completely random biomass trends,
324 would be likely to show just as many significant species-specific effects. Taken together, these
simulations suggest that the velocity model effectively combines both the temporal and spatial
326 dimensions of biotic and climate change, which provides support for our choice to focus on this
approach.

328 **Life-history and ecological correlates of climate sensitivity**

To assess potential ecological mechanisms and the extent to which the temporal and spatial scales
330 considered were appropriate for the different species, we used mixed-effect models to assess con-
cordance between species' life-history traits and ecology and the estimated effect of climate ve-
332 locity. We first assessed the independent effects of mean population age (among immature pop-
ulations only) and occupied depth (mean and range). We then tested for independent relation-
334 ships between climate sensitivity and ecological groupings (including range limits, foraging zones,
trophic level, and sociality), while controlling for the depth total ranges occupied (see Supplemen-
336 tary Methods).

Results

338 Climate trends and velocities

We estimated bottom temperature and DO values biennially between late May and early August
340 during 2008–2018 or 2007–2019, depending on the surveyed area. Seafloor temperature varied
from 4.6 °C to 10.2 °C (95% quantile range) across 4 × 4 km grid cells that had a mean depth within
342 the 99th quantile range of sampled depths (23 to 1112 m). For the same range of survey depths, DO
ranged between 0.7 ml/L and 5.7 ml/L (95% quantiles). For both temperature and DO, the highest
344 values were associated with the shallowest depths, while the lowest values were associated with
the deepest locations (Figure 1b, c).

346 Over this period, summer seafloor temperature increased by an average of 0.6 °C per decade
across the entire region (95% quantile range of -0.2 to 1.8 °C per decade; Figure 1d). In contrast, the
348 direction of change in seafloor DO was more variable (95% quantiles: -2.8 to 0.6 ml/L per decade;
Figure 1e). Warming tended to be most pronounced in the already warmer locations—mean of
350 1.3 °C/decade in cells shallower than 50 m (Figure S10b). Likewise, the greatest decreases in DO
occurred in the shallowest locations (mean: -2 ml/L per decade); however, the highest variability
352 in DO trend (95% quantiles: -1.7 to 0.6 ml/L per decade) occurred between 50 and 200 m depths
(Figure S10e). There was a tendency for the shallowest depths to be occupied by groundfish species
354 that have narrower depth ranges (e.g., Southern Rock Sole, *Lepidopsetta billineta*, vs. Dover Sole,
Microstomus pacificus; Figure S10g, Table S1).

356 When these local climate trends were placed in their geographic context by converting to
gradient-based velocity estimates (Eq. 12), they implied that an organism would have to move an
358 average of 10.5 km/decade (mean of absolute values) to maintain its starting thermal environment
and an average of 11 km/decade to maintain initial DO levels. Temperature velocities averaged pos-
360 itive, representing warming conditions (mean: 10.1; 95% interquantile range of -12 to 87; Figure 1f),
while DO velocities averaged negative, representing declining DO levels (-6.26; -91 to 24; Figure 1g).
362 Most locations of high climate velocity occurred in patches throughout Queen Charlotte Sound
and Hecate Strait (dark red patches in Figure 1f). The most negative DO velocities occurred in
364 shallower portions of Hecate Strait (largest green patch in Figure 1g). The largest velocities tended
to be found across a broader range of depths than the largest climate trends (Figure S10).

366 Linking biotic changes with climate

Geostatistical models linking climatic (Figure 1d–g) and biotic trends (Figures S12 and S13) or velocities (Figures S14 and S15) resolved different aspects of biotic change (Figures S4 and S8). The effect of temperature velocity on biotic velocity was weakly positive across species (β : 0.28 km/decade with 95% CI -0.04 to 0.60; point range for “T change” shown in Figure 2b), despite a significant overall 0.55% decline in biomass (-0.87 to -0.22) per 1 SD increase in warming (0.8 °C per decade) based on local temperature trend only (point range for “T change” shown in Figures 2a). However, mean local temperature influenced the effect of temperature velocity on biotic velocity (β : -1.09, -1.48 to -0.70; “T interaction” in Figure 2b), such that when temperature velocity was high in the warmest parts of a species’ range, local biomass was more likely to decline and exhibit larger negative or smaller positive biotic velocities. When temperature velocity was high in the coolest parts of a species range, local biomass was more likely to increase, and to result in smaller negative or larger positive biotic velocities.

Interactions between mean climate and climate velocity for each maturity class of each species can be illustrated as the predicted relationships between climate and biotic velocities at different mean local conditions (e.g., in Figures 3c and S11a, the blue and red lines are the predicted relationships for locations at the 0.025 and 97.5 quantile of mean local temperatures, respectively). For Redbanded Rockfish (*Sebastes babcocki*) the horizontal blue line indicates stable biomass (small absolute biotic velocities), while the red line with a negative slope means that biomass was more likely to be declining across a local area where conditions were warmest on average and getting warmer across more of the surrounding area (Figure 3b). The slopes of all predicted relationships (e.g., as illustrated in Figure 3c and Figure S11a) are plotted for all species-maturity combinations in Figure 4. Consistent with the overall interaction, the majority of species-maturity combinations with significant interactions between local mean temperature and temperature velocity had negative interactions (31 of 33 coloured dots and lines with red coefficients to the left of blue coefficients in Figure 4a). Over a third of these cases predicted a positive effect of increased temperature velocities for both the warmest and coolest locations, but that the relationship was more strongly positive in the cooler locations (13 of 31 species-maturity combinations with negative interactions).

To assess whether these relationships predicted that specific species’ biotic velocities were increasing or decreasing under different climate velocities, the lines displayed in Figures 3c and S11a

396 can be “sliced” at either the minimum temperature velocity experienced by each species (left end of
lines) or at the maximum (right end of lines). The expected biotic velocity was near zero for most
398 species-maturity combinations in locations experiencing minimum climate velocity (Figure 5a)
regardless of mean temperature. However, the expected biotic velocity was strongly negative for
400 a number of species-maturity combinations (19 of 69) in the warmest locations when experiencing
maximum climate velocity and tended to be positive in cooler locations experiencing the same
402 high climate velocity (e.g., Pacific Halibut, *Hippoglossus stenolepis*; Figure 5b).

After controlling for temperature, the average effect of DO velocity on biotic velocity was
404 negative across species (β : -0.48 km/decade, -0.82 to -0.15; point and range for “DO change” in
Figure 2b) despite there being a positive effect of DO trend on biomass trend (β : 0.34 % increase in
406 biomass, 0.16 to 0.52; point and range for “DO change” in Figure 2a). Thus, while increasing DO
was associated with increases in biomass at a local scale, DO velocity was not on average correlated
408 with biotic velocities. However, unlike for temperature, DO velocity did not interact with mean
DO availability consistently across species (β : 0.25, -0.05 to 0.55). Only two species (those with
410 green point ranges on the positive side of the x-axis in Figure 4b) showed the expected interaction
where locations with lower mean DO levels experiencing positive DO velocities were associated
412 with increases in biotic velocity and/or negative DO velocities were associated with decreases in
biotic velocity (e.g., immature Lingcod, *Ophiodon elongatus*; Figure 3). In contrast, several species
414 experienced declines in biotic velocity when DO velocity increased across the range of mean DO
levels (black point ranges on negative side of x-axis in Figure 4b).

416 **Life-history and ecological correlates of climate sensitivity**

We examined possible relationships between responses to climate velocities and each species’ tax-
418 onomy, traits, and depth distributions. Relationships with biotic velocities that were negative
at high temperatures or positive at low temperatures occurred in members of both the largest
420 families represented in our analysis, Sebastidae (rockfish) and Pleuronectidae (righteye flounders)
suggesting no strong patterns of similarity among species belonging to the same genus or fam-
422 ily (Figures 4a and S8; see also non-significant family-level effects from hierarchical model, Fig-
ure S16). However, the effects of temperature velocities at high temperatures were most negative
424 for Chondrichthyan biotic velocities (-1.8 km/decade per SD in temperature velocity, same units

apply elsewhere) and rockfish species occupying shelf habitats (-1.3), neutral for continental slope
426 rockfish (0.1) and flatfish (-0.1), and most positive for sablefish (1.0; mean across red values in
Figure 4a).

428 Life-history failed to explain substantial variation in climate sensitivity in the warmest loca-
tions, although more negative effects tended to be clustered in shallow depths and among younger
430 immature populations (Figure S17). However, the positive effects of temperature velocities on bi-
otic velocities in the coolest locations were strongest in species occupying a larger range of depths
432 (β : 0.57, 0.21 to 0.92) and for immature populations with younger mean age (β : -1.0, -2.0 to 0).
Ecological factors were somewhat better at accounting for negative effects in the warmest loca-
434 tions. The effects of temperature velocity at high mean temperatures differed significantly between
species depending on diet (lower biotic velocities in zooplantivores than species at higher trophic
436 levels; β : -0.96, -1.44 to -0.48), and use of foraging zones (higher biotic velocities in demersal
species relative to benthopelagic; β : 0.98, 0.47 to 1.49) after accounting for mean depth occupied
438 (Figure S18 top row). The strongest negative effects of warming temperature velocities (estimated
for the warmest parts of a species distribution) were for species occurring at intermediate depths,
440 whereas most species with mean encounter depths deeper than 290 m appeared to increase in
biotic velocity with more positive temperature velocities (Figure S19c).

442 In contrast, DO velocities at low mean DO locations only showed a strong positive effect on
Lingcod biotic velocities (0.7) and negative effects were strongest for both continental slope rock-
444 fish (-1.1) and flatfish (-1.4; mean across green values in Figure 4b). These negative relationships
represent declining biotic velocity with increasing DO, or visa versa, and tended to be stronger
446 both for species occupying deeper locations on average (β : -0.43, -0.73 to -0.13; Figure S19d) and
a larger range of depths (β : -0.30, -0.6 to 0). It is notable, however, that the effect of trends in
448 DO on percent change in biomass were also negative at these depths despite being mostly positive
at intermediate depths (Figure S19b). At these intermediate depths (the mean occupied depth for
450 species in this analysis of about 175 m), the effects of DO velocity at low DO was also most negative
for species foraging at higher trophic levels (β : -0.33, -0.81 to 0.16), in the demersal zone (β : -0.79,
452 -1.32 to -0.26), and with more solitary habits (β : -0.63, -1.21 to -0.06; Figure S18 bottom row).

Discussion

454 Using novel geostatistical models fit to bottom temperature, DO, and demersal fish biomass from
scientific trawl surveys, we related trends and velocities between climatic and biotic variables
456 across 38 species. Local declines in demersal fish biomass were, on average, associated with warm-
ing trends and decreases in DO. However, after converting trends to velocities, a clear interac-
458 tion between temperature velocity and mean bottom temperature emerged. On average, and for
roughly half the species-maturity combinations, temperature velocity had a more negative effect
460 on biotic velocity in already warm locations than in relatively cool locations. Converting these
interaction effects into expected values, approximately one quarter of species-maturity combina-
462 tions experienced declines (negative biotic velocities) in the warmest locations when experiencing
maximum warming. In contrast, locations experiencing minimal warming or cool locations ex-
464 perience maximum warming experienced stable or increasing biotic velocities. Characteristics
such as trophic level, foraging zone, and sociality—as well as potentially confounding variables
466 such as commercial fishing effort or catch—explained little of the observed effects. Although DO
velocity results were more equivocal, planktivores responded more positively to DO velocity un-
468 der low DO conditions (Figure S18f) than species with more diverse or higher trophic-level diets.
This suggests that the prevalence of strong negative relationships between DO and biotic veloci-
470 ties (Figure 2b) might be explained by increases in primary production in benthic environments,
causing decreases in DO due to increased rates of decomposition (Keister *et al.* 2020).

472 Scale and context dependence

Our analysis is the first, to our knowledge, to explore how the interaction between climate veloc-
474 ities and local mean climate conditions affect fine-scale biotic velocities, and the first to contrast
patterns between trend and velocity indices. Globally, the impact of temperature change in marine
476 environments appears to be highly dependent on local mean temperatures, whether measured in
range shifts relative to temperature velocity (e.g., Lenoir *et al.* 2020) or species richness and abun-
478 dance in response to temperature trends (e.g., Antão *et al.* 2020). Specifically, this latter meta-
analysis of patterns in marine taxa found that abundance was positively correlated with warming,
480 except in the warmest of locations (Antão *et al.* 2020). While our trend model indicated an overall

negative effect of rising temperatures on local fish density, the velocity model was consistent with
482 the global pattern in showing that most negative relationships occurred only in already warm lo-
cations (Figure 2). Large climate velocities reflect more spatially uniform environments—where
484 an organism would need to move greater distances to maintain constant climate—and likewise,
small velocities reflect more spatially heterogeneous environments (Loarie *et al.* 2009). As a re-
486 sult, more spatially uniform regions have greater weight in the velocity model than in the trend
model, and this stretching and compressing of trend values based on spatial heterogeneity likely
488 explains why the negative interactive effect of mean temperature was only detected for veloci-
ties. Overall, we focused primarily on the velocity results since they represent a more ecologically
490 meaningful measure than trends alone, given that they account for the local reality species face
if tracking a constant environment (Brito-Morales *et al.* 2018) or prey that themselves track the
492 environment.

For many species, we do not know how far individuals travel on a daily or seasonal basis, so
494 uncertainty remains as to the extent to which the modelled spatial resolution is appropriate for
each of the species in this analysis. While the trend- and velocity-based models capture slightly
496 different spatial scales (4×4 km focal cell vs. 12×12 km encompassed when considering pat-
terns among neighbouring cells as well), both resolutions are smaller than what is often used for
498 analyses of climate change in the marine environment (Oestreich *et al.* 2020, Pinsky *et al.* 2020),
substantial environmental changes can occur at even smaller scales, and these local-scale effects
500 may be especially important for species with high site fidelity (e.g., Yelloweye Rockfish *Sebastes*
ruberrimus, Hannah and Rankin 2011). However, in order to detect the impact of climate change
502 on rockfish (many of which have generation times > 20 yrs), one would require either data in
excess of 20 years, or to contrast patterns of change between age classes. Indeed, responses to
504 environmental change can be expected to differ between species, depending on the life history of
species including physiological tolerances, lifespan, and dispersal patterns (Massiot-Granier *et al.*
506 2018). Furthermore, reaching reproductive maturity frequently results in shifts in dispersal pat-
terns, habitat selectivity, physiological tolerances (Laurel *et al.* 2007), and therefore represents a
508 potentially important break point for understanding the impacts of climate change. Given the rel-
atively short timescale encompassed in our analysis (one decade), we expected to find stronger
510 patterns in shorter-lived/immature portions of populations and more pelagic species. Within im-

mature populations, those with a younger mean age were found to exhibit the most extreme re-
512 sponses to temperature velocity (positive in coolest locations and negative in warmest locations;
Figure S17c); however, immature populations did not have overall stronger responses than mature
514 populations (Figure S22b). Ecological responses were somewhat complicated by interactions with
depths occupied; but, contrary to expectation, more extreme responses tended to belong to dem-
516 ersal foraging and solitary species, rather than those with more pelagic or schooling behaviours
(Figure S18c, g, h).

518 Aggregate metrics such as the centre of gravity have also demonstrated that demersal fishes
use both shifts in latitude and depth to track changes in ocean temperatures (e.g., [Perry et al. 2005](#),
520 [Dulvy et al. 2008](#), [Li et al. 2019](#)), but evidence that range edges on the North American continental
shelf have shifted further north than expected or even contracted southward, suggest roles for
522 competition, climate-independent mortality and/or density-dependent habitat selection ([Li et al.](#)
[2019](#), [Fredston et al. 2020](#)). Indeed, fishing pressure on the Atlantic shelf was found to be more
524 important than average bottom temperature for predicting centre of gravity for five groundfish
species, despite temperature being more correlated with variance in biomass ([Adams et al. 2018](#)).
526 This latter result suggests that there was spatial variability in temperature, or responses to temper-
ature, which were not fully captured by the centre of gravity ([VanDerWal et al. 2013](#)). Fine-scale
528 local effects may contribute to the relatively greater influence of temperature relative to fishing
pressure in our analysis. Groundfish species in the eastern Bering Sea also do not show a strong
530 correlation even for local climate and biotic velocities, but no interaction with mean conditions
was reported ([Alabia et al. 2018](#)). Another potential explanation for stronger negative effects on
532 Canadian Pacific groundfish is that species here are closer to the southern ends of their distribu-
tions and may therefore be closer to the warm end of their temperature tolerances, especially in
534 the warmest locations. However, although we found the strongest negative biotic velocities in
these warmer locations, species nearer to their northern range limit were not more likely to show
536 a positive response to temperature.

Limitations and implications

538 There are a number of limitations to our analysis. First, our analysis cannot separate fish movement
in response to climate from a host of other possible explanations. For example, local changes in

540 biomass density can be a result of movement, local population growth, age cohorts beyond our
two maturity categories, changes in average body size (Shackell *et al.* 2010, Laurel *et al.* 2007),
542 or effects of fishing not captured by the metrics of total catch or hours fished. Indeed, some of
the hypothesized effects of warming climate and lower DO on fishes include higher metabolism
544 and ability to store fat, reduced productivity, and slower growth resulting in generally smaller fish
(Klein *et al.* 2017, Madeira *et al.* 2017). Furthermore, changes in local density may be correlated
546 with climate, not because of groundfish thermal preference, but because groundfish seek prey or
avoid predators that have themselves shifted their distribution in response to climate. Second,
548 there are limitations to our data. The CTD climate data from Canadian Pacific trawl surveys are
only available from 2008 onward, the surveys occur in one seasonal period (May to August) and
550 cover a given region only once every two years. Also, some of the species (e.g., shallower rockfish
species) may be better sampled by longline gear than trawl gear. This spatial and temporal scope
552 will miss overlap in major life-history events for some species (e.g., Sablefish; Beamish 2008), or
seasonal movements (e.g., Pacific Halibut; Loher 2011). Importantly, the input data for our meta-
554 analytic model are predictions from our first-stage geostatistical models. Third, it is possible that
climate conditions may themselves affect survey catchability. For example, groundfish may flee
556 gear more slowly or aggregate to avoid low DO conditions (Craig 2012), thereby making fish more
catchable and biasing observations.

558 This analysis suggests multiple future research directions. First, future efforts may aim to iden-
tify common spatial patterns across species using spatial dimension reduction tools such as spatial
560 factor analysis (Thorson *et al.* 2015a). Areas where species overlap in their response would repre-
sent important areas for conservation (Brito-Morales *et al.* 2018), but also areas where competition
562 may be expected to increase or new fisheries interactions may occur. Second, some rockfish are
better sampled by longline survey gear and future analyses could use such survey data, or com-
564 bine survey data from multiple gear types (Webster *et al.* 2020), to develop a composite density
estimate. Third, our analysis used CTD data, which was only available for spring or summer from
566 2008 onwards and required a statistical model to extrapolate to the full region. An alternative
would be a ROMS (Regional Ocean Modeling System) model (Peña *et al.* 2019), which could extend
568 the temporal scope, allow for accounting of climate at other times of the year (e.g., temperature
during spawning; Laurel and Rogers 2020), allow for inclusion of variables not typically measured

570 with survey data (e.g., primary production), and allow for forward projections. Preliminary inves-
572 tigations indicated a strong correlation between our CTD projections and recently updated ROMS
574 bottom temperatures. With the greater spatial and temporal extent that ROMS data will provide,
576 calculation of more geographically precise analog-based climate velocities could be used to further
578 refine the identification of areas important for conservation (Brito-Morales *et al.* 2018).

Climate change is expected to have large impacts on fish stocks and their management, par-
576 ticularly with respect to changes in species distribution (e.g., Tommasi *et al.* 2017, Karp *et al.* 2019,
578 Free *et al.* 2019). Legislation and policy in jurisdictions around the world (e.g., the US *Magnuson-*
580 *Stevens Act*, Canada's *Fisheries Act*, the European Marine Strategy Framework Directive) require
582 that environmental conditions affecting fish stocks be accounted for in management decisions
584 such as setting sustainable catch limits and developing rebuilding plans. However, there is of-
586 ten a mismatch between scale of climate predictions, the scale at which species respond, and the
588 scale of management decisions (Stock *et al.* 2011, Maureaud *et al.* 2021). For example, the popula-
590 tions analyzed in this study are managed at the mesoscale, with catch limits often determined for
592 individual substocks (DFO 2019). The metrics presented in our paper represent fine-scale indica-
594 tors of response to a changing environment, which are useful for assessing risk and conservation
596 planning (Brito-Morales *et al.* 2018). Shifts in distribution, such as those reported here, can have
implications for calculation of indices of abundance, and estimates of stock size and stock status,
which in turn may impact harvest recommendations (Szuwalski and Hollowed 2016, Karp *et al.*
2019). Analyses such as ours can be incorporated into frameworks for improving advice for the
management of fisheries under climate change (e.g. Plagányi *et al.* 2011, Punt *et al.* 2014, Karp *et al.*
2019).

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598 Data Availability Statement

The biological data that used in this study are openly available through <https://open.canada.ca>
600 at <https://open.canada.ca/data/en/dataset/a278d1af-d567-4964-a109-ae1e84cbd24a> and associated
environmental measurements are available from [https://www.pac.dfo-mpo.gc.ca/stats/index-](https://www.pac.dfo-mpo.gc.ca/stats/index-eng.html)
602 [eng.html](https://www.pac.dfo-mpo.gc.ca/stats/index-eng.html). All of the code underlying this analysis is available at [https://github.com/pbs-](https://github.com/pbs-assess/gfvelocities)
[assess/gfvelocities](https://github.com/pbs-assess/gfvelocities).

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Tables

Table 1: Gradient-based velocity metrics and their definitions. Climatic variables are temperature and dissolved oxygen (DO); biotic variables are biomass density for the mature and immature components of a species. Climatic and biotic variables are represented generically by A . Our analysis treated gradient-based velocity as a scalar, using only the magnitude component of the velocity vector.

| Term | Notation | Definition | Magnitude | Sign |
|-------------------------|---|---|---|--|
| Local trend | $m_s^A = \frac{\Delta A_s}{\Delta t}$ | Change in local biotic or climatic scalar A per decade | Temporal rate of change in A | Increasing (+) or decreasing (-) local trend in A |
| Spatial gradient | \vec{g}_s^A | Vector sum (magnitude, angle) of mean north or south and east or west gradients of A in a 3×3 cell spatial neighbourhood | Spatial rate of change in A | Vector magnitude and angle always positive (+) |
| Gradient-based velocity | $\vec{V}_s^A = \frac{m_s^A}{\vec{g}_s^A}$ | Vector velocity (magnitude, angle) from local trend of A divided by vector local spatial gradient of A | Speed of travel predicted to maintain initial A | Increasing (+) or decreasing (-) based on the local trend in A |

Figures

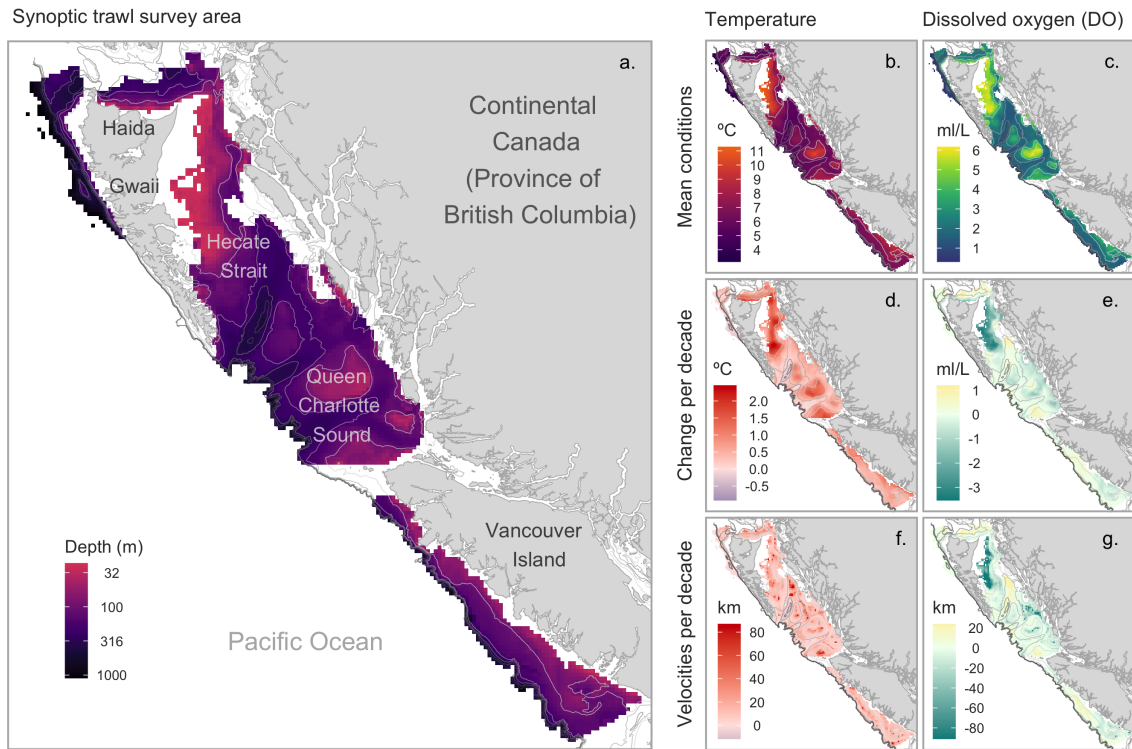


Figure 1: Maps of study area (a), predicted mean conditions (b, c), decadal trends (d, e), and decadal velocities (f, g) of bottom temperature and dissolved oxygen (DO) for 2008–2018 off the coast of British Columbia, Canada. Values are estimated using geostatistical spatiotemporal models of CTD sensor data collected during late-spring/early-summer groundfish trawl surveys. Bathymetry lines at every 100 m are overlaid in shades of grey that increase with depth.

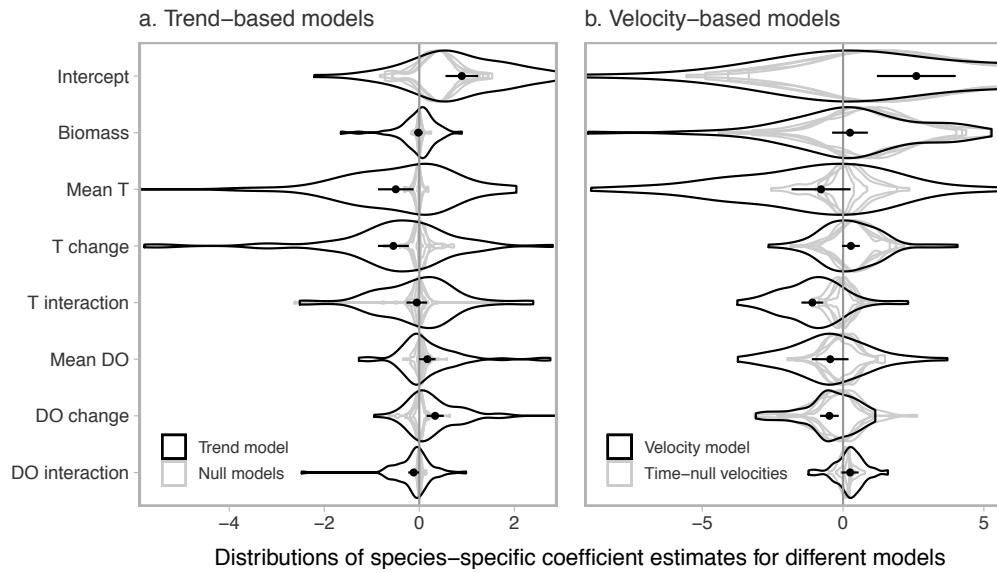


Figure 2: Distribution of species-specific (random effect) coefficients from the model fitted to observed data (black violins) compared with coefficients from four simulated null models (gray violins). Each “violin” is based on a single model including all species (a: trend-based models where climate and biotic change variables are all local trends; b: velocity models where climate and biotic change variables are all velocities). Black points with ranges represent the observed-data global (fixed effect) coefficient estimates with 95% CIs. Null models used fitted covariate values, but simulated response data. Simulated time-null velocities used these same simulated trends divided by the real spatial gradients. The x-axes have been truncated slightly for interpretability.

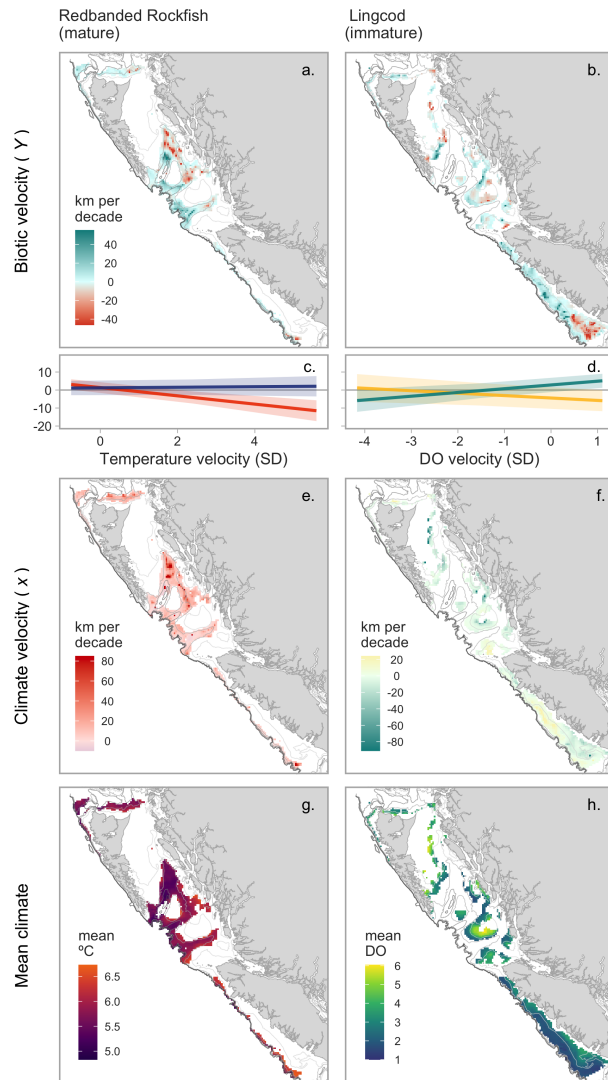


Figure 3: Maps and interaction plots for two illustrative species representing the most frequent relationship with temperature (left column) and the expected response with DO (right column). Mature *Sebastes babcocki* had stable, near-zero, biotic velocities regardless of amount of warming in the coolest regions it occupied, and decreases in biomass when temperatures increased in warmer regions (a,c,e,g). Immature *Ophiodon elongatus* biotic velocities increased with positive DO velocities in low mean DO locations only (b,d,f,h). In panel c, a blue line represents predicted biotic velocity (Y , y -axis) for different temperature velocities (x , x -axis) in the coolest locations (0.025 quantile of those occupied by 95% of the estimated biomass of each species) and a red line represents the same for the warmest locations (0.975 quantile). Likewise, for predictions at different DO velocities, green represents the lower quantile of mean DO and yellow the higher (d). Both the colours and slopes illustrated correspond with those in Figure 4. The maps include biotic velocity estimates for all locations that cumulatively account for 95% of the estimated biomass of each species (a, b), and the same climate estimates as in Figure 1, but trimmed to include only the values for the same locations as the biotic velocities for each species predicted relationships.

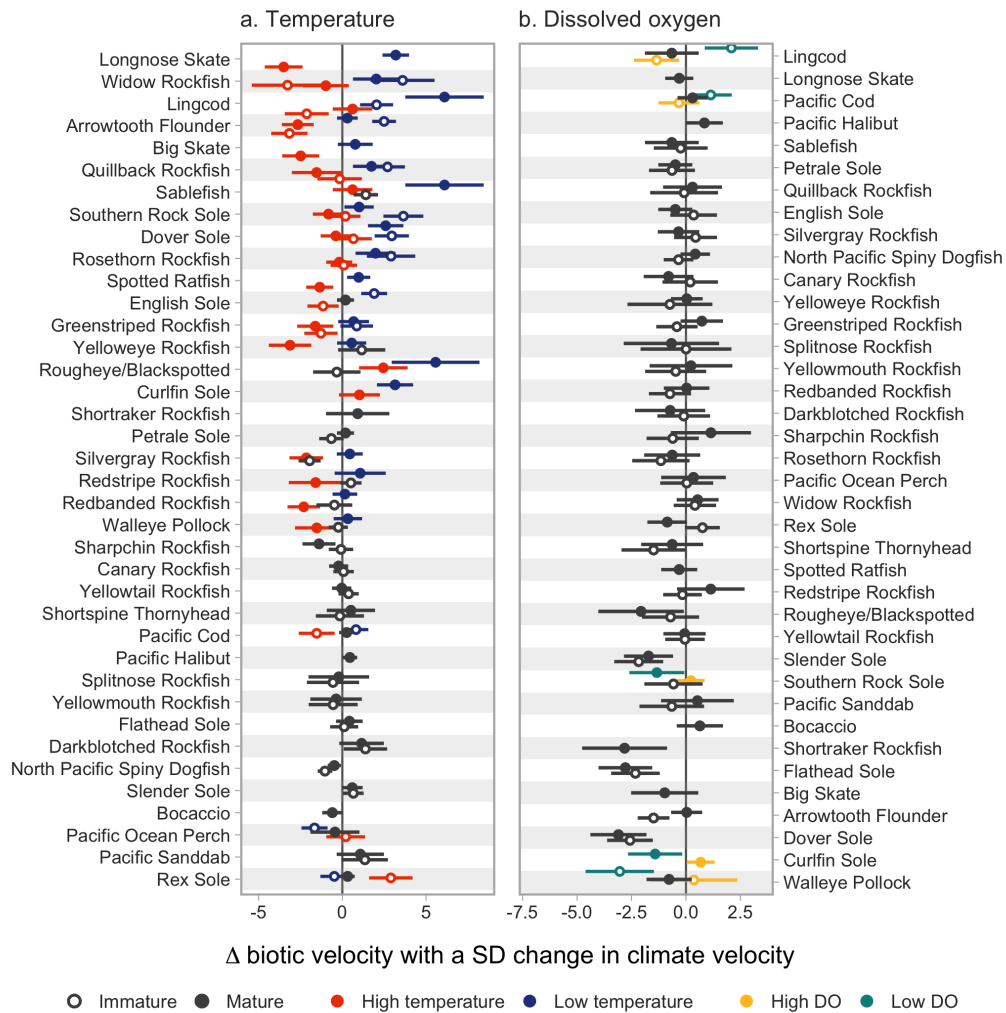


Figure 4: Mean climate and climate change interact in predicting biotic velocities (km/decade) for 38 groundfish species. Coloured dot-whiskers indicate slopes and 95% CIs of the predicted biotic velocities with 1 SD of change in climate velocity for the low and high 95% quantiles of mean local climate (i.e., the slopes of lines in interaction plots like those in Figure 3c, d). Species are ordered by the difference between the slopes at the highest and lowest quantiles of mean climate such that the more intuitive results are at the top: increases in climate velocity have a more positive impact on biotic velocity when starting at a low mean temperature (a) or DO level (b). Open circles indicate patterns for immature fish and closed circles represent individuals large enough to have a 50% chance of having reached reproductive maturity, or belonging to species for which maturity data was not available. Black dot-whiskers represent the slopes for each maturity class when the interaction is not significant.

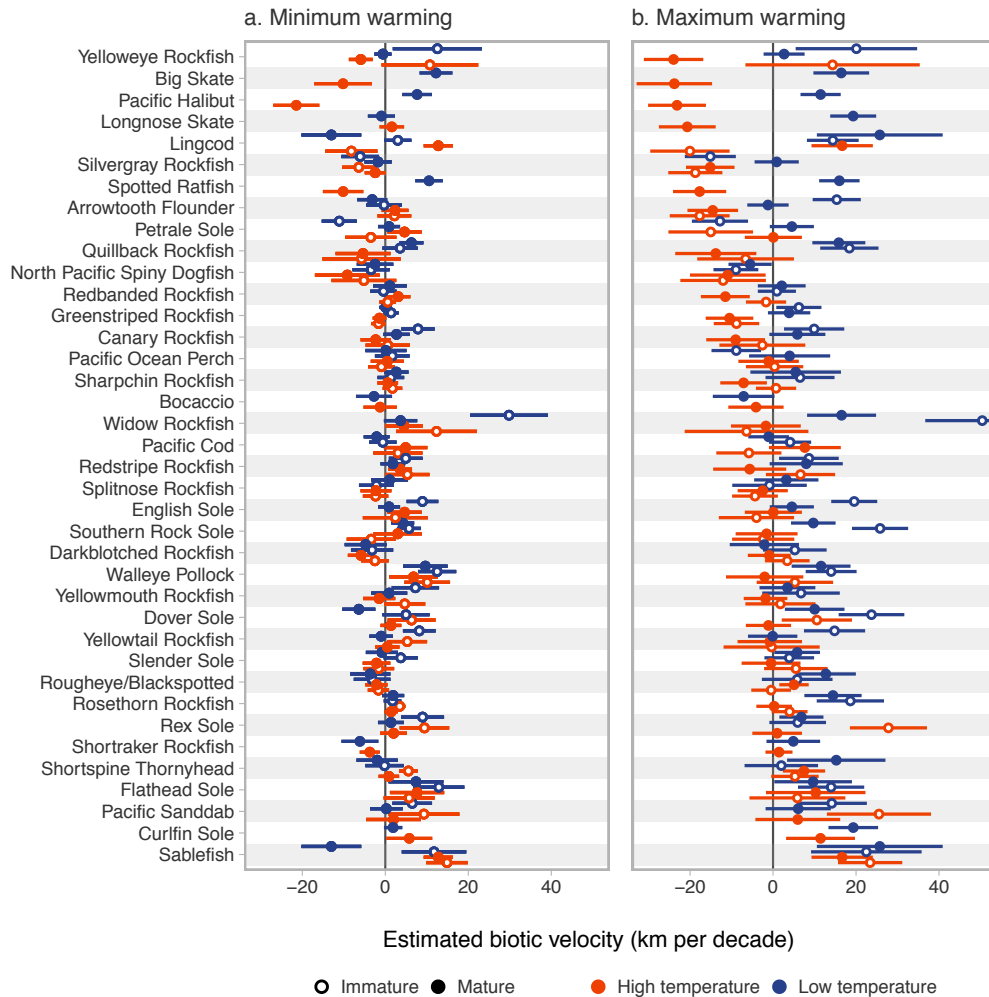


Figure 5: Estimates of biotic velocities (km/decade with 95% CI) for 38 groundfish species under different mean temperatures (blue and red represent low and high 95% quantiles) occupied and at (a) the minimum and (b) maximum temperature velocities experienced for each species. Open circles indicate patterns for immature fish and closed circles represent individuals large enough to have a 50% chance of being reproductively mature, or belonging to species for which maturity data were not available. Species are ordered by the minimum estimates at the maximum climate velocity experienced for each species. Therefore, species most likely to experience population declines with increasing temperatures are at the top.

Supporting Methods, Tables, and Figures

2 Maturity and length-weight models

When maturity data were collected for a species in all years for all surveys (> 250 samples across
4 all years and > 40 each year), we included a random intercept for year to allow for temporal change
in size at maturity:

$$M_i \sim \text{Bernoulli}(p_i), \quad (1)$$

$$p_i = \text{logit}^{-1}(\alpha + \alpha_t + \beta L_i), \quad (2)$$

$$\alpha_t \sim \text{Normal}(0, \sigma_\alpha^2), \quad (3)$$

6 where M_i represents the mature (1) or immature (0) status of fish i , p_i represents the probability of
maturity of fish i , α represents a global intercept, α_t represents a year-specific deviation for year t
8 that is allowed to vary with a variance of σ_α^2 , β represents a coefficient, and L_i represents the length
of fish i . We used year-specific 50% maturity probability thresholds to split observed catches into
10 maturity classes. For species not meeting the above thresholds, we used a random effect of tow
instead of year, and split catches based on the global estimate.

12 For all catches exceeding the species-specific threshold count of individual fish on a survey,
either a random subset of roughly 50 fish or all individuals were measured for both length and
14 weight. We therefore filled in occasional missing weights as

$$\log(W_i) \sim \text{Student-t}(3, \log(a) + b \log(L_i), \sigma), \quad (4)$$

with W_i and L_i representing the weight and length for fish i , a and b being the species-specific
16 parameter estimates of the length-weight relationship $W_i = aL_i^b$, σ representing the observation
error scale, and 3 representing a degrees of freedom parameter fixed to allow for outlying residuals.

18 Alternative spatiotemporal models of fish biomass density

We tried including the proportion of muddy sediment and proportion of sediment with any rocks
20 as covariates in biomass density models, but the values we used were likely not specific enough to
the trawl path sampled, and therefore not helpful to our models. Certainly more spatially precise
22 estimates would be possible with refined substrate variables, but likely irrelevant to this analysis
given the resolution and uncertainty in our climate variables. Furthermore, the spatial random
24 effects can account for spatial factors that are constant across time, like substrate type, while
spatiotemporal random effects account for factors that vary from year to year spatially such as
26 bottom temperature, water circulation patterns, species interactions, and species movement.

Velocity calculation considerations

28 An alternative to gradient-based velocity calculations is to search for analogous conditions in the
second time period and calculate the shortest actual distance to an analogous cell. This method
30 requires a threshold of change below which cells are deemed analogous which is often derived from
historical variability in climate. We calculated analog-distance velocities that were qualitatively
32 similar to gradient-based velocities by using twice the minimum standard deviation of each climate
variable as our threshold and time periods defined by prior-to and post onset of the same marine
34 heatwave. However, models including these values tended to have more difficulty converging,
so we relied instead on the gradient-based values and the component values for all our analyses
36 (Figs 1 and S9).

Alternative model configurations for linking biotic changes with climate

38 We tested additional covariates that we chose not to include in the final model. We calculated av-
erage hours fished by commercial bottom trawl for each 4×4 km grid cell per year between 2008
40 and 2018, as well as the percent change in time spent fishing during this time (Figure S20). The
log of mean fishing intensity, the trend in fishing intensity, and the interaction between the two
42 were all included as covariates in a climate trend model, but none of these variables showed any
more significant negative relationships than might be expect by chance (Figure S21). We tested
44 for an overall effects of maturity (treating mature fish as the intercept) on the main effects of all
climate variables (all two-way interactions), and on the interactions (model with 3-way interac-
46 tions). For each maturity class of each species, the model estimated an independent random spatial
field either with or without genus or family as taxonomic grouping factors (Figure S16); however,
48 final models do not include any grouping factors because they did not change any of the model
estimates qualitatively. Finally, we attempted to assess the importance of the gradient component
50 in velocity estimates by adding temperature gradient to a model of biomass change in response
to temperature trends, and including a three-way interaction between temperature trend, mean,
52 and gradient. None of the important effects we focus on in the results (Figure S22) were changed
qualitatively by any of these added variables.

54 How climate sensitivity varies with life history

We calculated weighted means and interquartile ranges of depths from maturity-specific biomass
56 densities for all survey catches. Because climate conditions experienced vary with depth and a
narrower species depth range might increase other ecological effects, we include these variables
58 as covariates. From the individual fish caught in these trawl surveys, we calculated the maximum
recorded body mass of each species and average age (estimated from otoliths or fin clips when
60 available) for each maturity class of each species Given that age data were available for only a

subset of species, we first assessed the independent effects of mean population age and occupied depth (mean and range) on species responses to climate (Figure S17). These models also included an interaction with whether the response slope estimated was at the high or low extreme of mean conditions, and a random intercept for species (to capture the non-independence of the estimates for high and low climate extremes). Finally, to reduce leverage of extreme slope estimates, these extreme values were collapsed down to be equal to the 0.005 and 0.995 quantiles of all slope estimates. We then tested for relationships between ecological groupings and slope estimates (at both the high or low extreme of mean conditions) across both maturity classes, while controlling for the mean depth occupied. These models also used collapsed slope estimates (see previous paragraph), included a fixed effect of the mean climate (high or low) that the response slope was estimated for, and a random intercepts for both species and maturity classes nested within species.

How climate sensitivity varies with ecology

The species and life history stages varied with respect to their trophic level, behaviour, and overarching distribution (Table S1). Species were classified into either zooplanktivores or higher trophic level feeders based on the majority of their diet components from available literature (Love *et al.* 2002, Yang *et al.* 2006, Bizzarro *et al.* 2017). Species were classified as solitary and demersal (flatfishes, Lingcod, Sablefish, skates and some rockfishes) or benthopelagic and schooling (cods and some rockfishes). Rockfishes were classified based on Love *et al.* (2002). British Columbia occupies a unique oceanographic position at the bifurcation of the North Pacific Current (Royer 1998, Masson and Fine 2012). As such, the distribution of some groundfish species is limited to the north of British Columbia (such as for many of the rockfish species). Although species can occur in Alaska, British Columbia demarcates a northern boundary of relatively high abundance. It was expected that some of the groundfish species in this analysis might be responsive to these larger scale species distribution patterns. Thus, each species was qualitatively categorized based on bottom trawl survey catches in British Columbia, Washington State and Alaska as either occurring in the middle (high catches of the species in all three areas), northern (lowered catches of the species in Southeast Alaska) or southern (lowered catches in Washington State) portions of the species range. There were only three species in the southern portion of their range (Walleye Pollock, Flathead Sole and Arrowtooth Flounder), so in the analysis these were combined with the species in the middle of their distribution.

Table S1: Ecological data for 38 species analyzed, ordered by frequency of occurrence on trawl survey sets between 2008-2018. Classification codes: N = near northern range limit, S = nearer to centre of range or southern limit, L = zooplanktivore, H = all higher trophic diets.

| Common name | Scientific name | Sets | Depth occupied (m) | | | | Mean age (years) | | Range limit | Trophic level | | Foraging zone | Sociality |
|--------------------------------|--|------|--------------------|-----|--------|-----|------------------|------|-------------|---------------|------|----------------------------|------------------------|
| | | | Immature | | Mature | | Imm. | Mat. | | Imm. | Mat. | | |
| | | | Mean | IQR | Mean | IQR | | | | | | | |
| Arrowtooth Flounder | <i>Atheresthes stomias</i> | 85% | 166 | 69 | 168 | 73 | 3 | 10 | S | L | H | Demersal | Solitary |
| Rex Sole | <i>Glyptocephalus zachirus</i> | 82% | 139 | 55 | 165 | 67 | - | - | S | H | H | Demersal | Solitary |
| Spotted Ratfish | <i>Hydrolagus collicii</i> | 80% | - | - | 97 | 69 | - | - | N | - | H | Demersal | Schooling |
| Dover Sole | <i>Microstomus pacificus</i> | 74% | 167 | 65 | 219 | 145 | 7 | 14 | S | H | H | Demersal | Solitary |
| Sablefish | <i>Anoplopoma fimbria</i> | 55% | 232 | 145 | 295 | 220 | 2 | 14 | S | H | H | Demersal | Solitary |
| North Pacific Spiny Dogfish | <i>Squalus suckleyi</i> | 54% | 115 | 61 | 124 | 74 | - | - | N | L | H | Benthopelagic | Schooling |
| Pacific Ocean Perch | <i>Sebastes alutus</i> | 52% | 239 | 56 | 265 | 58 | 6 | 24 | S | L | L | Benthopelagic ⁺ | Schooling ⁺ |
| Pacific Cod | <i>Gadus macrocephalus</i> | 52% | 121 | 69 | 125 | 67 | 2 | 4 | S | H | H | Benthopelagic | Schooling |
| Silvergray Rockfish | <i>Sebastes brevispinis</i> | 46% | 181 | 51 | 198 | 60 | 11 | 25 | N | L | L | Benthopelagic | Solitary |
| Walleye Pollock | <i>Gadus chalcogrammus</i> | 46% | 133 | 56 | 140 | 73 | - | - | S | L | L | Benthopelagic | Schooling |
| Slender Sole | <i>Lyopsetta exilis</i> | 44% | 156 | 50 | 157 | 52 | - | - | N | H | H | Demersal | Solitary |
| English Sole | <i>Parophrys vetulus</i> | 44% | 72 | 46 | 89 | 43 | - | - | N | H | H | Demersal | Solitary |
| Redbanded Rockfish | <i>Sebastes babcocki</i> | 41% | 257 | 70 | 230 | 62 | 10 | 28 | S | L | L | Benthopelagic | Solitary |
| Petrale Sole | <i>Eopsetta jordani</i> | 41% | 117 | 46 | 120 | 48 | 5 | 9 | N | L | H | Demersal | Solitary |
| Pacific Halibut* | <i>Hippoglossus stenolepis</i> | 40% | - | - | 110 | 88 | - | - | S | - | H | Demersal | Solitary |
| Shortspine Thornyhead | <i>Sebastolobus alascanus</i> | 40% | 329 | 91 | 352 | 102 | - | - | S | H | H | Demersal | Solitary |
| Lingcod | <i>Ophiodon elongatus</i> | 34% | 126 | 51 | 145 | 70 | 3 | 7 | S | H | H | Demersal | Solitary |
| Longnose Skate* | <i>Raja rhina</i> | 32% | - | - | 222 | 131 | - | - | S | - | H | Demersal | Solitary |
| Flathead Sole | <i>Hippoglossoides elassodon</i> | 32% | 133 | 45 | 131 | 45 | - | - | S | H | H | Demersal | Solitary |
| Sharpchin Rockfish | <i>Sebastes zacentrus</i> | 29% | 213 | 50 | 235 | 25 | 7 | 16 | S | L | L | Benthopelagic | Schooling |
| Greenstriped Rockfish | <i>Sebastes elongatus</i> | 26% | 182 | 45 | 173 | 40 | 9 | 26 | N | L | L | Demersal | Solitary |
| Rougheye/Blackspotted Rockfish | <i>Sebastes aleutianus/melanostictus</i> | 24% | 356 | 50 | 371 | 60 | 16 | 36 | S | H | H | Demersal | Solitary |
| Redstripe Rockfish | <i>Sebastes proriger</i> | 23% | 134 | 65 | 182 | 50 | 5 | 15 | S | L | L | Benthopelagic | Schooling |
| Southern Rock Sole | <i>Lepidopsetta bilineata</i> | 22% | 46 | 32 | 50 | 33 | 4 | 8 | S | H | H | Demersal | Solitary |
| Yellowtail Rockfish | <i>Sebastes flavidus</i> | 22% | 116 | 43 | 148 | 36 | 6 | 15 | N | L | L | Benthopelagic | Schooling |
| Rosethorn Rockfish | <i>Sebastes helvomaculatus</i> | 20% | 228 | 65 | 249 | 69 | - | - | N | H | H | Demersal | Solitary |
| Canary Rockfish | <i>Sebastes pinniger</i> | 19% | 147 | 53 | 164 | 34 | 8 | 18 | N | L | L | Benthopelagic | Schooling |
| Pacific Sanddab | <i>Citharichthys sordidus</i> | 18% | 76 | 35 | 83 | 26 | - | - | N | H | H | Demersal | Solitary |
| Yellowmouth Rockfish | <i>Sebastes reedi</i> | 15% | 217 | 25 | 232 | 46 | 11 | 33 | N | L | L | Benthopelagic | Schooling |
| Splitnose Rockfish | <i>Sebastes diploproa</i> | 14% | 250 | 39 | 294 | 33 | 7 | 19 | N | L | L | Benthopelagic | Schooling |
| Darkblotched Rockfish | <i>Sebastes crameri</i> | 11% | 256 | 91 | 306 | 48 | - | - | N | L | L | Demersal | Solitary |
| Curlfin Sole** | <i>Pleuronichthys decurrens</i> | 10% | - | - | 58 | 28 | - | - | N | - | H | Demersal | Solitary |
| Bocaccio** | <i>Sebastes paucispinis</i> | 10% | - | - | 162 | 38 | - | 22 | N | - | H | Benthopelagic | Solitary |
| Quillback Rockfish | <i>Sebastes maliger</i> | 10% | 65 | 21 | 76 | 37 | 6 | 20 | N | L | H | Demersal | Solitary |
| Yelloweye Rockfish | <i>Sebastes ruberrimus</i> | 9% | 149 | 39 | 156 | 36 | - | - | S | L | H | Demersal | Solitary |
| Big Skate* | <i>Beringraja binoculata</i> | 9% | - | - | 75 | 58 | - | - | S | - | H | Demersal | Solitary |
| Widow Rockfish | <i>Sebastes entomelas</i> | 9% | 74 | 82 | 180 | 141 | 2 | 21 | N | L | L | Benthopelagic | Schooling |
| Shortraker Rockfish** | <i>Sebastes borealis</i> | 5% | - | - | 393 | 153 | - | 63 | S | - | H | Demersal | Solitary |

⁺Immature individuals use the alternate strategy

*Species for which maturity data not collected

**Species not captured frequently enough when immature to fit the spatial model

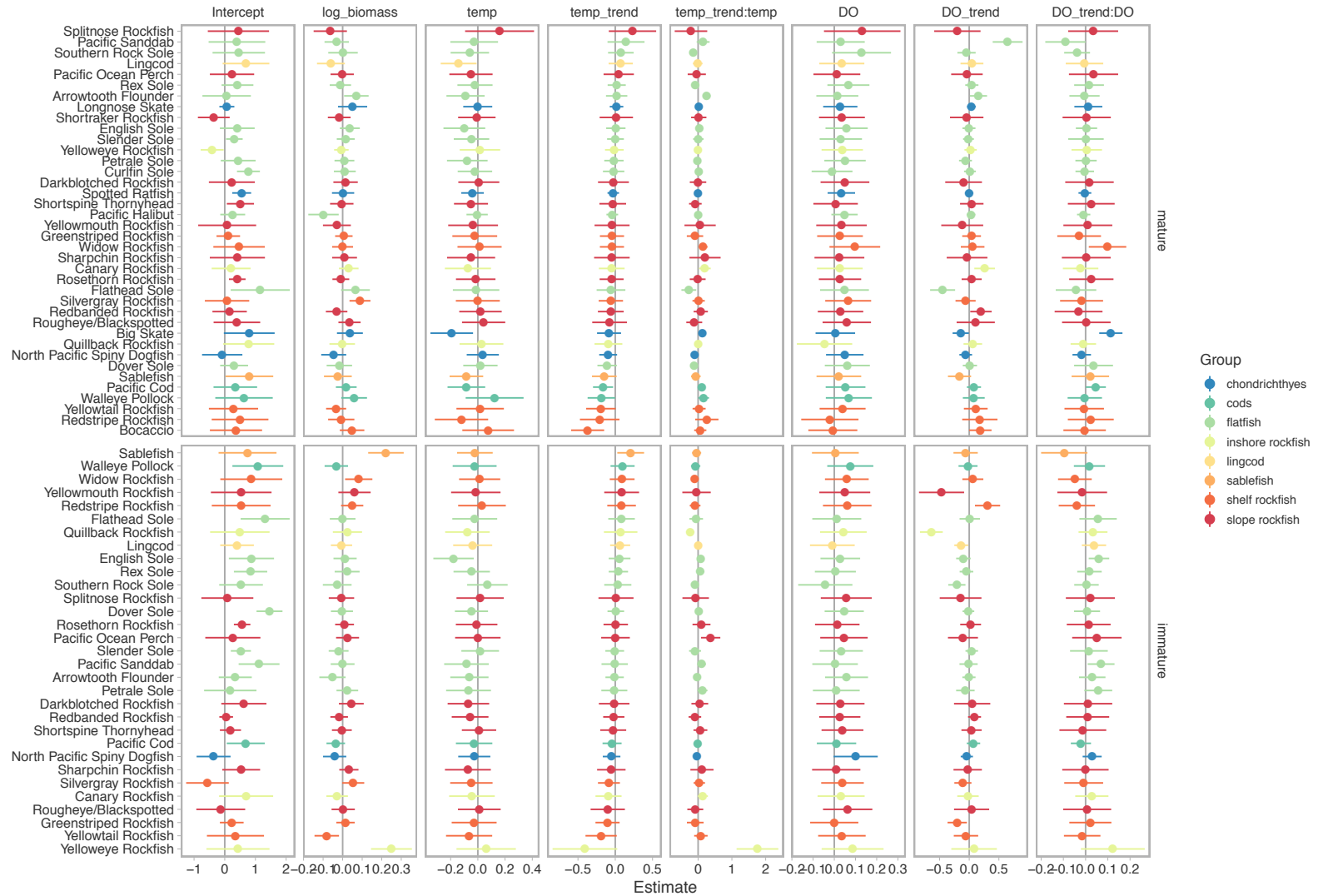


Figure S1: Species-specific coefficient estimates from one example of a simulated trends model (null #1) ordered by the estimated effect of temperature trend.

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Figure S2: Species-specific coefficient estimates from one example of a simulated trends model (null #2) ordered by the estimated effect of temperature trend.



Figure S3: Species-specific coefficient estimates from one example of a simulated trends model (null #3) ordered by the estimated effect of temperature trend.

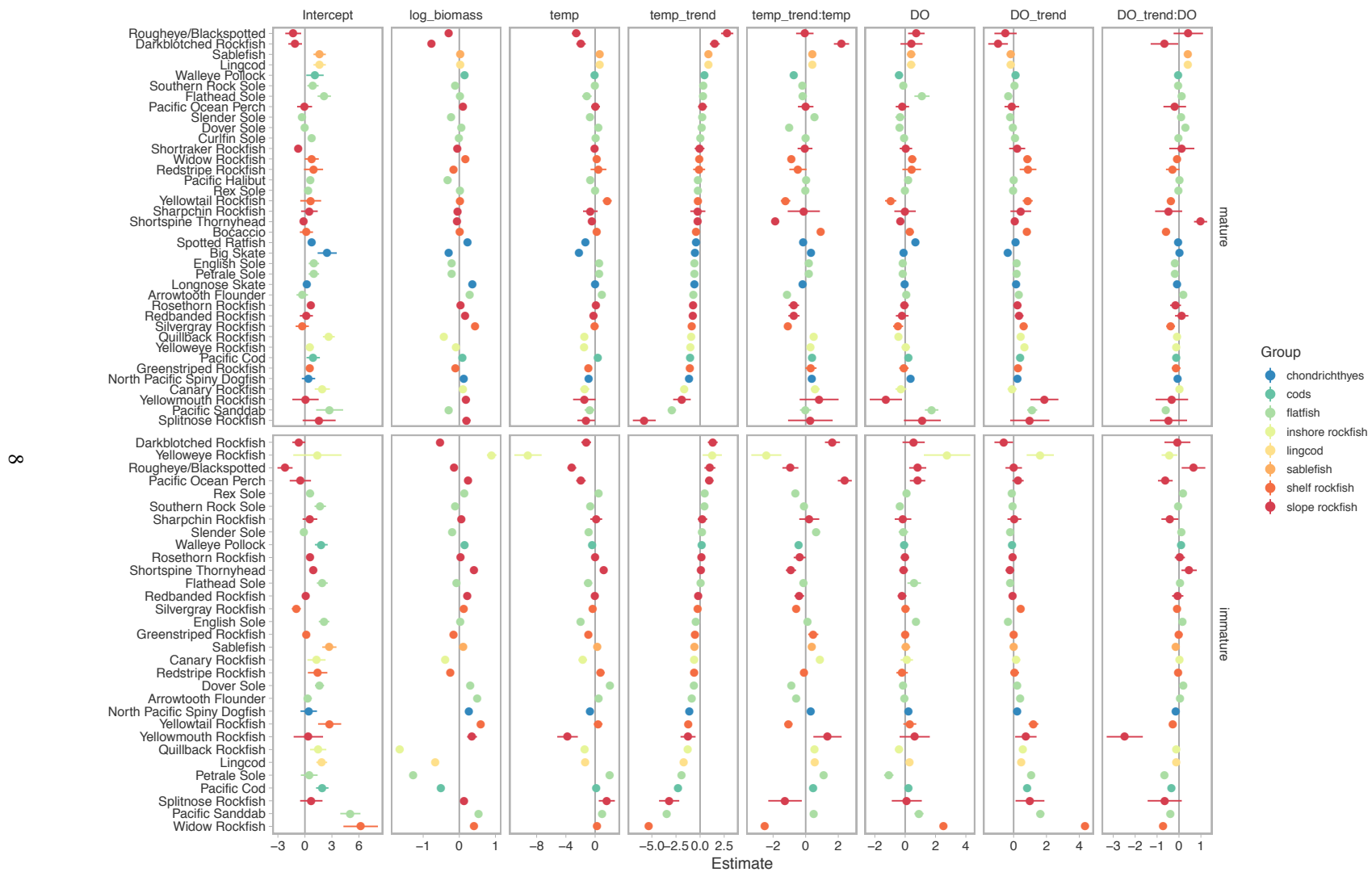


Figure S4: Species-specific coefficient estimates from trend model ordered by the estimated effect of temperature trend for a cell with an average biomass density and climate conditions and with no change in DO.



Figure S5: Species-specific coefficient estimates from one example of a simulated velocity model (null #1) ordered by the estimated effect of temperature velocity. The simulated biotic velocities used for this model were derived from simulated trends and true spatial gradients.



Figure S6: Species-specific coefficient estimates from one example of a simulated velocity model (null #2) ordered by the estimated effect of temperature velocity. The simulated biotic velocities used for this model were derived from simulated trends and true spatial gradients.



Figure S7: Species-specific coefficient estimates from one example of a simulated velocity model (null #3) ordered by the estimated effect of temperature velocity. The simulated biotic velocities used for this model were derived from simulated trends and true spatial gradients.



Figure S8: Species-specific coefficient estimates from velocity model ordered by the estimated effect of temperature velocity, which represents the change in the velocity of biomass change for a cell with an average biomass density and climate conditions and with no change in DO.

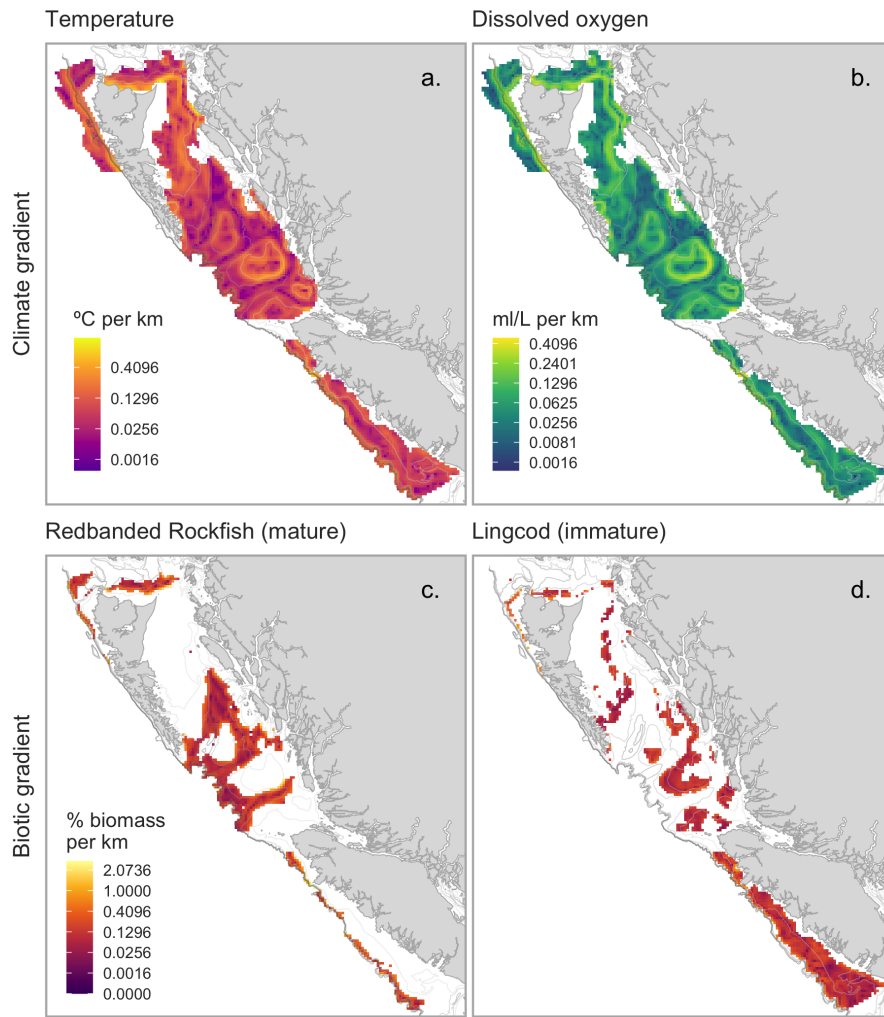


Figure S9: Maps of the gradient component of velocity calculations for both climate and biomass. Biotic gradient panels are for example species.

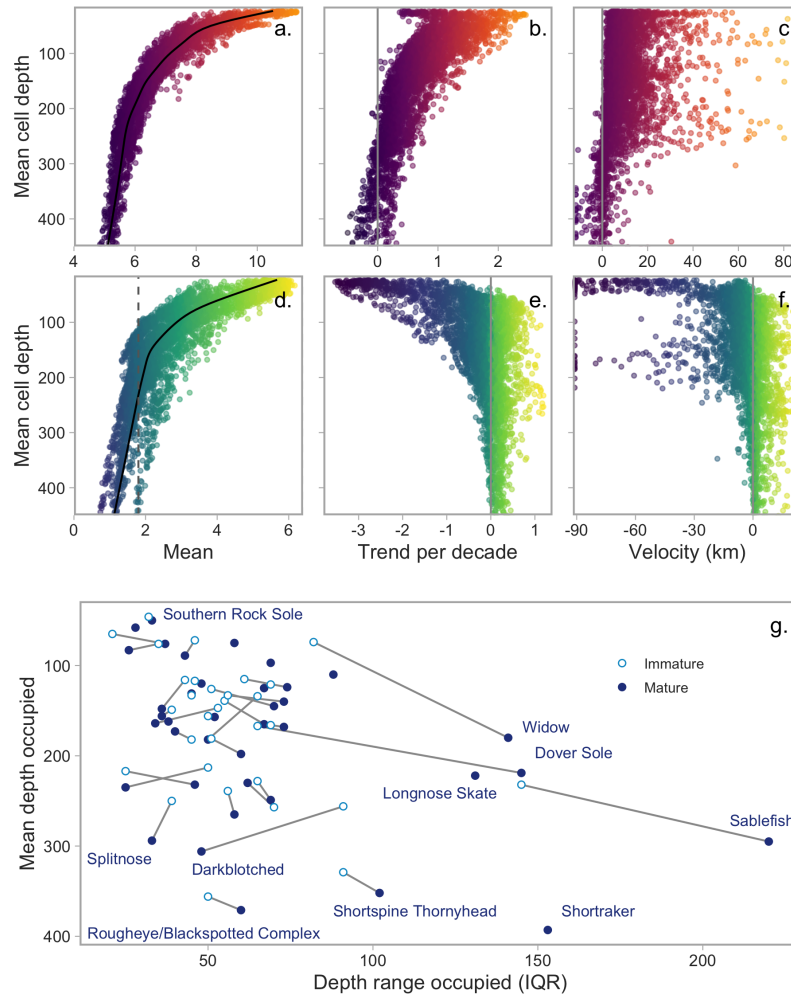


Figure S10: The climate conditions of each cell across depths (y-axes of upper panels) are indicated by both colours and the values on the x-axes of the 6 upper plots. Mean depth occupied by groundfish species co-varies with interquartile depth range occupied (g) and many of these species move deeper (lower on y-axis) with maturity (classes linked by grey lines) often with a corresponding increase in depth range (to right on x-axis).

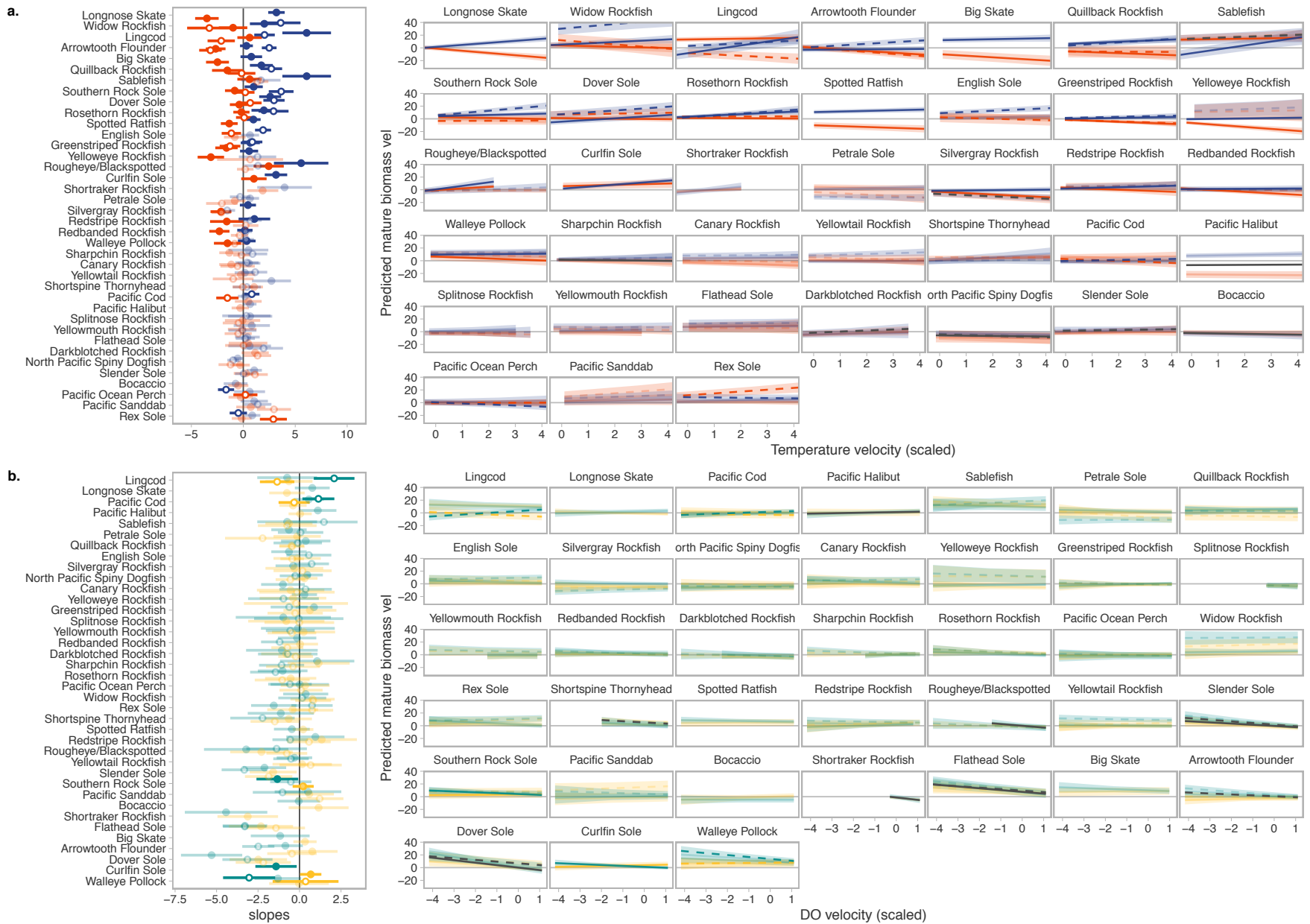


Figure S11: Slopes of predicted biotic velocity based on interaction between (a) seafloor temperature velocity and the mean temperature, or (b) seafloor DO velocity and mean DO levels. Colours, symbols, and order are the same as in Figure ??.



Figure S12: Biomass trends for mature fish populations (top and bottom 5th quantiles are not included in the colour scale, but are coloured by the nearest scale value).

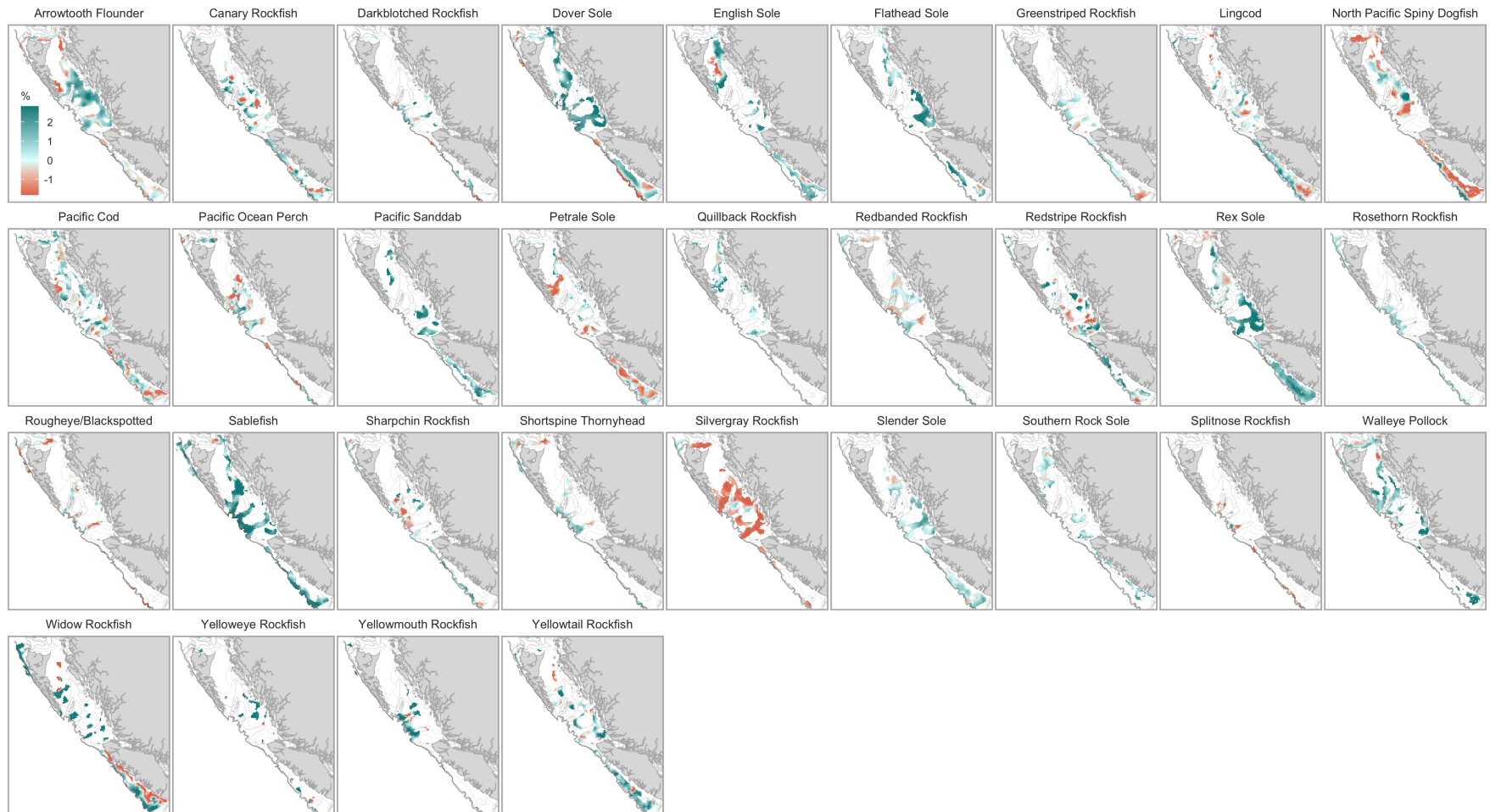


Figure S13: Biomass trends for immature fish populations on same scale as Figure S12.



Figure S14: Biotic velocities for mature fish populations.

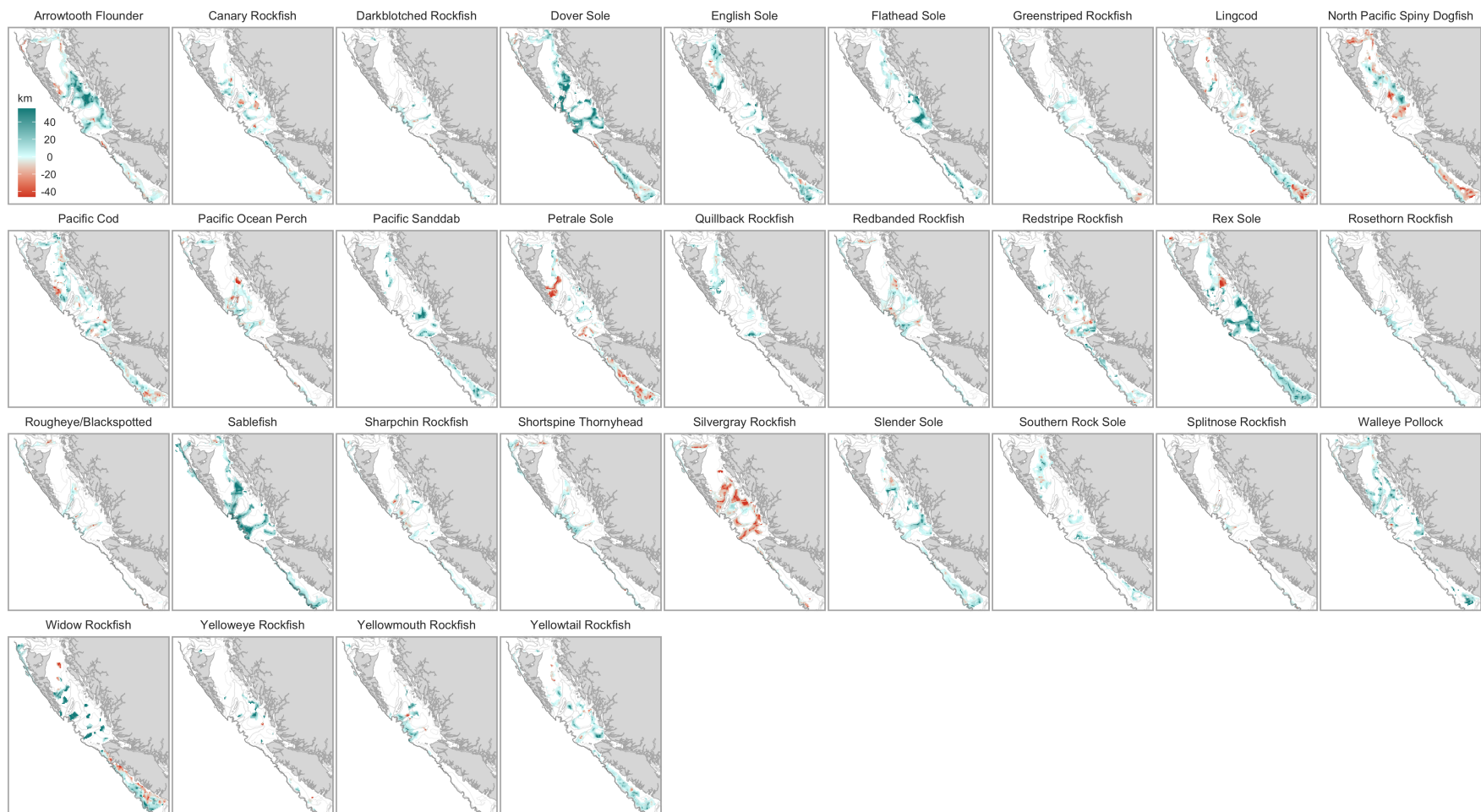


Figure S15: Biotic velocities for immature fish populations.

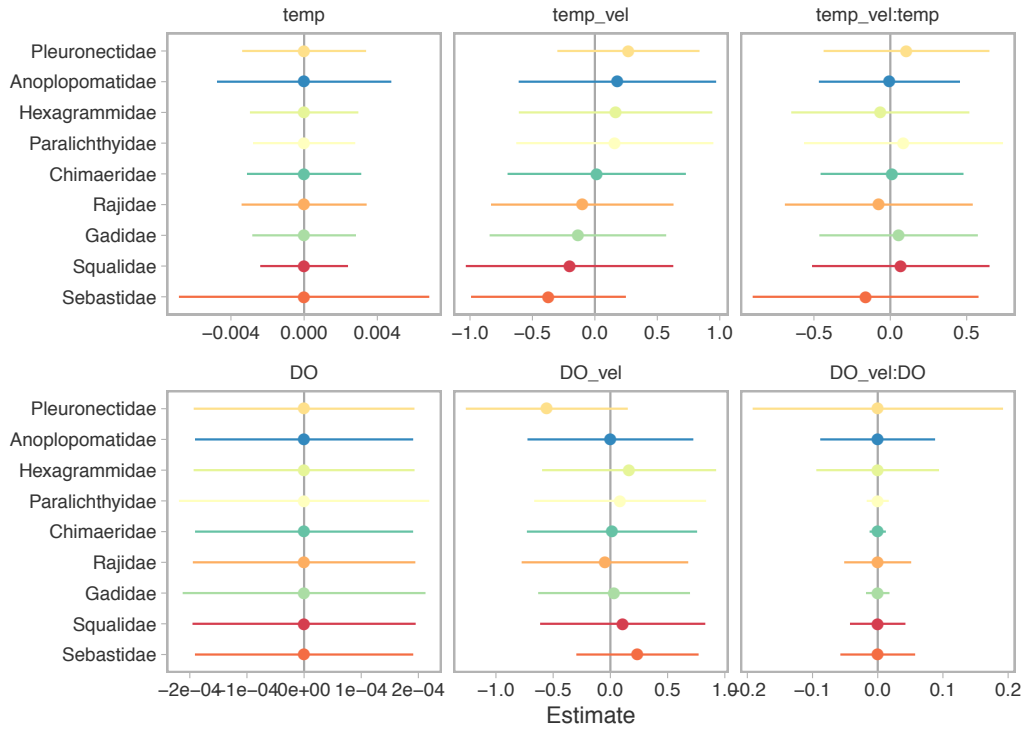


Figure S16: Family-level coefficient estimates for climate variables all have confidence intervals overlapping zero. Families are ordered by decreasing biotic velocity with increasing temperature velocity. This model includes the same climate variables as the “Velocity” models in Figures 2b and S22.

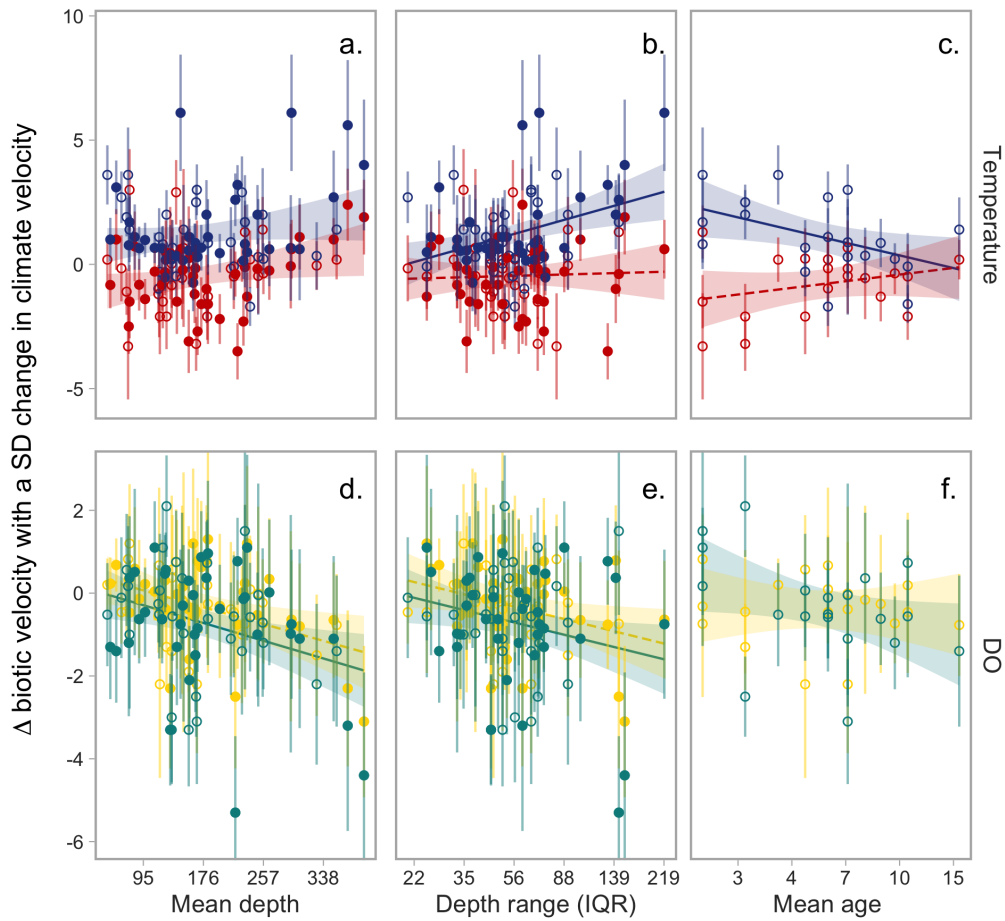


Figure S17: Occupied range of depths and immature population age correlate with the effect of warming temperature velocities on biotic velocities at low temperatures (a-c) and/or DO levels (e). Mean depth occupied only correlated with effects of DO (d). Each panel illustrates a separate model with a random effect of species and a fixed effect of mean local climate as a high or low 95th quantile for temperature or DO levels (colours and shapes match Figure 4). Points with ranges represent each species' raw slope estimates from the spatial models and their CI. Regression lines indicate significant relationships and corresponding uncertainties are based only on fixed-effects, and do not account for uncertainty in the slope estimates.

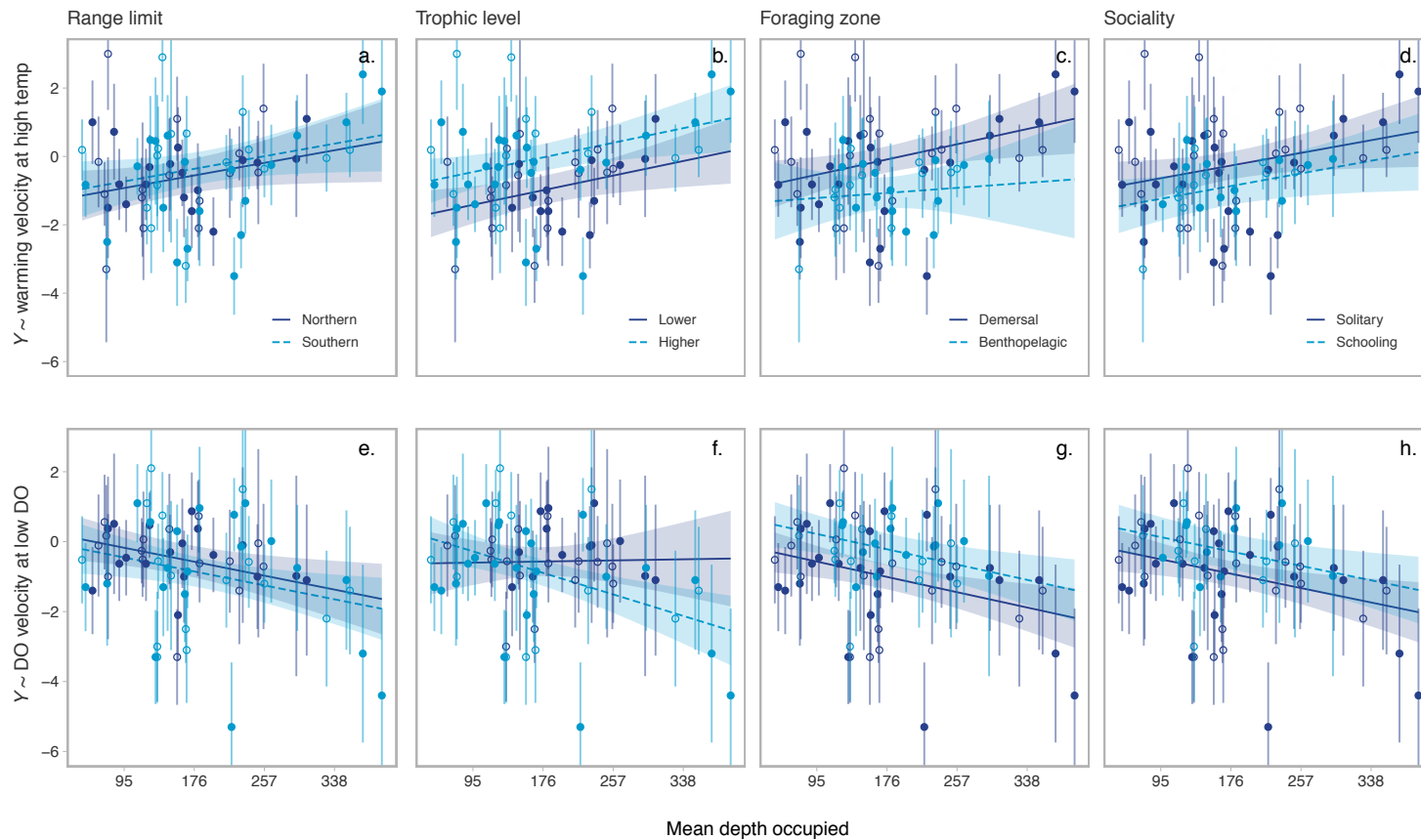


Figure S18: Ecological traits overlaid on responses to climate velocities, while controlling for the mean depth occupied by different maturity classes of each species. Points represent each species' raw slope estimates and their CI from the velocity model each coloured based on species and maturity-class specific ecology, with open circles for immature, and closed circles for mature biomass. Regression lines are derived from mixed-effect models with random intercepts for species and maturity classes nested within species; however, uncertainties are based only on fixed-effects and do not account for uncertainty in the slope estimates. In addition to the variables illustrated, each model contains slopes for both high and low mean conditions, but only the raw data and the estimated relationship for the stronger effect (highest temperatures and lowest DO) are plotted here. An interaction between ecology and mean depth is included only when statistically significant.

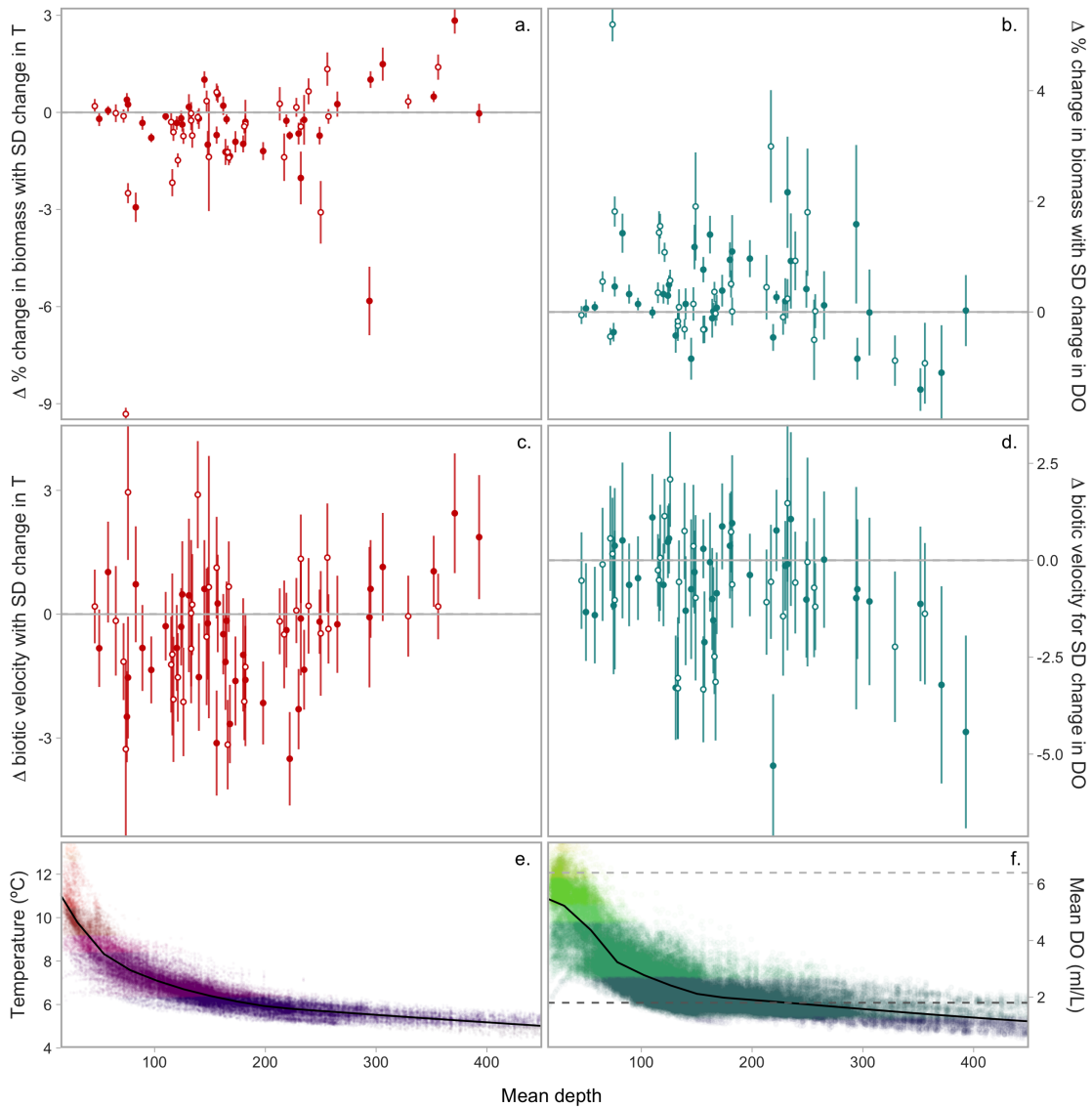


Figure S19: The slopes of the relationship between changes in biomass and climate, when calculated for the environmental extremes expected to have the greatest physiological impact—(b) highest temperature locations and (c) lowest DO locations—do not change predictably with mean occupied depth. Line segments on points represent 95% CIs on slope estimates from spatial models. Bottom panels illustrate relationships (smoothed solid lines are GAMs) between estimated temperature (d) and DO (e) with mean depth in each 4x4 km survey grid cell (dots). Dashed lines (e) represent complete saturation of seawater at 1 bar, 10 degree C, 35 salinity (upper), or threshold for mildly hypoxic conditions (< 1.8 ml/L; lower).

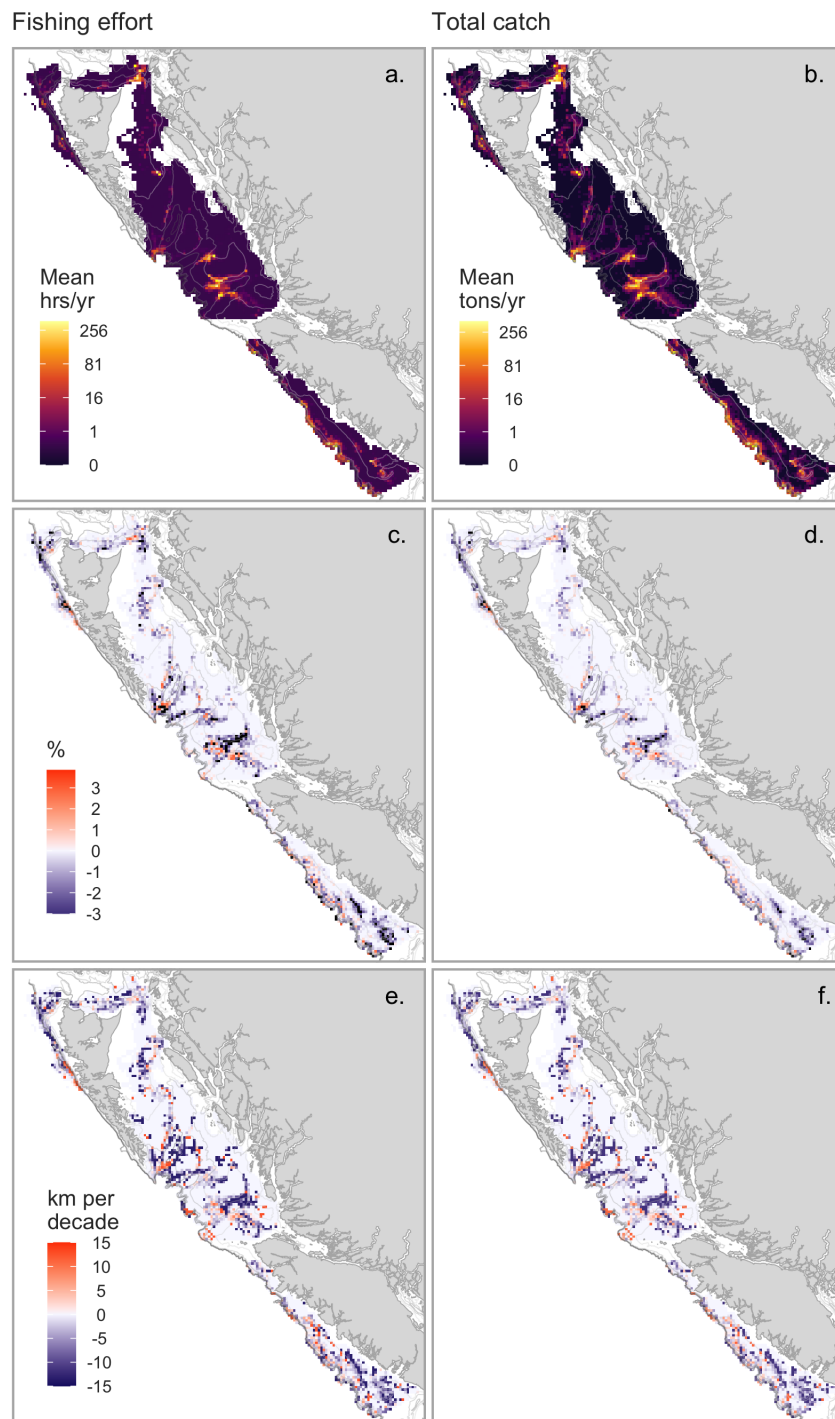


Figure S20: Variables capturing cell-specific commercial trawl fishing intensity: mean hours of commercial trawl fishing conducted (a) and mean tons of fish caught (b) per year, the % change in each estimate of fishing pressure (c, d), and the velocity of change in fishing pressure (e, f) between 2008 and 2018 for each 4×4 km cell within the survey footprint.

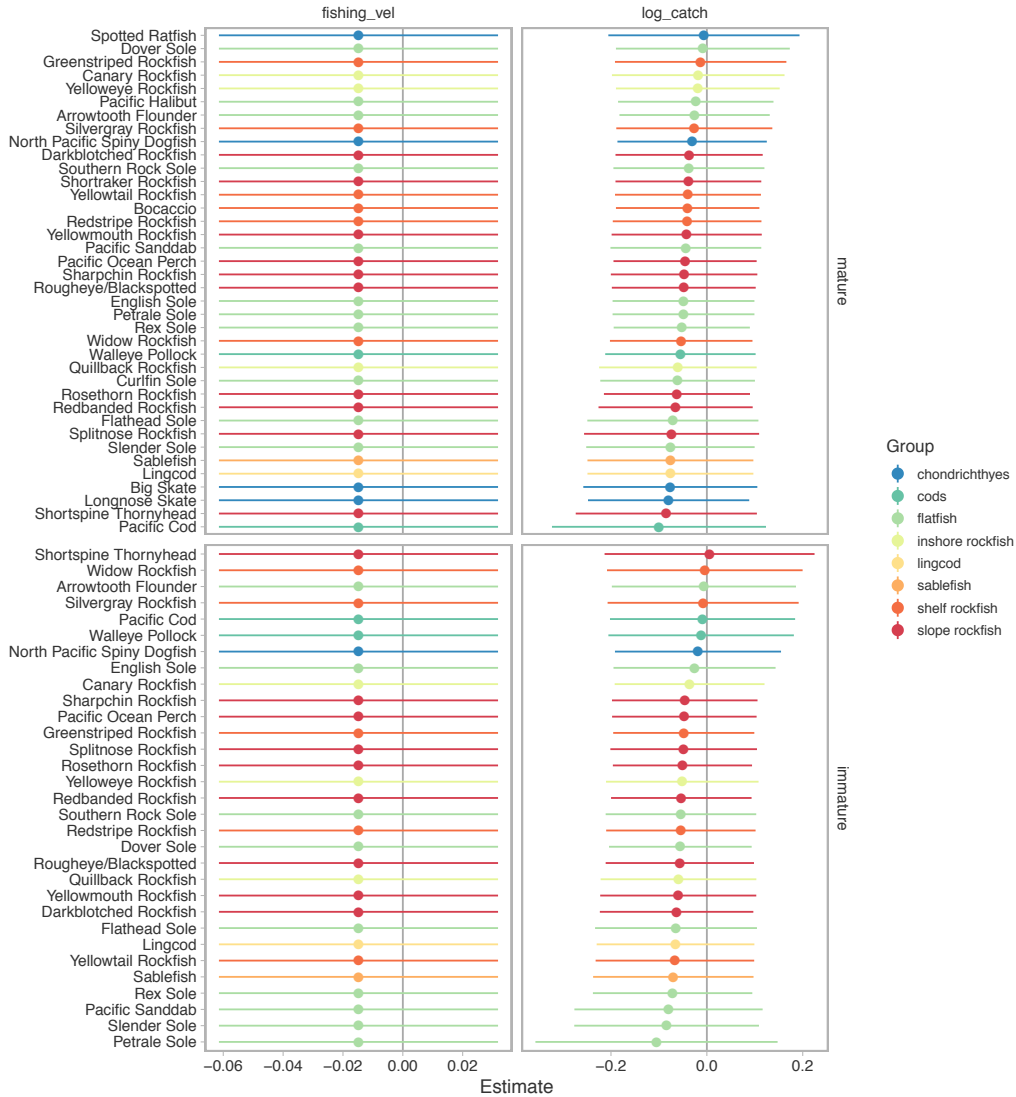


Figure S21: Species-specific coefficient estimates for variables accounting for fishing effort. This model includes the same climate variables as the “Velocity” models in Figures 2b and S22, as well as two variables capturing cell-specific commercial trawl fishing intensity: the velocity of change in mean hours of fishing that occurred annually between 2008 and 2018 (fishing_vel) and the mean tons of fish captured annually across those years (log_catch). Other variables illustrated in Figure S20 were explored, including interactions between mean and change values, but the rest were not estimate-able in models including the full set of climate variables.

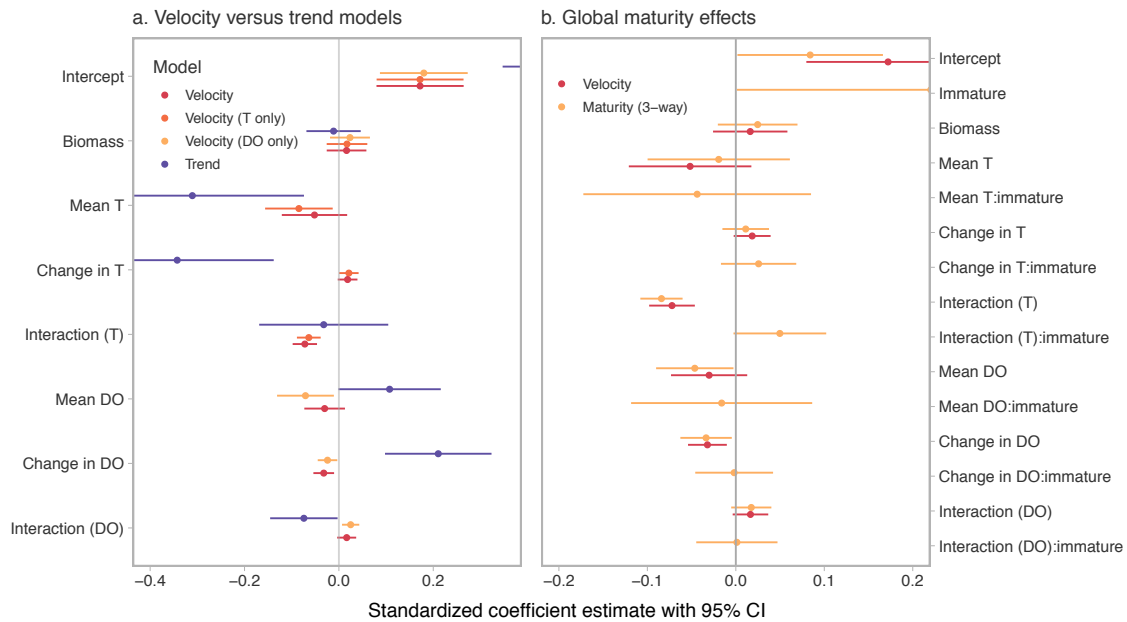


Figure S22: Global coefficient estimates for all fixed effects in a range of model configurations. All ‘velocity’ models predicted biotic velocity in response to climate changes calculated as gradient-based velocities (trend/spatial gradient). ‘Trend’ model predicts % change in biomass in response to climate changes measured as trends. Unless noted in parentheses, both temperature (T) and dissolved oxygen (DO) are included in each model. ‘Interactions’ are between the change in each climate variable (included in parentheses) and the mean conditions for that same climate variable. All models incorporate some degree of density-dependence by including the mean estimated biomass across all years. The model with a maturity effect (b. yellow dot-whisker-climate velocities and means interact with maturity) treats mature populations as the intercept.

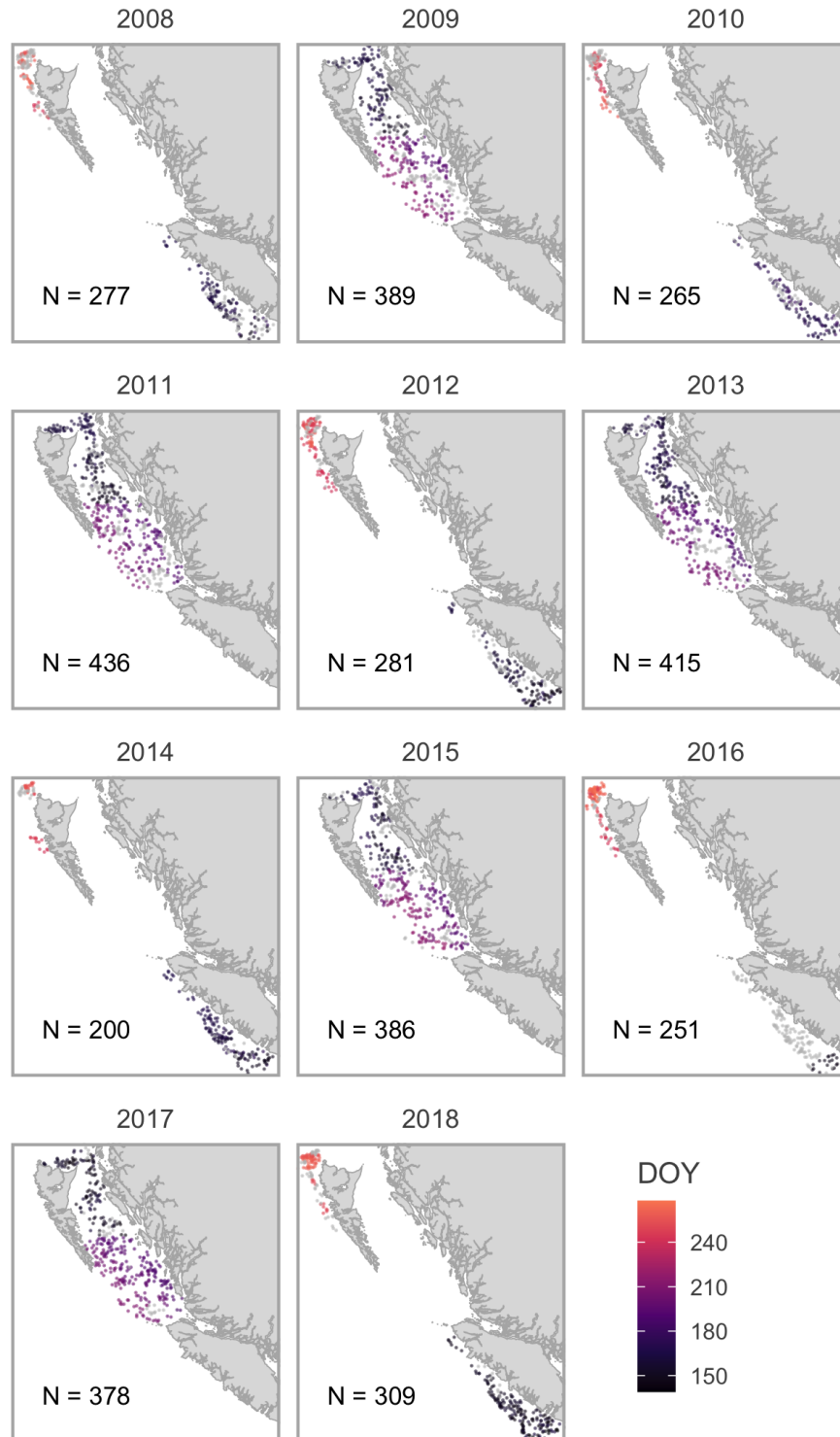


Figure S23: Distribution of synoptic survey trawls from 2008 through 2018 by year, day of year (DOY), and in space (UTM coordinates correspond to those in Figure 1). N is the total trawls analyzed for each year. Grey points are trawls that lack DO sensor data.

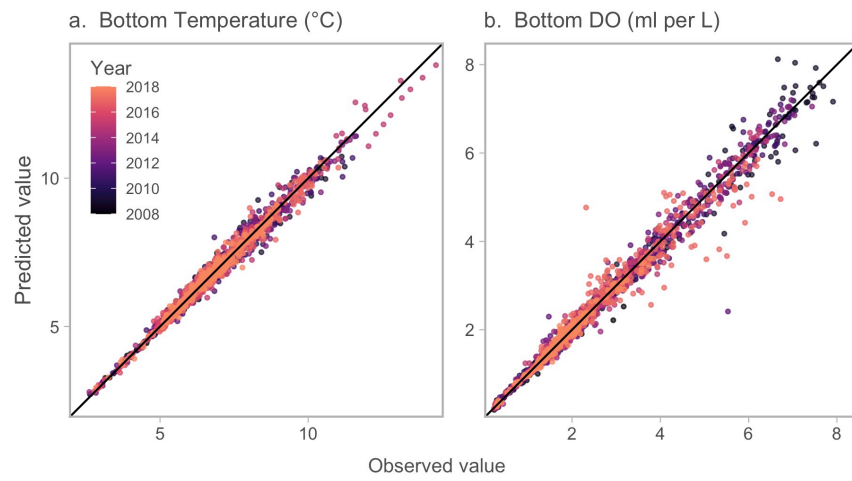


Figure S24: Predictions from models of bottom temperature (a) and DO (b) vs. observed sensor measurements on the trawl surveys.

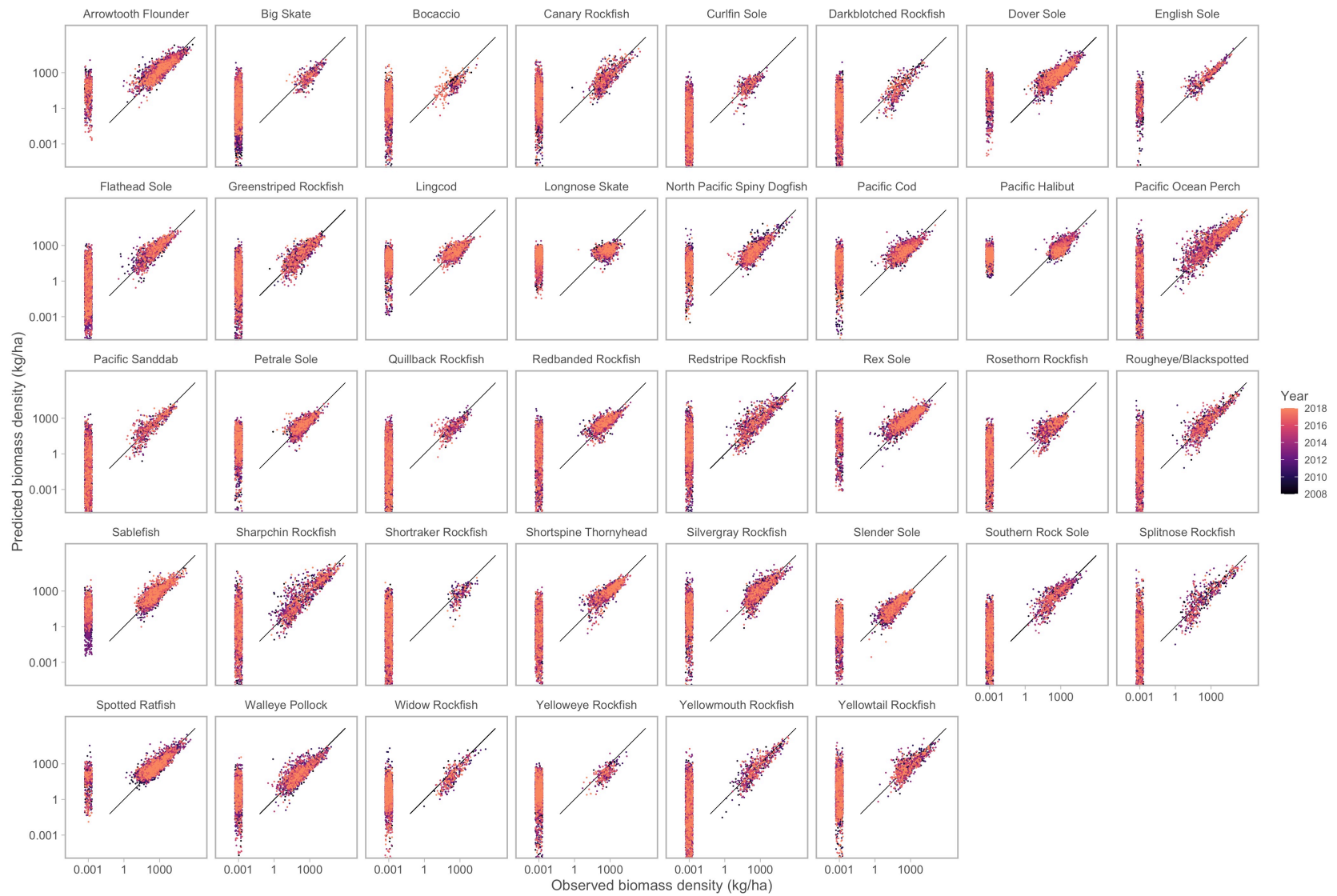


Figure S25: Predicted vs. observed mature biomass densities. Observed absences have been assigned 0.001 kg/ha and given some horizontal random jitter to improve visibility of data points and the 1:1 line is truncated to not intersect these adjusted values.

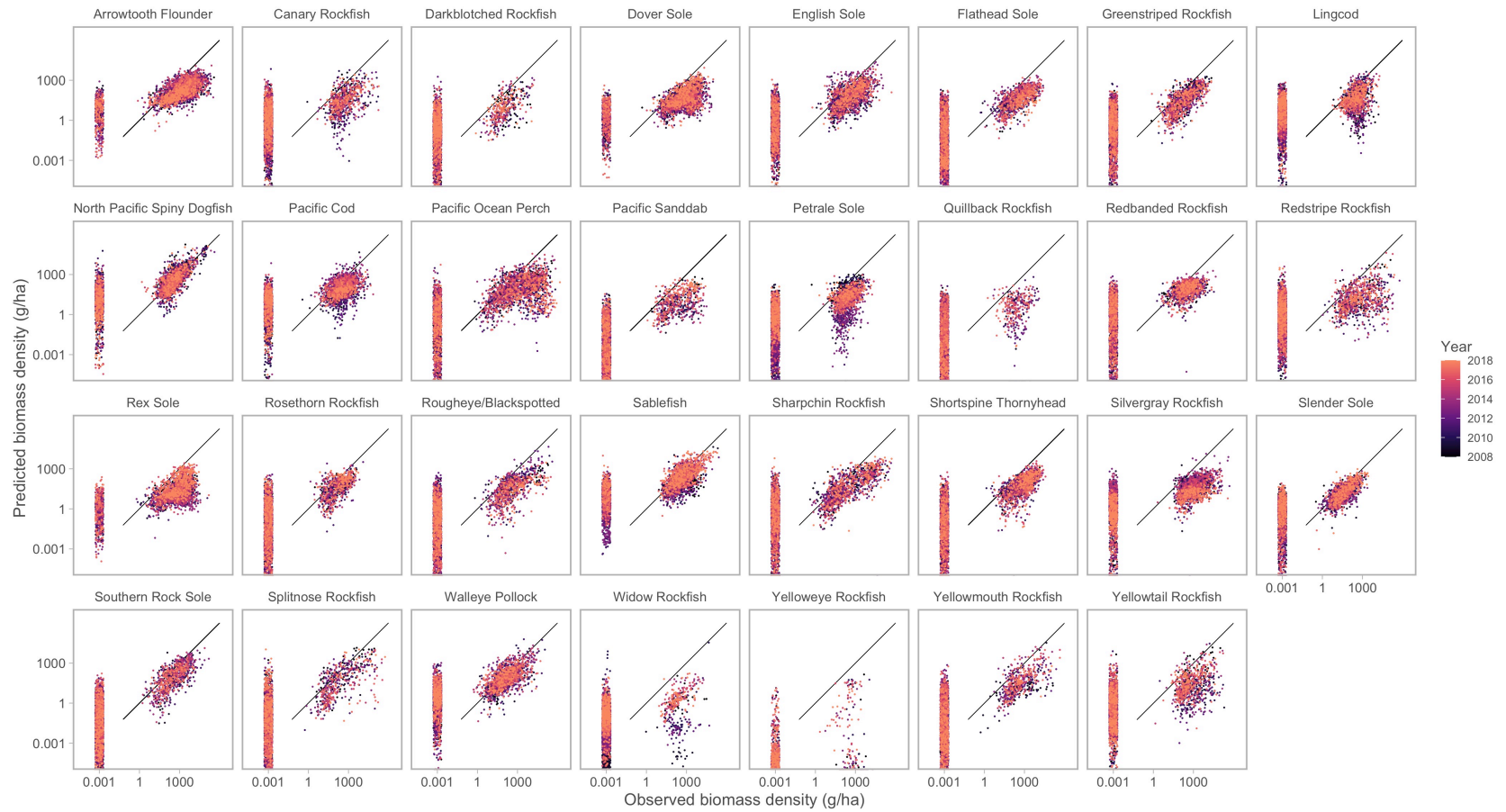


Figure S26: Predicted vs. observed **immature** biomass densities. Same treatment as Figure S25 except that units are g per hectare instead of kg per hectare. Relatively few positive samples for Widow and Yelloweye Rockfish result in relatively poor model fit to the positive sample component.

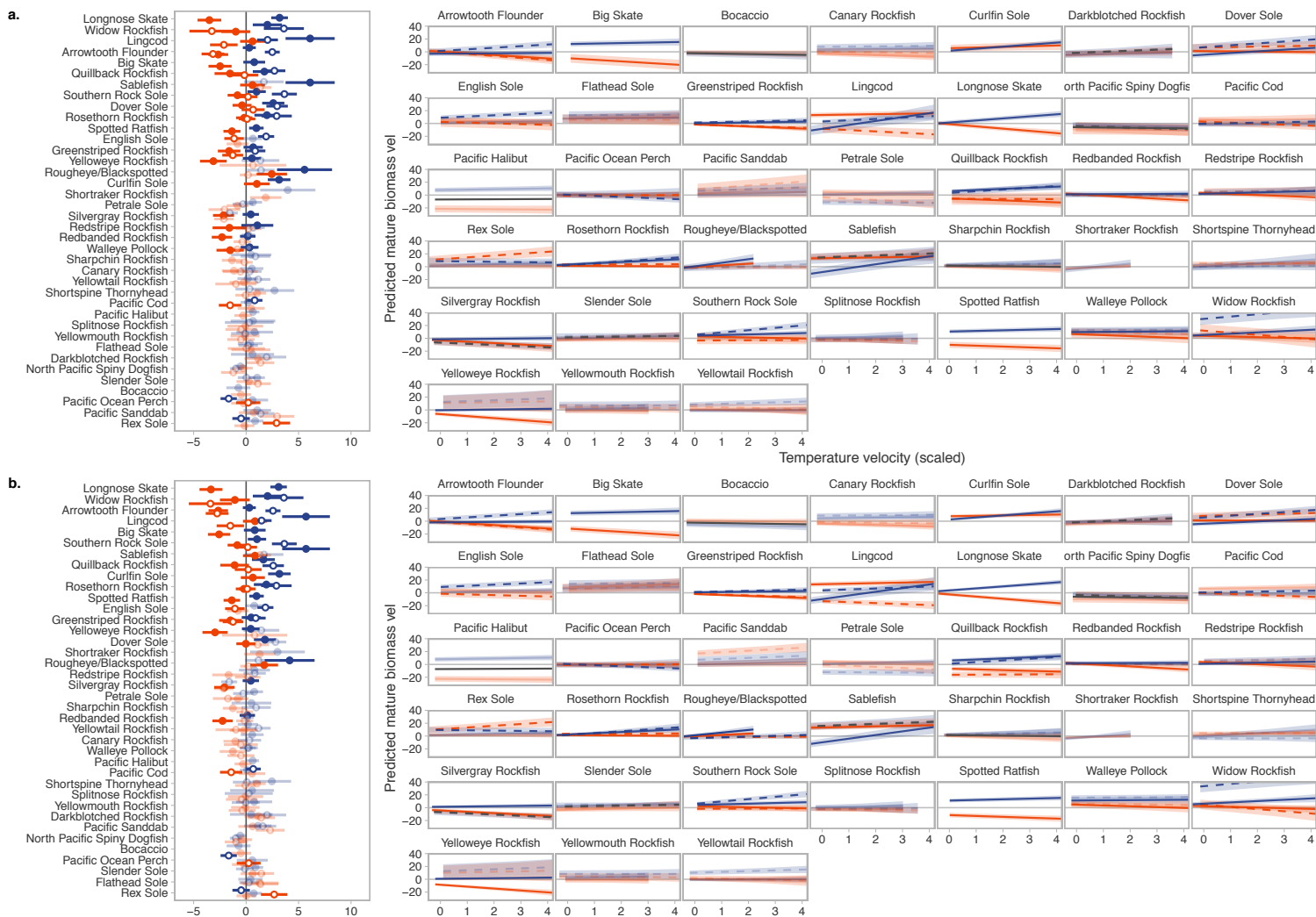


Figure S27: Here, (a) we duplicate the same slopes and predicted relationships as in Figure 4, but this time the species plots are ordered alphabetically for ease of comparison with (b) results from a similar model that lacks all of the DO variables. Differences in the ordering of the species in the left hand panels show that the precise values do change slightly, however the patterns and significance of effects are not changed by including DO in the model.