

# 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 the fine-scale changes that are most relevant to conservation and fisheries management.  
4 We develop 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  
6 of warming 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  
8 and climate were converted to velocities—the speed and direction a population would have to  
move to maintain consistent conditions—the effect of temperature change differed depending on  
10 local conditions. In the warmest locations, warming velocities were associated with negative bi-  
otic velocities for 19 of 69 species-maturity combinations, and yet were almost always associated  
12 with stable or positive biotic velocities in the coolest locations (64 of 69). These spatially consis-  
tent biomass declines (negative biotic velocities) in the warmest locations and increases in cooler  
14 locations suggest a redistribution of species with the potential for new ecological and fisheries  
interactions. After controlling for temperature, the more spatially consistent effects of dissolved  
16 oxygen were often negative, suggesting a mechanism other than hypoxia avoidance—potentially  
changes in primary production. Our approach identifies the species and locations that are most  
18 sensitive to observed changes in the environment at any scale, thus facilitating future vulnerability  
assessments.

20

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

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## 44 Introduction

Managing the impacts of a rapidly changing climate on ecological communities, particularly those  
46 that provide food for humans, is a critical challenge facing society (e.g., [Doney et al. 2012](#)). An  
increase in atmospheric CO<sub>2</sub> is not only causing increases in both mean ocean temperature and the  
48 frequency of extreme heat waves ([Frölicher et al. 2018](#)), but is also affecting patterns of circulation,  
productivity, and marine chemistry ([Pörtner et al. 2019](#)). Combined, these environmental changes  
50 can impact the distribution and abundance of many ecologically and commercially important fish  
species, leading to local loss of some species, colonizations, and changes in species interactions  
52 and bycatch composition (e.g., [Pinsky and Fogarty 2012](#), [García Molinos et al. 2016](#), [Morley et al.  
2018](#)). Furthermore, such changes can cause the efficiency of fishing to increase if population  
54 density increases faster than range expansion during population growth, or temporarily maintain  
catch rates despite population decline if organisms move towards preferred habitat as it becomes  
56 available (the basin model of density-dependent habitat selection theory; [MacCall 1990](#), [Thorson  
et al. 2016b](#)). Because traditional stock assessment methods, fisheries regulations, and choices  
58 regarding habitat protection generally assume stationary species distributions, new methods that  
anticipate and incorporate the effects of climate change on species distributions will be crucial for  
60 successful resource management in the future ([Hare et al. 2010](#), [Bell et al. 2020](#)).

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



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

Local velocities are commonly used to quantify changes at finer spatial scales than captured in  
82 population-wide indices (e.g., center of gravity; Brito-Morales *et al.* 2018). A local climate velocity  
represents the movement of an isocline—a boundary along which a climate metric is constant.  
84 More intuitively, a climate velocity gives the speed and direction a population must move to main-  
tain a constant climate condition (e.g., temperature) (Loarie *et al.* 2009). Gradient-based estimates  
86 of climate velocity 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  
88 magnitude and 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 neigh-  
90 bourhood of 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  
92 cell conditions (Hamann *et al.* 2015). While analog-based velocity estimates can be more geograph-  
ically precise, the choice of thresholds and other statistical properties (e.g., clumpiness) make them  
94 less 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  
96 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  
98 the minimum distance one would have to move to maintain an equivalent degree of habitat suit-  
ability (Carroll *et al.* 2015, Comte and Grenouillet 2015). Similar to climate velocity, a positive local  
100 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  
102 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

104 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.

106 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  
108 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).  
110 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  
112 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,  
114 these species occupy a large range of depths, especially along the shelf edge where short move-  
ments can result from large environmental changes, and vary in their potential for behavioural  
116 responses to climate. For example, some species are migratory or highly mobile (e.g., Sablefish  
(*Anoplopoma fimbria*, Anoplopomatidae) and many flatfish species (Pleuronectidae)), while others  
118 are relatively sedentary (e.g., many species of rockfish, *Sebastes* spp. (Sebastidae)). Furthermore, a  
warmer ocean is expected to hold less oxygen, while becoming more stratified (Levin and Le Bris  
120 2015), and groundfish species occupying different depths vary in their sensitivity to hypoxia (Keller  
*et al.* 2017).

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

134 spatiotemporal models applied to a decade of survey-derived climate and species density data,  
and then assess relationships between velocities of biotic and climatic change for 38 commonly  
136 encountered species using a geostatistically explicit hierarchical analysis that controls for change  
in both temperature and DO.

## 138 **Methods**

### **Survey data**

140 We analyzed biomass density distributions and morphometric data for 38 species of groundfish  
that were regularly encountered by fisheries-independent bottom-trawl surveys and are widely  
142 distributed within Canadian Pacific waters (DFO 2020, Table S1). The surveys were stratified  
within four regions, two of which were surveyed in odd years (Hecate Strait and Queen Char-  
144 lotte Sound) and two in even years (West Coast Vancouver Island and West Coast Haida Gwaii)  
since at least 2005. Each region was sampled over the same month-long period between late May  
146 and early August in each survey year (Fig. S1). These surveys share similar random depth-stratified  
designs, fishing gear and fishing protocols (Sinclair *et al.* 2003). Combined, they covered most of  
148 the upper continental slope and shelf in Pacific Canada, and resulted in a mean of 326 samples per  
year (range from 200 to 436). We only included tows of > 15 minutes duration and converted total  
150 biomass of each species to a biomass density based on the speed, distance covered, and net open-  
ing (e.g., Williams *et al.* 2018, Anderson *et al.* 2019). Biological sampling protocols varied among  
152 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 subsampled  
154 and, for commercially important species, maturity data and otoliths for aging were collected.

### **Estimating spatiotemporal variation in maturity-specific biomass density**

156 Because ontogenetic shifts in habitat, particularly depth, are well documented for groundfish  
species (e.g., Mindel *et al.* 2016, Barbeaux and Hollowed 2018, Li *et al.* 2019), we estimated biomass  
158 densities separately for mature and immature size classes whenever possible. Maturity was not  
assessed for certain Chondrichthyans, or when catches were particularly low. To do this, we first  
160 estimated length at 50% maturity as defined by gonadal development stages using ogives fit as sex-

specific logistic regressions to individual specimens (see Supporting Methods). To split the estimated biomass density per tow into mature and immature components, we calculated the 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 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 measured 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 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 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 \(2011\)](#).

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 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., that effects are constant through both time and space). Instead, we use a climate-agnostic version of a species distribution model with a spatiotemporal random effect structure to estimate local variability in biomass density change. Our models relied on spatial random effects to capture unmeasured components of habitat suitability and allow suitability to change through time 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 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 to dramatically improve precision of overall estimates ([Thorson and Barnett 2017](#)), and maintaining independent estimates should make identification of shared climate responses more conservative.

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](#)

et al. 2019):

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

190

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

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

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

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

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

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

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

locations, we used bilinear interpolation to approximate a continuous spatial field (Rue *et al.* 2009,  
 210 Lindgren *et al.* 2011).

We fit our models in R version 3.6.1 (R Core Team 2019) with the R package sdmTMB (Anderson  
 212 *et al.* 2019, 2020), which interfaces automatic differentiation and the Laplace approximation in the  
 TMB (Template Model Builder) R package (Kristensen *et al.* 2016) with the SPDE (Stochastic Partial  
 214 Differential Equation) approximation to Gaussian Markov fields from the INLA (Integrated Nested  
 Laplace Approximation) R package (Rue *et al.* 2009) to find the value of the fixed effects that min-  
 216 imizes the the marginal negative log likelihood. We confirmed that the non-linear optimizer had  
 converged by checking that the Hessian matrix was positive definite and the maximum absolute  
 218 gradient across fixed effects was  $< 0.005$ .

### Climate trends and velocities

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

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

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

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

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

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

Here  $C_{s,t}$  represents the climate variable (bottom temperature or log DO) in space  $s$  and time  $t$ ,  $\mu$   
 226 represents the mean, and  $\sigma$  represents the observation error standard deviation. The symbol  $\mathbf{X}_{s,t}$   
 represents a vector of predictors (described below) and  $\boldsymbol{\beta}$  represents a vector of corresponding  
 228 parameters. The spatial random effects  $\omega_s$  were defined as in Eq. 5 whereas the spatiotemporal  
 random effects were structured to follow a stationary AR1 process with first-order correlation  
 230  $\rho$ . Because DO is known to be influenced by both water temperature and seasonal biological

processes, we included a quadratic effect for temperature and a linear effect for day of year along  
232 with estimated means for each year. Although not shown above for simplicity, we again allowed  
the quadratic depth covariates to follow a random walk through time as in Eq. 3. Our bottom  
234 temperature model fixed effects included only depth and estimated means for each year, because  
including day of year did not improve model fit based on AIC (Akaike Information Criterion).  
236 Because bottom temperature data (but not DO) have been collected in synoptic surveys since 2003,  
we included these earlier data in the temperature model to provide more information for estimating  
238 the fixed spatial random field  $\omega_s$ .

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

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

where  $A$  is any temporally varying feature of focal cell  $s$ . Depending on the portion of the survey  
248 grid considered, we calculated the trend through time for biennial time-steps between 2008 and  
2018 (6 surveys across 11 years) or 2009 and 2017 (5 surveys across 9 years). In order to compare  
250 between survey areas with different sampling years, we converted values for all cells to a rate of  
change, or trend, per decade (Table 1). The spatial gradient  $g_s$  was calculated as the vector sum of  
252 the mean north-south and east-west gradients based on a  $3 \times 3$  cell neighbourhood (Burrows *et al.*  
2011); however, the values of  $A$  from which a spatial gradient is calculated can be based on any  
254 particular subset of times  $t$ , or the mean of all  $\Delta t$ . The input information related to a cell and any  
cell near enough to share spatial information in a gradient or in the overall spatial models (this  
256 includes all response and predictor variables) all share the same sample years.

The magnitudes of gradients  $g_s$  strongly influence the distribution of velocities  $V$ . Most prior  
258 applications of gradient-based velocities have used  $g_s$  calculated from the mean cell conditions of  
the entire period analyzed (e.g., Burrows *et al.* 2011, Molinos *et al.* 2019). Estimated velocities will

260 tend to be larger (as  $g_s \rightarrow 0$ ,  $V_s \rightarrow \infty$ ) when more estimates (in this case sample years) are averaged  
 for the cells included in the  $g_s$  calculation, because a larger sample reduces the variability between  
 262 the mean values of adjacent cells. Furthermore, the gradients most relevant to the actual distance  
 a population would need to travel are those present after changes have begun to occur. Given that  
 264 samples were collected only once every two years and that there is variability among species in  
 terms of when dispersal occurs and how long it takes, we used the last two sample periods in our  
 266 estimates of spatial gradients (2015–2018). This time period begins the first survey season following  
 the onset of the 2014–2016 marine heat wave in the north-eastern Pacific (Peterson *et al.* 2015) and  
 268 is approximately the end point of the transition to warmer conditions in the Bering sea (Alabia  
*et al.* 2018). We calculated spatial gradients using the `vocc` R package (Brown and Schoeman  
 270 2018), which produces identical results when applied to the same data as the newer package `VoCC`  
 (García Molinos *et al.* 2019). Finally, we collapsed the most extreme velocity estimates to their 0.005  
 272 and 0.995 quantiles to reduce the impact of outliers from the resulting heavy-tailed distributions.

### Linking biotic changes with climate

274 To explore the relationship between change in estimated local climate and percent changes in  
 estimated biomass densities for each  $4 \times 4$  km grid cell, we used similar spatial GLMMs to control  
 276 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)  
 278 and an interaction between the mean climate of each cell and its local rate of change:

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

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

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

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

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

where  $\bar{T}_s$  and  $\Delta T_s$  represent the mean temperature and decadal trend in temperature for spatial  
 280 location  $s$ . A row of data represents a given spatial grid cell  $s$  and species-maturity  $k$  combination.  
 The symbols  $\bar{O}_s$  and  $\Delta O_s$  represent mean dissolved oxygen and decadal trend in dissolved oxygen,



282 and the symbol  $\bar{Y}_{k[s]}$  represents log biomass density for species-maturity  $k$ . Parameters  $\beta_0$  through  
284  $\beta_7$  (indexed by  $r$ ) represent coefficients that are allowed to vary as random effects across species  
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.

286 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  
288 changes were correlated with changes in climate at the  $4 \times 4$  km grid cell scale. The velocity-  
based models assessed whether changes in biomass, especially those with low local variability  
290 in biomass, were correlated with the predicted speed of climate isoclines within the  $12 \times 12$  km  
neighbourhood of cells. We did not include both trends and velocities in the same model because  
292 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  
294 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-  
296 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)  
298 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  
300 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  
302 included them in the final models because they did not change our conclusions (see Supplementary  
Methods).

### 304 **Simulation study**

We conducted a simulation study to assess: (1) the ability of the geostatistical models to cope with  
306 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  
308 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  
310 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  
312 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  
314 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,  
316 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-  
318 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  
320 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.

322 Null models based on simulated biotic trends and observed climate trends showed fewer signif-  
icant relationships at the species level than would be expected by chance (Figures S5, S6, and S7),  
324 confirming that the spatial random effects in our models (e.g. Figure S8) successfully controlled  
for the spatial autocorrelation. In contrast, models predicting time-null biotic velocities did pro-  
326 duce more significant effects than would be expected by chance (Figures S9, S10, and S11 vs. S12).  
These associations were likely due to the simulated velocities being based on the observed spatial  
328 gradients (Figure S13); 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  
330 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  
332 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,  
334 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  
336 dimensions of biotic and climate change, which provides support for our choice to focus on this  
approach.

### 338 **Life-history and ecological correlates of climate sensitivity**

To assess potential ecological mechanisms and the extent to which the temporal and spatial scales  
340 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-  
342 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-  
344 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-  
346 tary Methods).

## **Results**

### 348 **Climate trends and velocities**

We estimated bottom temperature and DO values biennially between late May and early August  
350 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  
352 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  
354 values were associated with the shallowest depths, while the lowest values were associated with  
the deepest locations (Figure 1b, c).

356 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  
358 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  
360 1.3 °C/decade in cells shallower than 50 m (Figure S14b). Likewise, the greatest decreases in DO  
occurred in the shallowest locations (mean: -2 ml/L per decade); however, the highest variability  
362 in DO trend (95% quantiles: -1.7 to 0.6 ml/L per decade) occurred between 50 and 200 m depths  
(Figure S14e). There was a tendency for the shallowest depths to be occupied by groundfish species  
364 that have narrower depth ranges (e.g., Southern Rock Sole, *Lepidopsetta billineta*, vs. Dover Sole,  
*Microstomus pacificus* (Pleuronectidae); Figure S14g, Table S1).

366 When these local climate trends were placed in their geographic context by converting to  
gradient-based velocity estimates (Eq. 12), they implied that a population would have to move an  
368 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  
370 positive, representing warming conditions (mean: 10.1; 95% interquantile range of -12 to 87; Fig-  
ure 1f), while DO velocities averaged negative, representing declining DO levels (-6.26; -91 to 24;  
372 Figure 1g). Most locations with high climate velocities occurred in patches throughout Queen  
Charlotte Sound and Hecate Strait (dark red patches in Figure 1f). The most negative DO veloci-  
374 ties occurred in 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  
376 (Figure S14).

### Linking biotic changes with climate

378 Geostatistical models linking climatic (Figure 1d–g) and biotic trends (Figures S17 and S18) or veloc-  
ities (Figures S19 and S20) resolved different aspects of biotic change (Figures S8 and S12). The effect  
380 of temperature velocity on biotic velocity was weakly positive across species ( $\beta$ : 0.28 km/decade  
with 95% CI -0.04 to 0.60; point range for “T change” shown in Figure 2b), despite a significant  
382 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,  
384 mean local temperature influenced the effect of temperature velocity on biotic velocity ( $\beta$ : -1.09,  
-1.48 to -0.70; “T interaction” in Figure 2b), such that when temperature velocity was high in the  
386 warmest parts of a species’ range, local biomass was more likely to decline and exhibit larger neg-  
ative or smaller positive biotic velocities. When temperature velocity was high in the coolest parts  
388 of a species range, local biomass was more likely to increase and to result in larger positive biotic  
velocities (or to decrease less and result in less negative biotic velocities).

390 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  
392 mean local conditions (e.g., in Figures 3c and S15a, the blue and red lines are the predicted relation-  
ships for locations at the 0.025 and 97.5 quantile of mean local temperatures, respectively). For Red-  
394 banded Rockfish (*Sebastes babcocki*, Sebastidae) the horizontal blue line indicates stable biomass

(small absolute biotic velocities), while the red line with a negative slope means that biomass  
396 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  
398 relationships (e.g., as illustrated in Figure 3c and Figure S15a) are plotted for all species-maturity  
combinations in Figure 4. Consistent with the overall interaction, the majority of species-maturity  
400 combinations with significant interactions between local mean temperature and temperature ve-  
locity had negative interactions (31 of 33 coloured dots and lines with red coefficients to the left of  
402 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  
404 more strongly positive in the cooler locations (13 of 31 species-maturity combinations with nega-  
tive interactions).

406 To assess whether these relationships predicted that specific species' biotic velocities were in-  
creasing or decreasing under different climate velocities, the lines displayed in Figures 3c and S15a  
408 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  
410 species-maturity combinations in locations experiencing minimum climate velocity (Figure 5a) re-  
gardless of mean temperature. However, in the warmest locations experiencing maximum climate  
412 velocity, the expected biotic velocity was strongly negative for 19 of 69 species-maturity combi-  
nations (Figure 5b). Meanwhile, in cooler locations experiencing the same high climate velocity,  
414 biotic velocities were often positive (e.g., Pacific Halibut, *Hippoglossus stenolepis*, Pleuronectidae).

After controlling for temperature, the average effect of DO velocity on biotic velocity was  
416 negative across species ( $\beta$ : -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 ( $\beta$ : 0.34 % increase in  
418 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  
420 with biotic velocities. However, unlike for temperature, DO velocity did not interact with mean  
DO availability consistently across species ( $\beta$ : 0.25, -0.05 to 0.55). Only two species (those with  
422 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  
424 with increases in biotic velocity and/or negative DO velocities were associated with decreases in

biotic velocity (e.g., immature Lingcod, *Ophiodon elongatus*, Hexagrammidae; Figure 3). In contrast, several species 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). Including DO in the model along with temperature did not substantially alter the effects of temperature for any species (Figure S16).

### Life-history and ecological correlates of climate sensitivity

We examined possible relationships between responses to climate velocities and each species' taxonomy, 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 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 family (Figures 4a and S12; see also non-significant family-level effects from hierarchical model, Figure S21). However, the effects of temperature velocities at high temperatures were most negative 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 rockfish (0.1) and flatfish (-0.1), and most positive for sablefish (1.0; mean across red values in Figure 4a).

Life-history failed to explain substantial variation in climate sensitivity in the warmest locations, although more negative effects tended to be clustered in shallow depths and among younger immature populations (Figure S22). However, the positive effects of temperature velocities on biotic velocities in the coolest locations were strongest in species occupying a larger range of depths ( $\beta$ : 0.57, 0.21 to 0.92) and for immature populations with younger mean age ( $\beta$ : -1.0, -2.0 to 0). Ecological factors were somewhat better at accounting for negative effects in the warmest locations. 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 levels;  $\beta$ : -0.96, -1.44 to -0.48), and use of foraging zones (higher biotic velocities in demersal species relative to benthopelagic;  $\beta$ : 0.98, 0.47 to 1.49) after accounting for mean depth occupied (Figure S24 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,

454 whereas most species with mean encounter depths deeper than 290 m appeared to increase in  
biotic velocity with more positive temperature velocities (Figure S25c).

456 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-  
458 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  
460 both for species occupying deeper locations on average ( $\beta$ : -0.43, -0.73 to -0.13; Figure S25d) and  
a larger range of depths ( $\beta$ : -0.30, -0.6 to 0). It is notable, however, that the effect of trends in  
462 DO on percent change in biomass were also negative at these depths despite being mostly positive  
at intermediate depths (Figure S25b). At these intermediate depths (the mean occupied depth for  
464 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 ( $\beta$ : -0.33, -0.81 to 0.16), in the demersal zone ( $\beta$ : -0.79,  
466 -1.32 to -0.26), and with more solitary habits ( $\beta$ : -0.63, -1.21 to -0.06; Figure S24 bottom row).

## Discussion

468 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  
470 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-  
472 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  
474 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-  
476 tions experienced declines (negative biotic velocities) in the warmest locations when experiencing  
maximum warming. In contrast, locations experiencing minimal warming or cool locations ex-  
478 perience maximum warming experienced stable or increasing biotic velocities. Characteristics  
such as trophic level, foraging zone, and sociality—as well as potentially confounding variables  
480 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-

482 der low DO conditions (Figure S24f) than species with more diverse or higher trophic-level diets.  
This suggests that the prevalence of strong negative relationships between DO and biotic velocities  
484 (Figure 2b) might be explained by increases in primary production, causing decreases in DO due  
to increased rates of decomposition in benthic environments (Keister *et al.* 2020).

#### 486 Scale and context dependence

Our analysis is the first, to our knowledge, to explore how the interaction between climate veloc-  
488 ities and local mean climate conditions affect fine-scale biotic velocities, and the first to contrast  
patterns between trend and velocity indices. Relationships between climate and biotic velocities  
490 have also been detected in marine species in the Arctic (Alabia *et al.* 2018) and between local climate  
velocities and species range shifts in tropical to subarctic zones along the Japanese archipelago  
492 (Kumagai *et al.* 2018) and along several portions of the continental shelf of North America (Pinsky  
*et al.* 2013, Fredston-Hermann *et al.* 2020). At a global scale, the impact of temperature change  
494 in marine environments appears to be highly dependent on baseline conditions, whether mea-  
sured in range shifts relative to temperature velocity (e.g., Lenoir *et al.* 2020) or species richness  
496 and abundance in response to temperature trends (e.g., Antão *et al.* 2020). Specifically, this lat-  
ter meta-analysis of patterns in marine taxa found that abundance was positively correlated with  
498 warming, except in the warmest of locations (Antão *et al.* 2020). The wide geographic scope of  
these analyses suggest that our focus on both local climate velocity and baseline environmental  
500 conditions may be broadly relevant to explaining climate change induced range shifts in marine  
taxa in regions around the globe.

502 While our trend model indicated an overall negative effect of rising temperatures on local fish  
density, the velocity model was consistent with the overall pattern in showing that most negative  
504 relationships occurred only in already warm locations (Figure 2). Large climate velocities reflect  
more spatially uniform environments—where a population would need to move greater distances  
506 to maintain constant climate—and likewise, small velocities reflect more spatially heterogeneous  
environments (Loarie *et al.* 2009). As a result, more spatially uniform regions have greater weight  
508 in the velocity model than in the trend model, and this stretching and compressing of trend values  
based on spatial heterogeneity likely explains why the negative interactive effect of mean temper-  
510 ature was only detected for velocities. Overall, we focused primarily on the velocity results since



they represent a more ecologically meaningful measure than trends alone, given that they account  
512 for the local reality species face if tracking a constant environment (Brito-Morales *et al.* 2018) or  
prey that themselves track the environment.

514 For many species, we do not know how far individuals travel on a daily or seasonal basis, so  
uncertainty remains as to the extent to which the modelled spatial resolution is appropriate for  
516 each of the species in this analysis. While the trend- and velocity-based models capture slightly  
different spatial scales ( $4 \times 4$  km focal cell vs.  $12 \times 12$  km encompassed when considering pat-  
518 terns among neighbouring cells as well), both resolutions are finer than what is often used for  
analyses of climate change in the marine environment (Oestreich *et al.* 2020, Pinsky *et al.* 2020),  
520 substantial environmental changes can occur at even finer scales, and these local-scale effects  
may be especially important for species with high site fidelity (e.g., Yelloweye Rockfish *Sebastes*  
522 *ruberrimus*, Hannah and Rankin 2011). However, in order to detect the impact of climate change  
on rockfish (many of which have generation times  $> 20$  yrs), one would require either data in  
524 excess of 20 years, or to contrast patterns of change between age classes. Indeed, responses to  
environmental change can be expected to differ between species, depending on the life history of  
526 species including physiological tolerances, lifespan, and dispersal patterns (Massiot-Granier *et al.*  
2018). Furthermore, reaching reproductive maturity frequently results in shifts in dispersal pat-  
528 terns, habitat selectivity, physiological tolerances (Laurel *et al.* 2007), and therefore represents a  
potentially important break point for understanding the impacts of climate change. Given the rel-  
530 atively short timescale encompassed in our analysis (one decade), we expected to find stronger  
patterns in shorter-lived/immature portions of populations and more pelagic species. Within im-  
532 mature populations, those with a younger mean age were found to exhibit the most extreme re-  
sponses to temperature velocity (positive in coolest locations and negative in warmest locations;  
534 Figure S22c); however, immature populations did not have overall stronger responses than mature  
populations (Figure S23b). Ecological responses were somewhat complicated by interactions with  
536 depths occupied; but, contrary to expectation, more extreme responses tended to belong to dem-  
ersal foraging and solitary species, rather than those with more pelagic or schooling behaviours  
538 (Figure S24c, g, h).

Aggregate metrics such as the centre of gravity have also demonstrated that demersal fishes  
540 use both shifts in latitude and depth to track changes in ocean temperatures (e.g., Perry *et al.* 2005,

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 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 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). This latter result suggests that there was spatial variability in temperature, or responses to temperature, which were not fully captured by the centre of gravity (VanDerWal *et al.* 2013). Fine-scale 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 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 Canadian Pacific groundfish is that species here are closer to the southern ends of their distributions and may therefore be closer to the warm end of their temperature tolerances, especially in the warmest locations. However, although we found the strongest negative biotic velocities in these warmer locations, species nearer to their northern range limit (designated by N under 'Range limit' in Table S1) were not more likely to show a positive response to temperature.

### 558 **Limitations and implications**

There are a number of limitations to our analysis. First, our analysis cannot separate fish population movement in response to climate from a host of other possible explanations. For example, local changes in 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), 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 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 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, there are limitations to our data. The CTD climate data from Canadian Pacific trawl surveys are

570 only available from 2008 onward, the surveys occur in one seasonal period (May to August) and  
cover a given region only once every two years. Also, some of the species (e.g., shallower rockfish  
572 species) may be better sampled by longline gear than trawl gear. This spatial and temporal scope  
will miss overlap in major life-history events for some species (e.g., Sablefish; [Beamish 2008](#)), or  
574 seasonal movements (e.g., Pacific Halibut; [Loher 2011](#)). Importantly, the input data for our meta-  
analytic model are predictions from our first-stage geostatistical models. Third, it is possible that  
576 climate conditions may themselves affect survey catchability. For example, groundfish may flee  
gear more slowly or aggregate to avoid low DO conditions ([Craig 2012](#)), thereby making fish more  
578 catchable and biasing observations.

This analysis suggests multiple future research directions. First, future efforts may aim to iden-  
580 tify common spatial patterns across species using spatial dimension reduction tools such as spatial  
factor analysis ([Thorson et al. 2015a](#)). Areas where species overlap in their response would repre-  
582 sent important areas for conservation ([Brito-Morales et al. 2018](#)), but also areas where competition  
may be expected to increase or new fisheries interactions may occur. Second, some rockfish are  
584 better sampled by longline survey gear and future analyses could use such survey data, or com-  
bine survey data from multiple gear types ([Webster et al. 2020](#)), to develop a composite density  
586 estimate. Third, our analysis used CTD data, which was only available for spring or summer from  
2008 onwards and required a statistical model to extrapolate to the full region. An alternative  
588 would be a ROMS (Regional Ocean Modeling System) model ([Peña et al. 2019](#)), which could extend  
the temporal scope, allow for accounting of climate at other times of the year (e.g., temperature  
590 during spawning; [Laurel and Rogers 2020](#)), allow for inclusion of variables not typically measured  
with survey data (e.g., primary production), and allow for forward projections. Preliminary inves-  
592 tigation indicated a strong correlation between our CTD projections and recently updated ROMS  
bottom temperatures. With the greater spatial and temporal extent that ROMS data will provide,  
594 calculation of more geographically precise analog-based climate velocities could be used to further  
refine the identification of areas important for conservation ([Brito-Morales et al. 2018](#)).

596 The spatial shifts we identified could have a number of management consequences. First, we  
observed changes over a decade and such redistribution is likely to compound over time. Redis-  
598 tribution can impact fishing opportunities and conservation of rarer species when “choke” species  
(species with limited quota that co-occur with species of fishing interest) limit fishing opportu-

600 nities (e.g., [Forrest et al. 2020](#)). Redistribution can also impact nations or peoples with relatively  
small defined spatial fishing rights and have consequences for marine spatial planning. For ex-  
602 ample, a marine reserve designed to protect a particular at-risk population may no longer be as  
effective after a local redistribution of abundance. Lastly, shifting distributions can affect calcu-  
604 lation 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](#)).

606 Climate change is expected to have large impacts on fish stocks and their management, par-  
ticularly with respect to changes in species distribution (e.g., [Tommasi et al. 2017](#), [Karp et al. 2019](#),  
608 [Free et al. 2019](#)). Legislation and policy in jurisdictions around the world (e.g., the US *Magnuson-*  
*Stevens Act*, Canada’s *Fisheries Act*, the European Marine Strategy Framework Directive) require  
610 that environmental conditions affecting fish stocks be accounted for in management decisions  
such as setting sustainable catch limits and developing rebuilding plans. However, there is often a  
612 mismatch between scale of climate predictions, the scale at which species respond, and the scale  
of management decisions ([Stock et al. 2011](#), [Maureaud et al. 2021](#)). For example, the populations  
614 analyzed in this study are managed at the mesoscale, with catch limits often determined for indi-  
vidual substocks ([DFO 2019](#)). The metrics presented in our paper represent fine-scale indicators of  
616 response to a changing environment, which are useful for assessing risk and conservation plan-  
ning ([Brito-Morales et al. 2018](#)). Analyses such as ours can be incorporated into frameworks for  
618 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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626 manuscript is based.

## Data Availability Statement

628 The biological data that used in this study are openly available through <https://open.canada.ca>  
at <https://open.canada.ca/data/en/dataset/a278d1af-d567-4964-a109-ae1e84cbd24a> and associated  
630 environmental measurements are available from [https://www.pac.dfo-mpo.gc.ca/stats/index-  
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-  
assess/gfvelocities](https://github.com/pbs-<br/>632 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 $3 \times 3$ 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

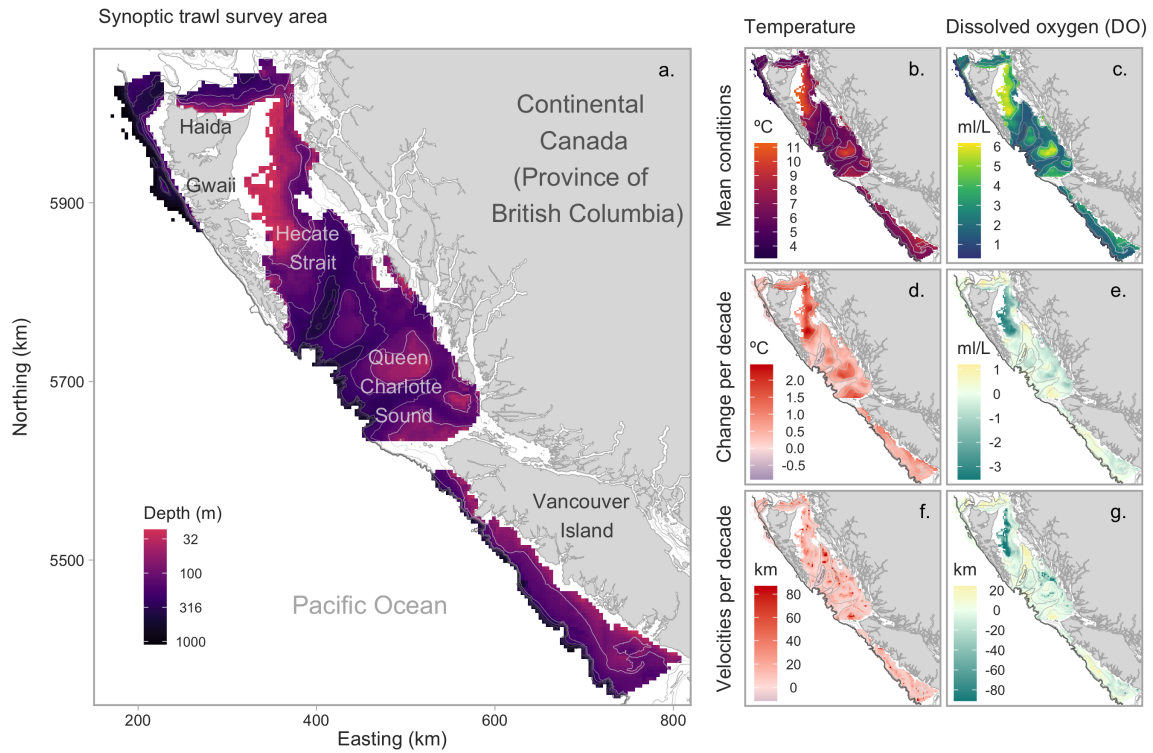


Figure 1: Maps of study area (a), predicted mean conditions (b, c), decadal trends (d, e), and decadal velocities (f, g) of bottom temperature and dissolved oxygen (DO) for 2008–2018 off the coast of British Columbia, Canada (UTM zone 9). Values are estimated using geostatistical spatiotemporal models 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.

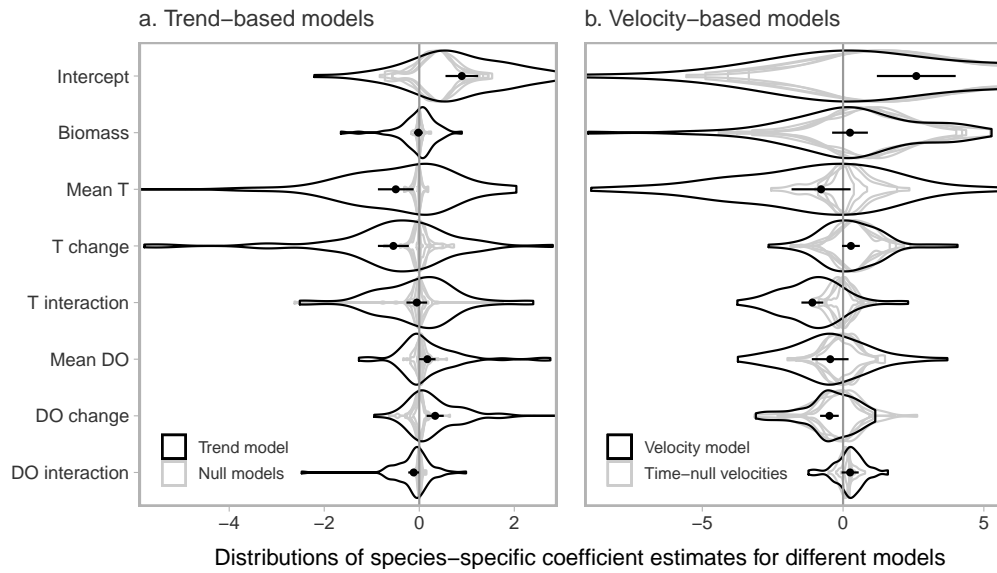


Figure 2: Distribution of species-specific (random effect) coefficients from the model fitted to observed data (black violins) compared with coefficients from four simulated null models (gray violins). Each “violin” is based on a single model including all species: (a) trend-based models where climate and biotic change variables are all local trends and (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.

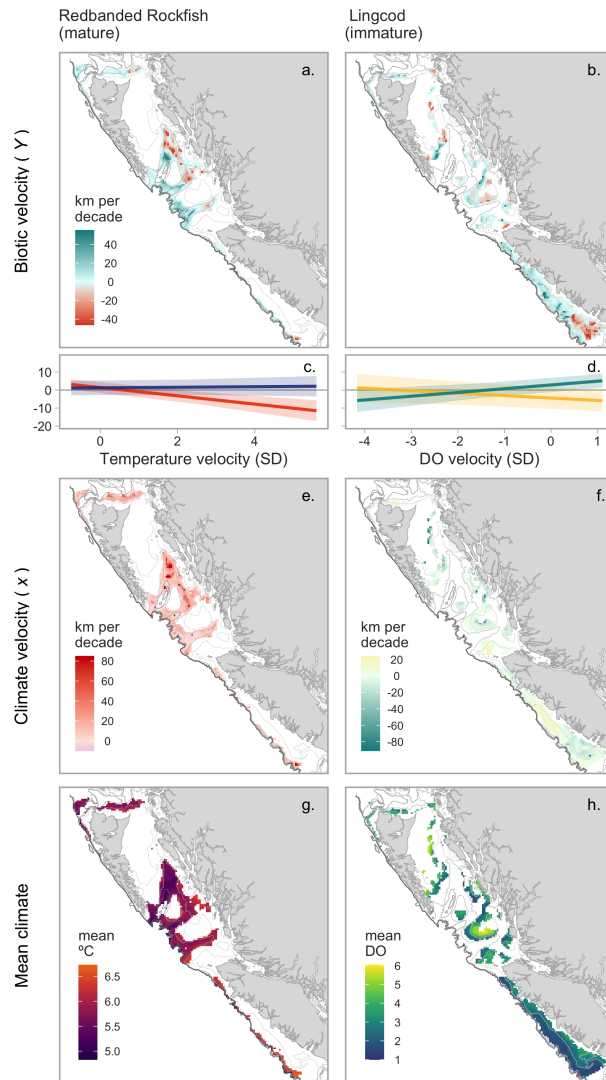


Figure 3: Maps and interaction plots for two illustrative species representing the most frequent relationship with temperature (left column) and the expected response with DO (right column). Mature Redbanded Rockfish had stable, near-zero, biotic velocities regardless of amount of warming in the coolest regions it occupied, and decreases in biomass when temperatures increased in warmer regions (a,c,e,g). Immature Lingcod 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.

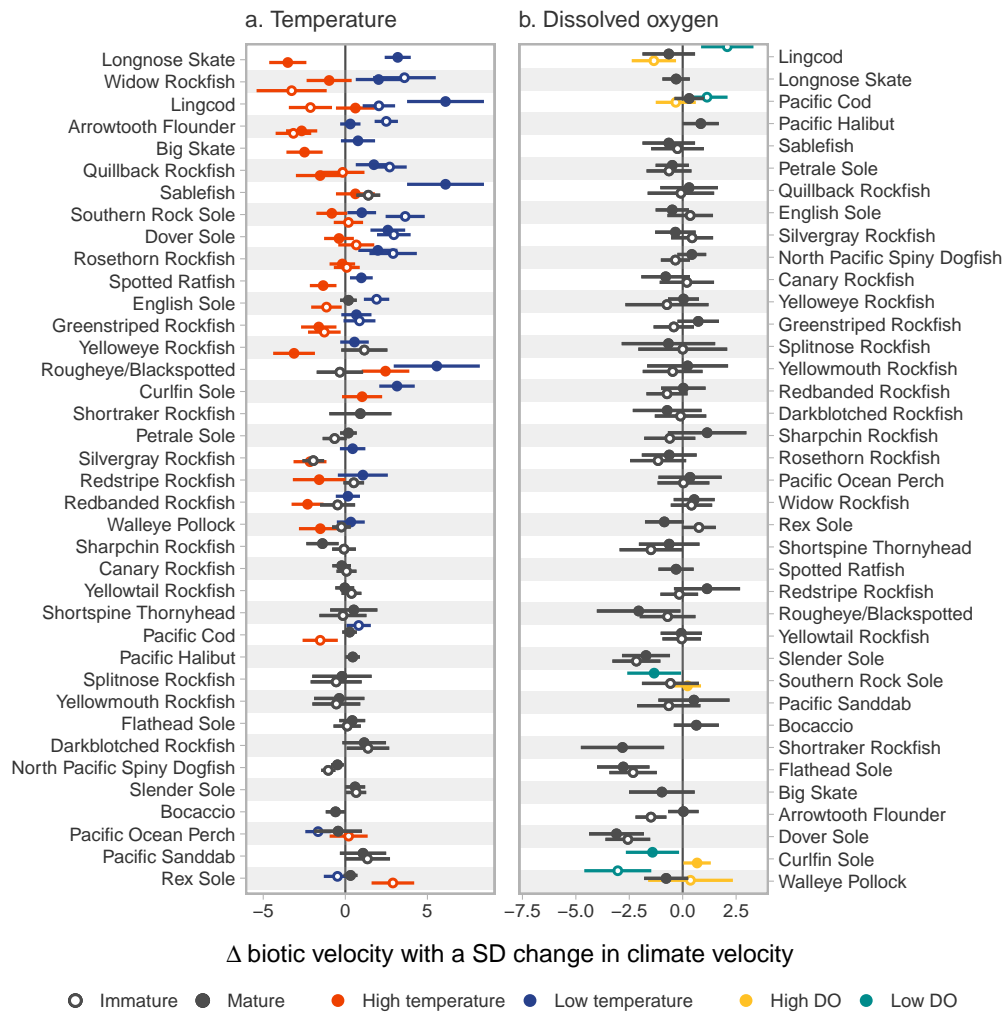


Figure 4: Mean climate and climate change interact in predicting biotic velocities (km/decade) for 38 groundfish species. Coloured dot-whiskers indicate slopes and 95% CIs of the predicted biotic velocities with 1 SD of change in climate velocity for the low and high 95% quantiles of mean local climate (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. See Table S1 for scientific names.

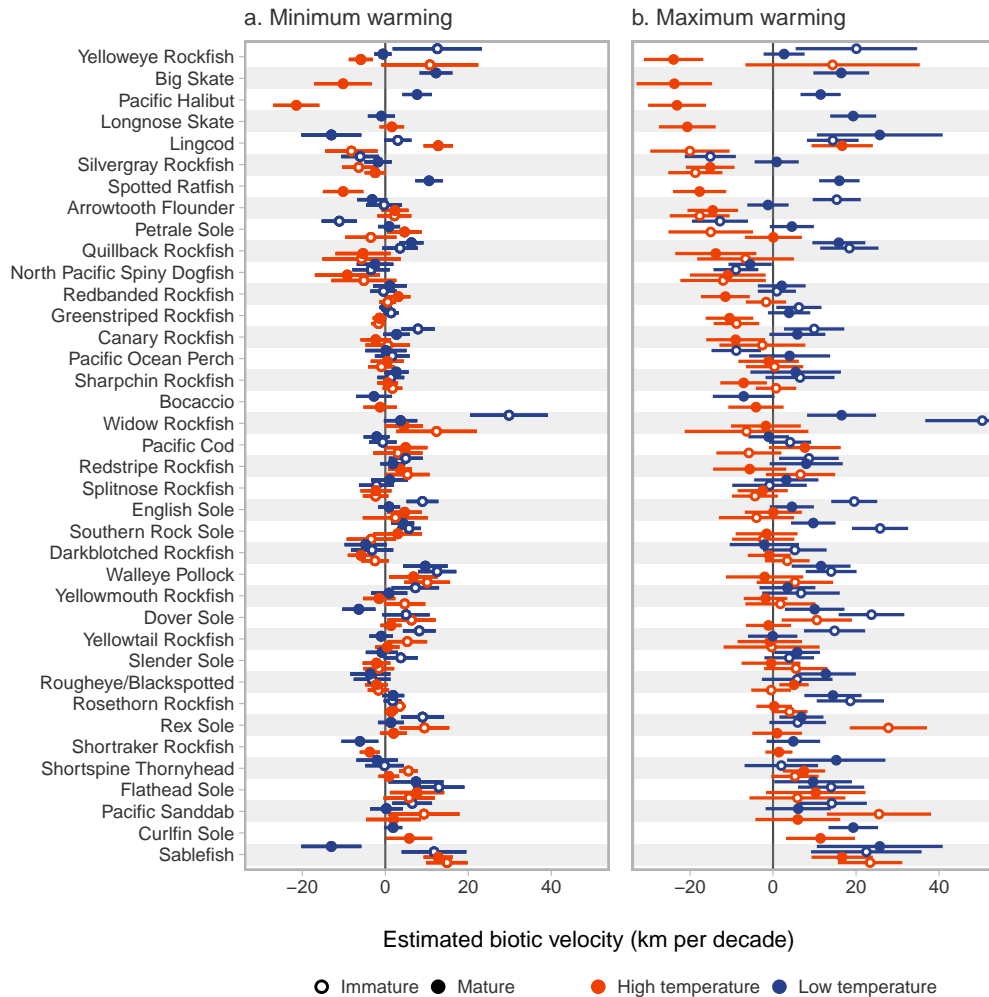


Figure 5: Estimates of biotic velocities (km/decade with 95% CI) for 38 groundfish species under different mean temperatures (blue and red represent low and high 95% quantiles) occupied and at (a) the minimum and (b) maximum temperature velocities experienced for each species. Open circles indicate patterns 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 Information

## Methods

### S1. Maturity and length-weight models

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

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

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

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

where  $M_i$  represents the mature (1) or immature (0) status of fish  $i$ ,  $p_i$  represents the probability of maturity of fish  $i$ ,  $\alpha$  represents a global intercept,  $\alpha_t$  represents a year-specific deviation for year  $t$  that is allowed to vary with a variance of  $\sigma_\alpha^2$ ,  $\beta$  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 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.

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 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 parameter estimates of the length-weight relationship  $W_i = aL_i^b$ ,  $\sigma$  representing the observation error scale, and 3 representing a degrees of freedom parameter fixed to allow for outlying residuals.

### S2. Alternative spatiotemporal models of fish biomass density

We tried including the proportion of muddy sediment and proportion of sediment with any rocks 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 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 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 bottom temperature, water circulation patterns, species interactions, and species movement.

### **S3. Velocity calculation considerations**

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 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 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 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 (Figs 1 and S13).

### **S4. Alternative model configurations for linking biotic changes with climate**

We tested additional covariates that we chose not to include in the final model. We calculated average hours fished by commercial bottom trawl for each  $4 \times 4$  km grid cell per year between 2008 and 2018, as well as the percent change in time spent fishing during this time (Figure S26). The log of mean fishing intensity, the trend in fishing intensity, and the interaction between the two were all included as covariates in a climate trend model, but none of these variables showed any more significant negative relationships than might be expected by chance (Figure S27). We tested 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 interactions). 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 S21); however, 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 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, and gradient. None of the important effects we focus on in the results (Figure S23) were changed qualitatively by any of these added variables.

### **S5. How climate sensitivity varies with life history and ecology**

We calculated weighted means and interquartile ranges of depths from maturity-specific biomass 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



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 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 S22). 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.

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

<sup>+</sup>Immature individuals use the alternate strategy

\*Species for which maturity data not collected

\*\*Complex that includes Rougheye Rockfish *Sebastes aleutianus* and a formerly unrecognized species, Blackspotted Rockfish *Sebastes melanostictus*

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

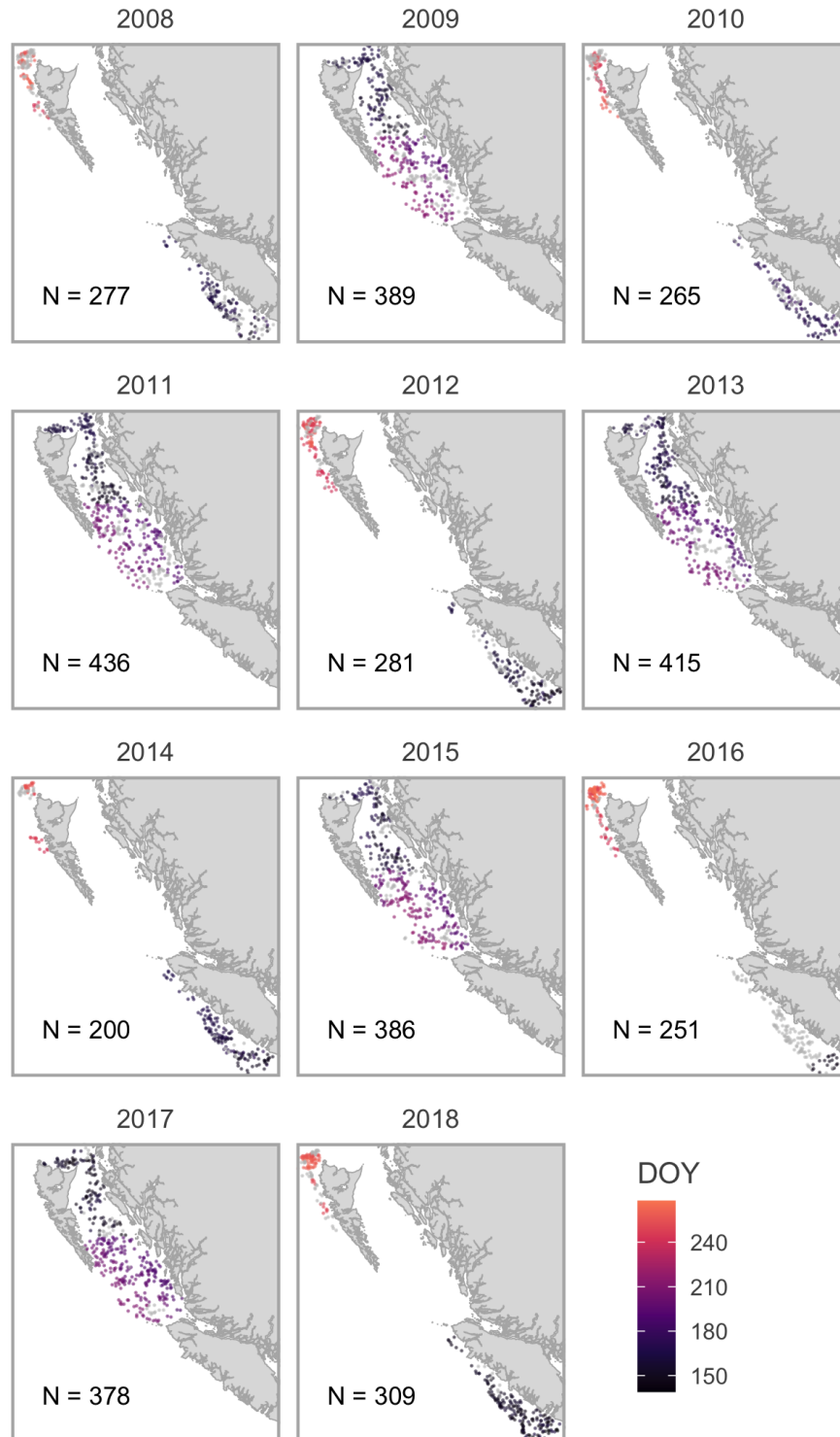


Figure S1: Distribution of synoptic survey trawls from 2008 through 2018 by year, day of year (DOY), and in space (UTM coordinates correspond to those in Figure 1). N is the total trawls analyzed for each year. Grey points are trawls that lack DO sensor data.

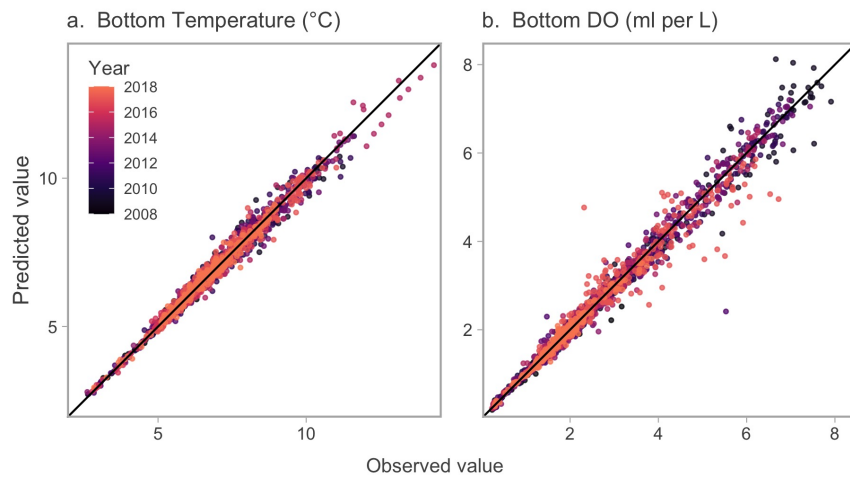


Figure S2: Predictions from models of bottom temperature (a) and DO (b) vs. observed sensor measurements on the trawl surveys.

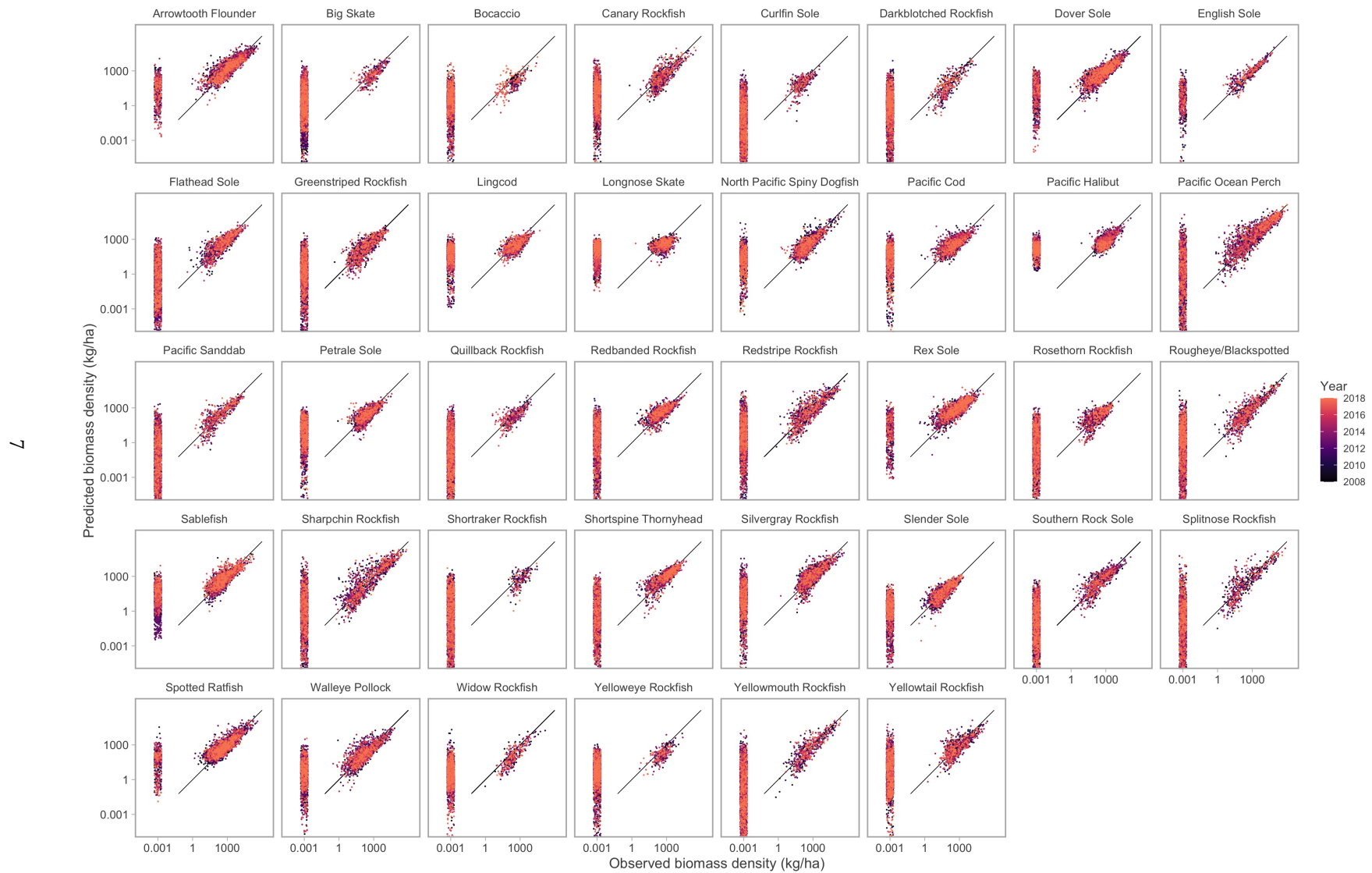


Figure S3: Predicted vs. observed mature biomass densities. Observed absences have been assigned 0.001 kg/ha and given some horizontal random jitter to improve visibility of data points and the 1:1 line is truncated to not intersect these adjusted values.

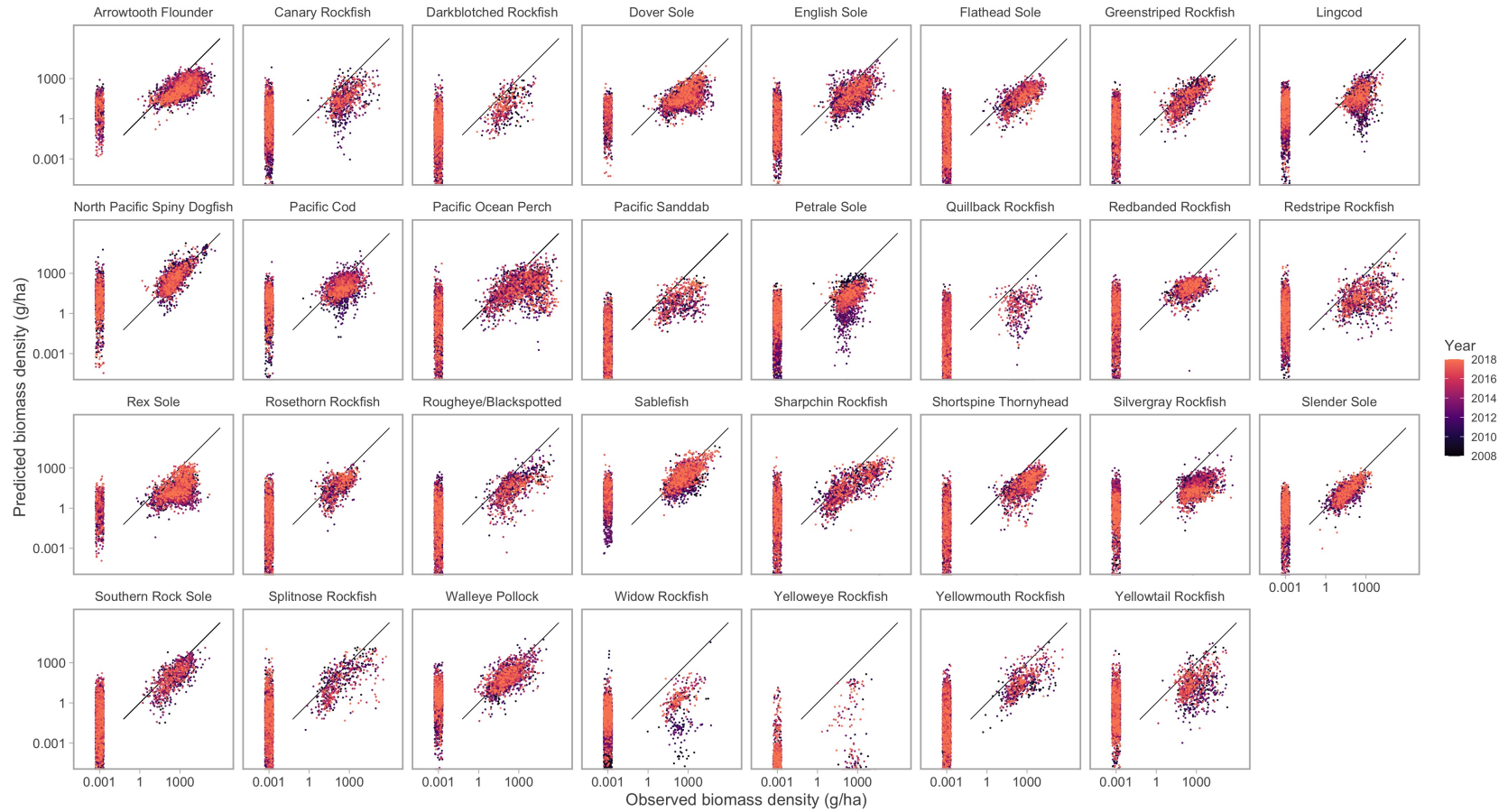
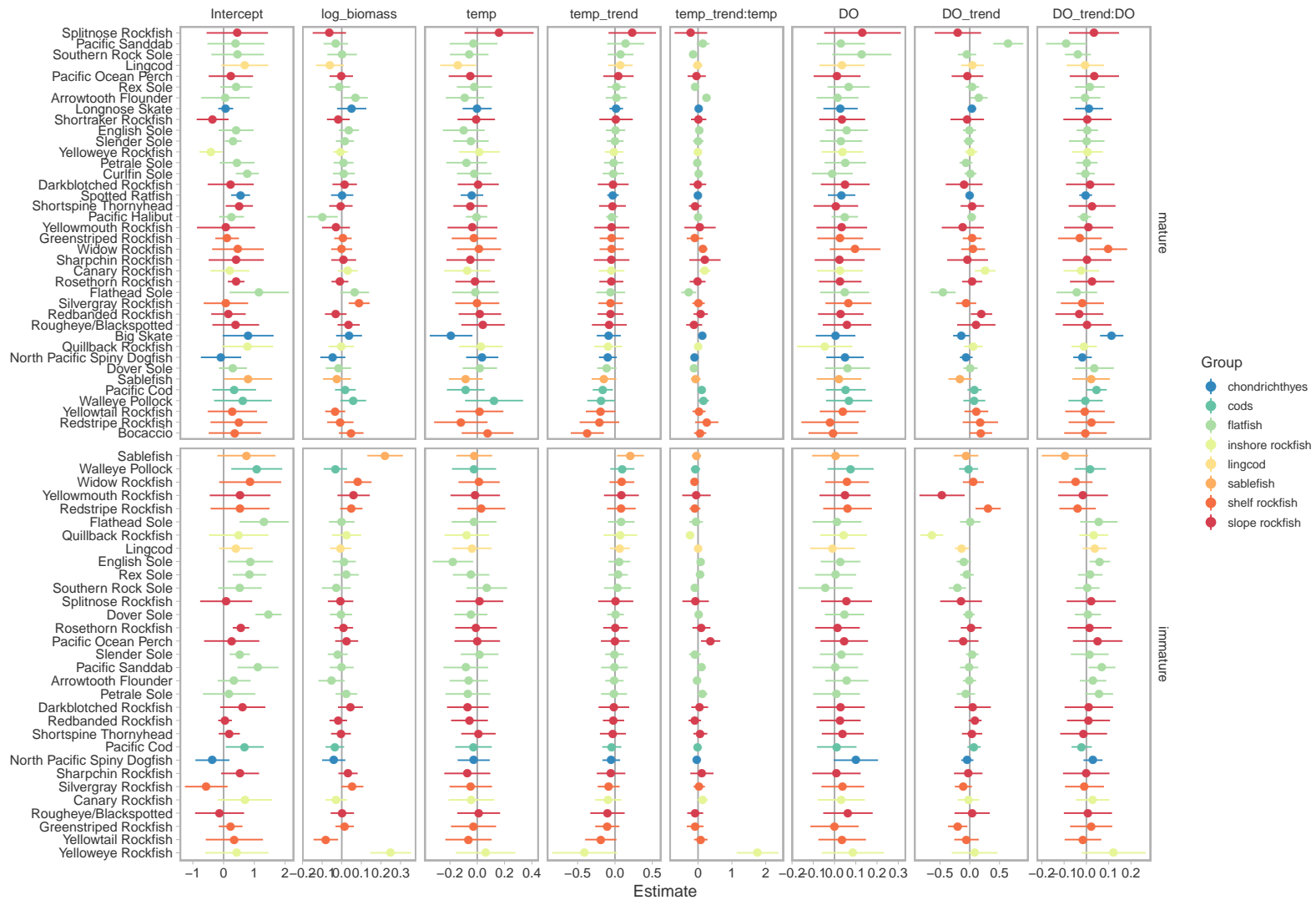


Figure S4: Predicted vs. observed **immature** biomass densities. Same treatment as Figure S3 except that units are g per hectare instead of kg per hectare. Relatively few positive samples for Widow and Yelloweye Rockfish result in relatively poor model fit to the positive sample component.



6

Figure S5: Species-specific coefficient estimates from one example of a simulated trends model (null #1) ordered by the estimated effect of temperature trend.

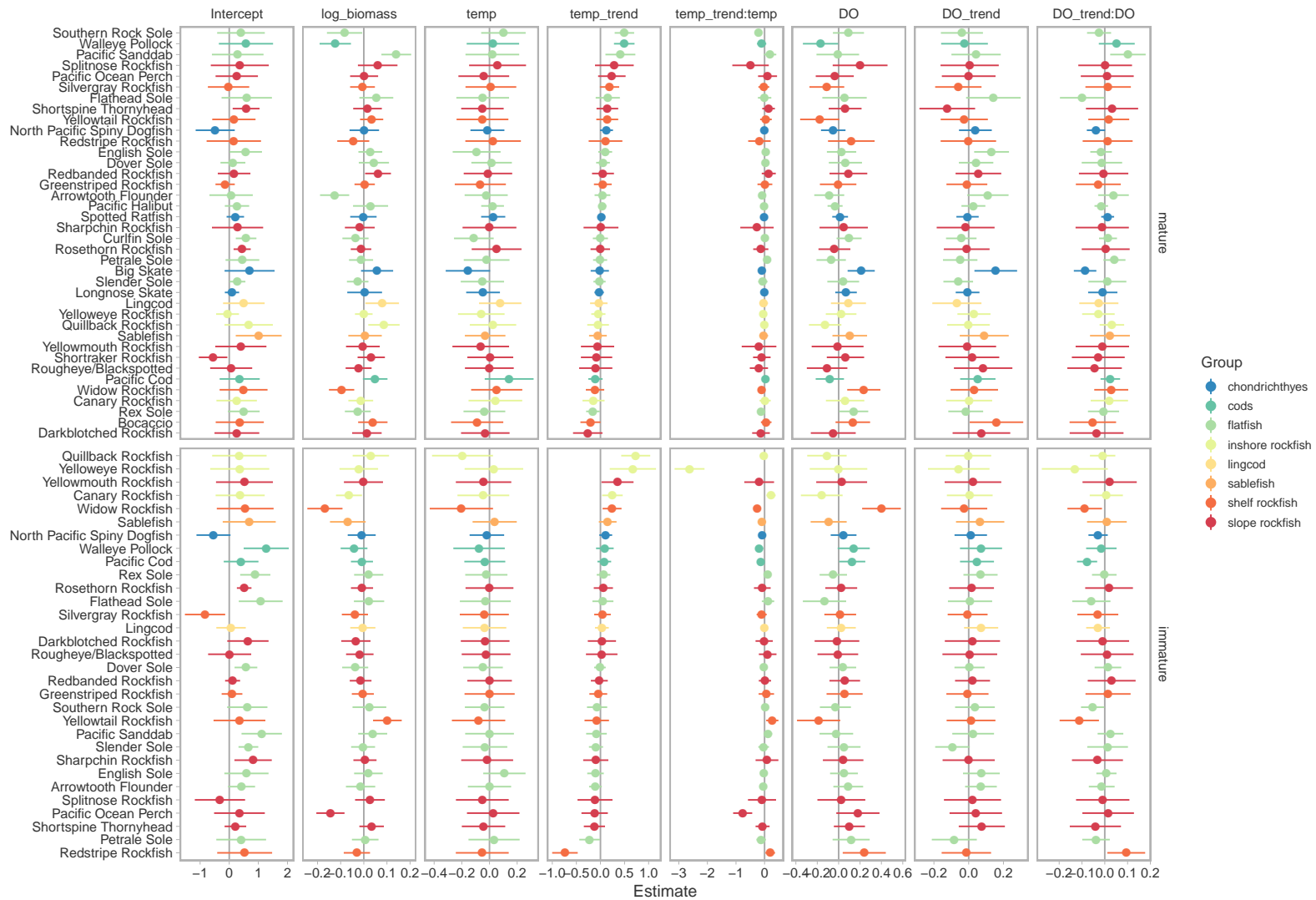


Figure S6: Species-specific coefficient estimates from one example of a simulated trends model (null #2) ordered by the estimated effect of temperature trend.



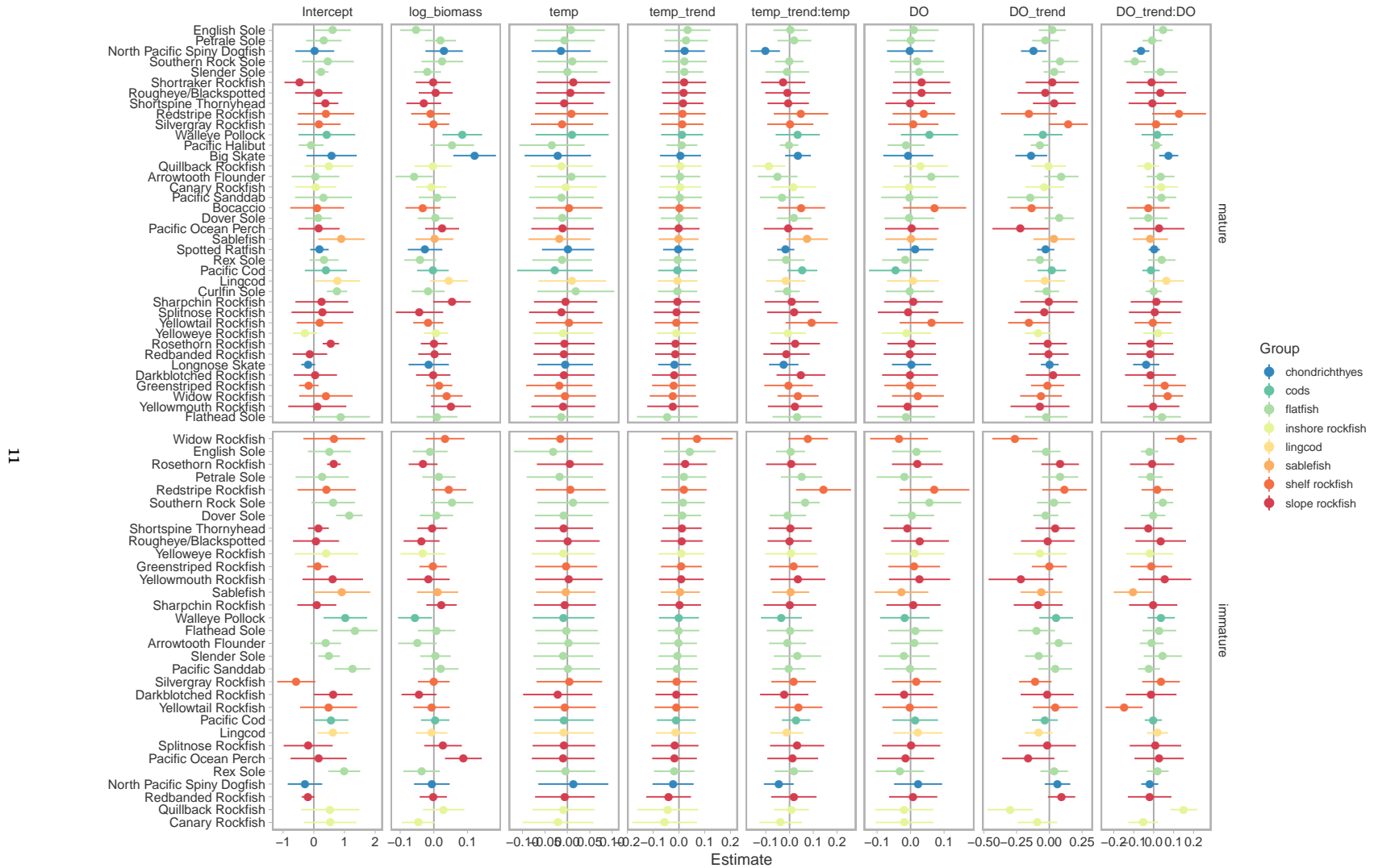


Figure S7: Species-specific coefficient estimates from one example of a simulated trends model (null #3) ordered by the estimated effect of temperature trend.

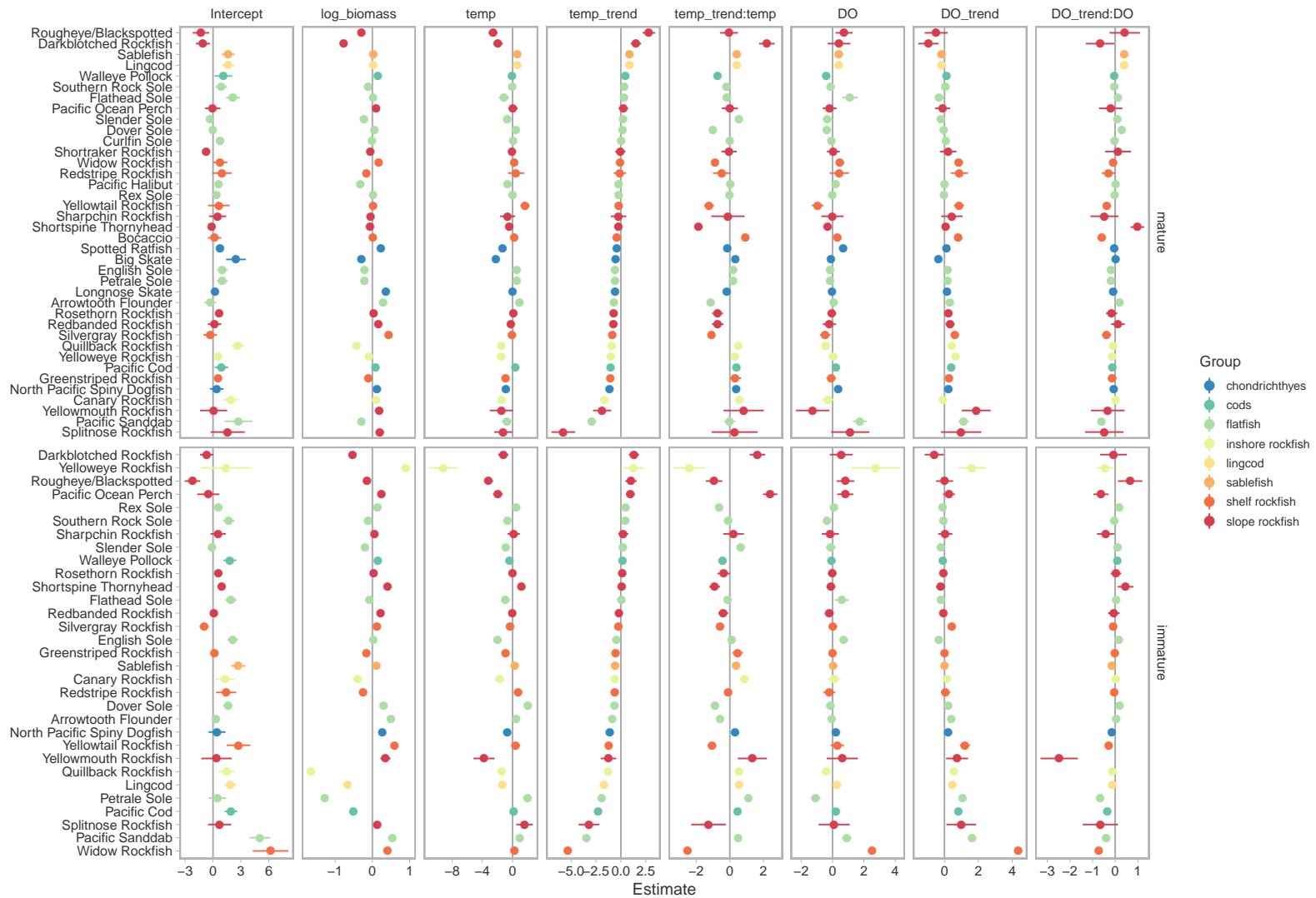


Figure S8: Species-specific coefficient estimates from trend model ordered by the estimated effect of temperature trend for a cell with an average biomass density and climate conditions and with no change in DO.



Figure S9: 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 S10: 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 S11: 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 S12: 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.

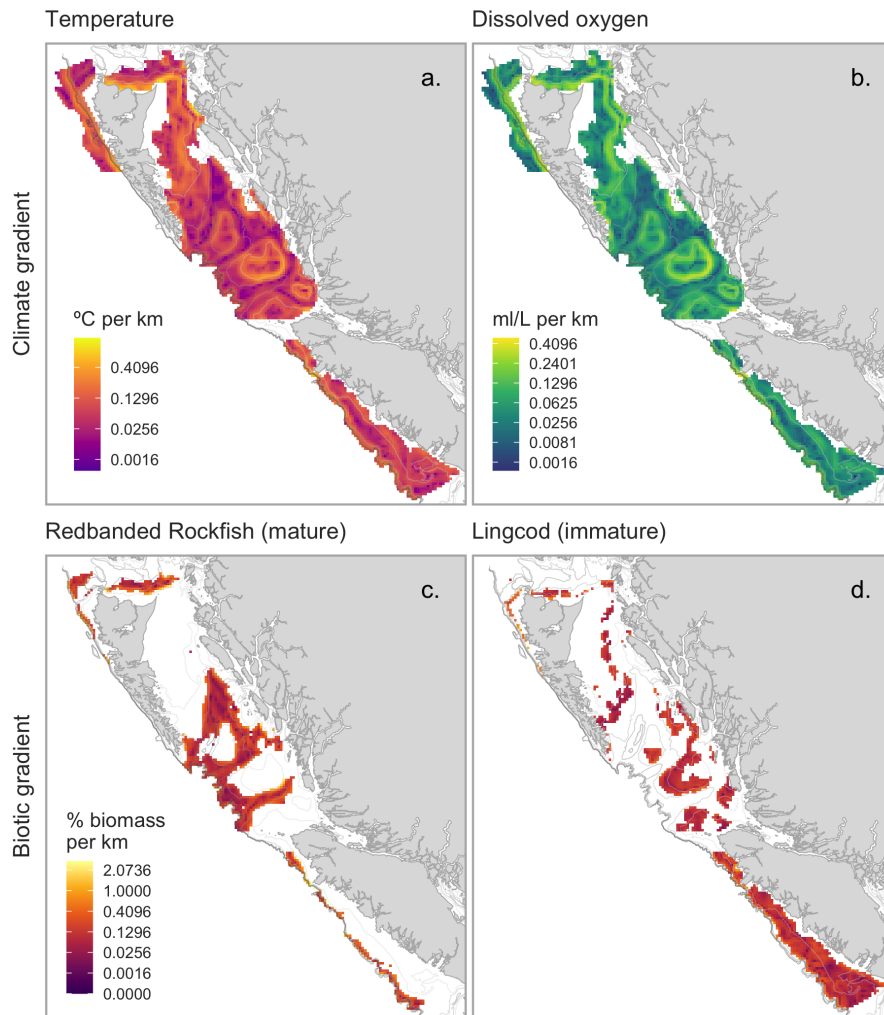


Figure S13: Maps of the gradient component of velocity calculations for both climate and biomass. Biotic gradient panels are for example species.

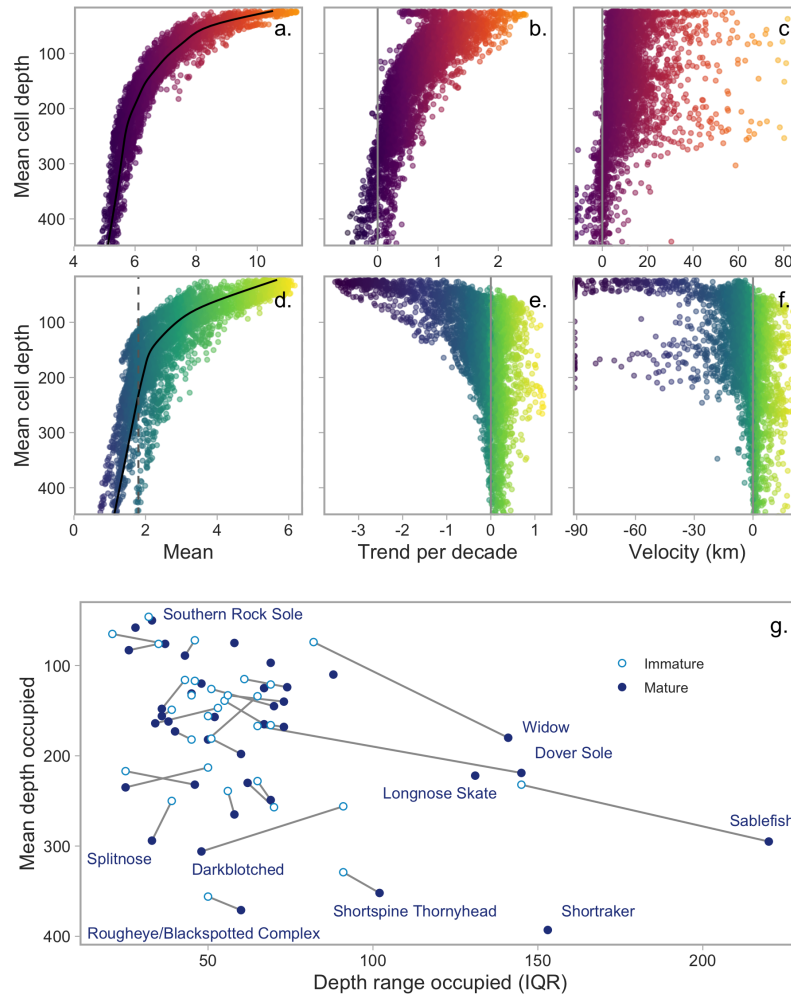
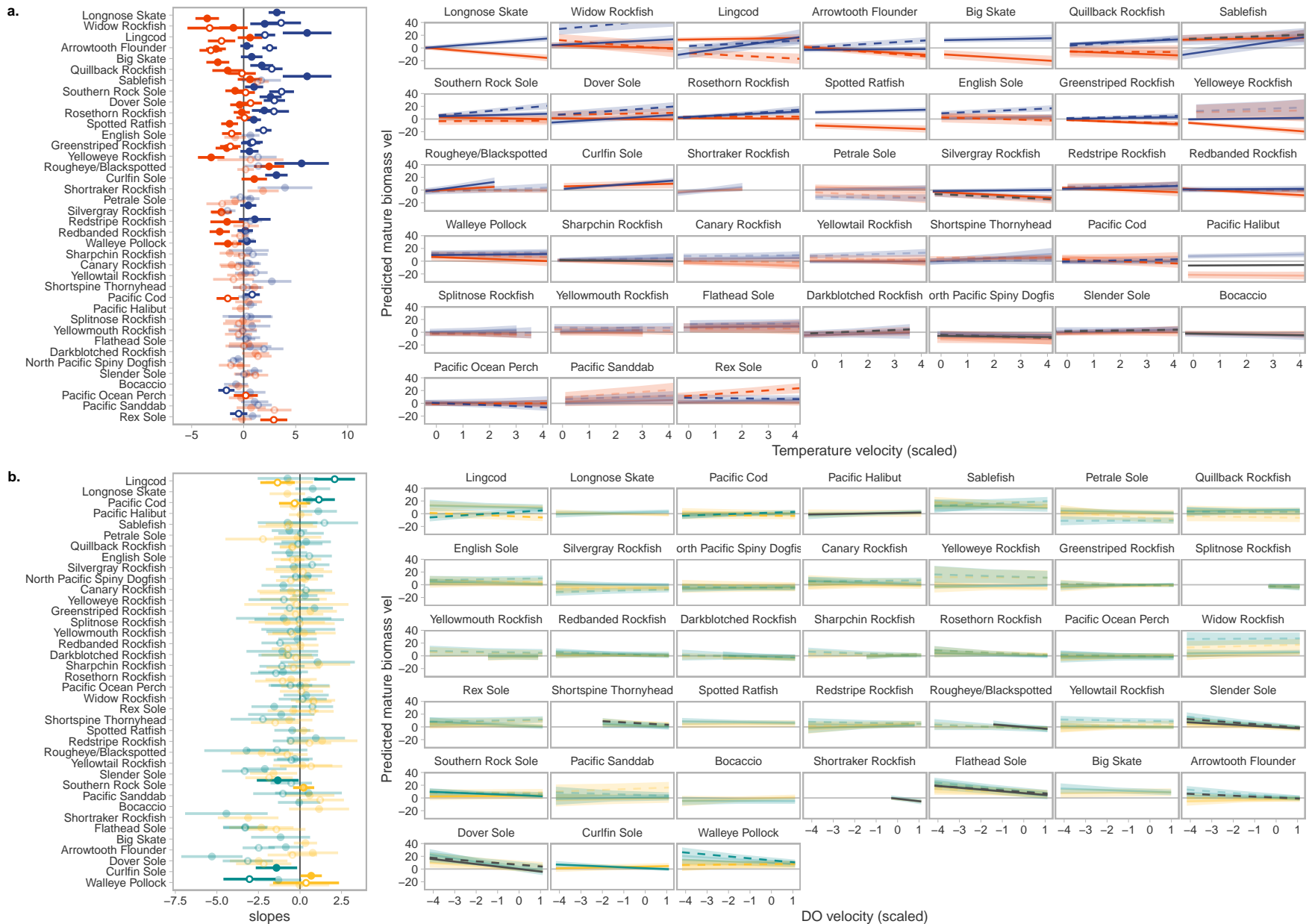


Figure S14: The climate conditions of each cell across depths (y-axes of upper panels) are indicated by both colours and the values on the x-axes of the 6 upper plots. Mean depth occupied by groundfish species co-varies with interquartile depth range occupied (g) and many of these species move deeper (lower on y-axis) with maturity (classes linked by grey lines) often with a corresponding increase in depth range (to right on x-axis).





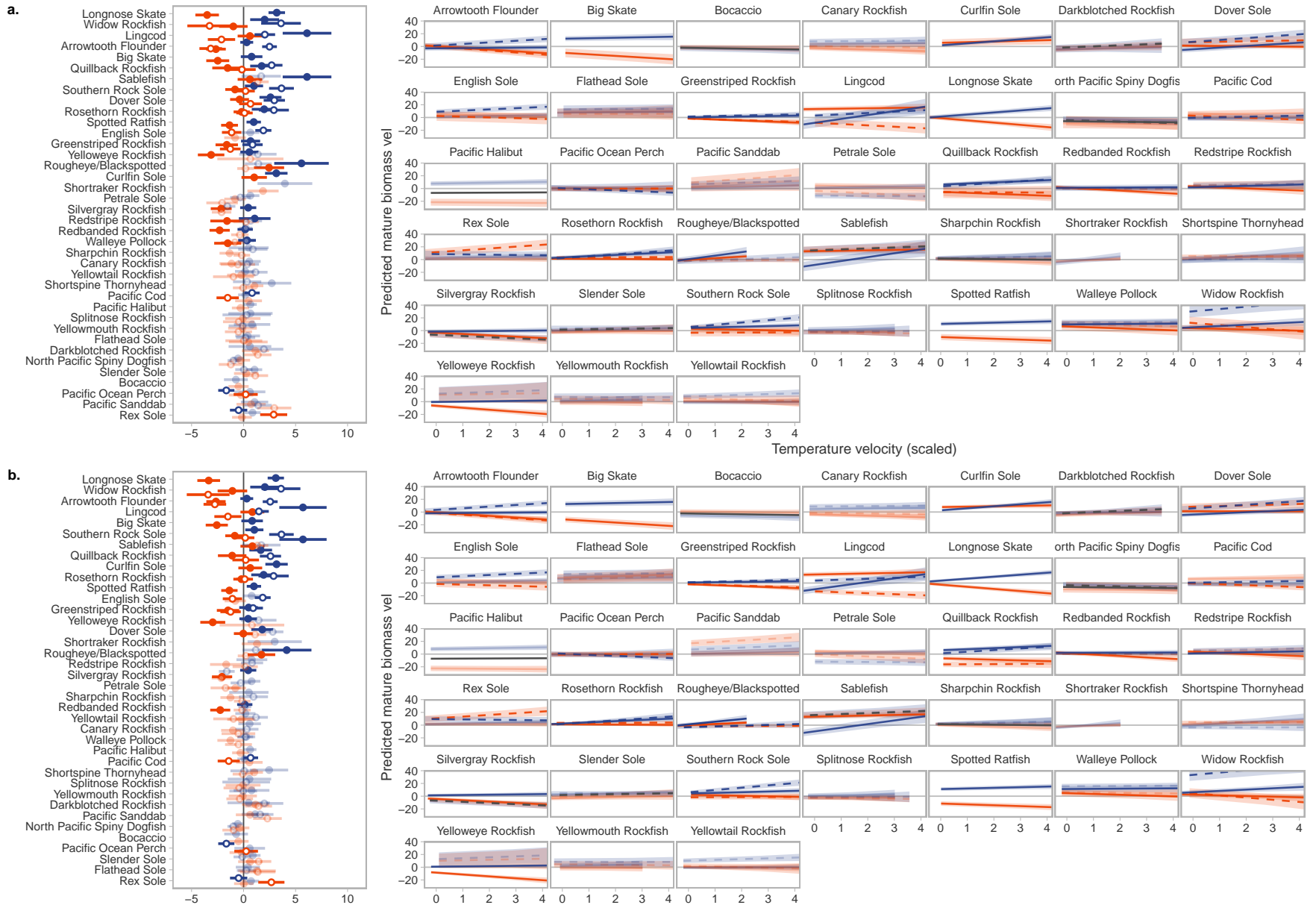


Figure S16: Here, (a) we duplicate the same slopes and predicted relationships as in Figure 4, but this time the species plots are ordered alphabetically for ease of comparison with (b) results from a similar model that lacks all of the DO variables. Differences in the ordering of the species in the 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.



Figure S17: 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).

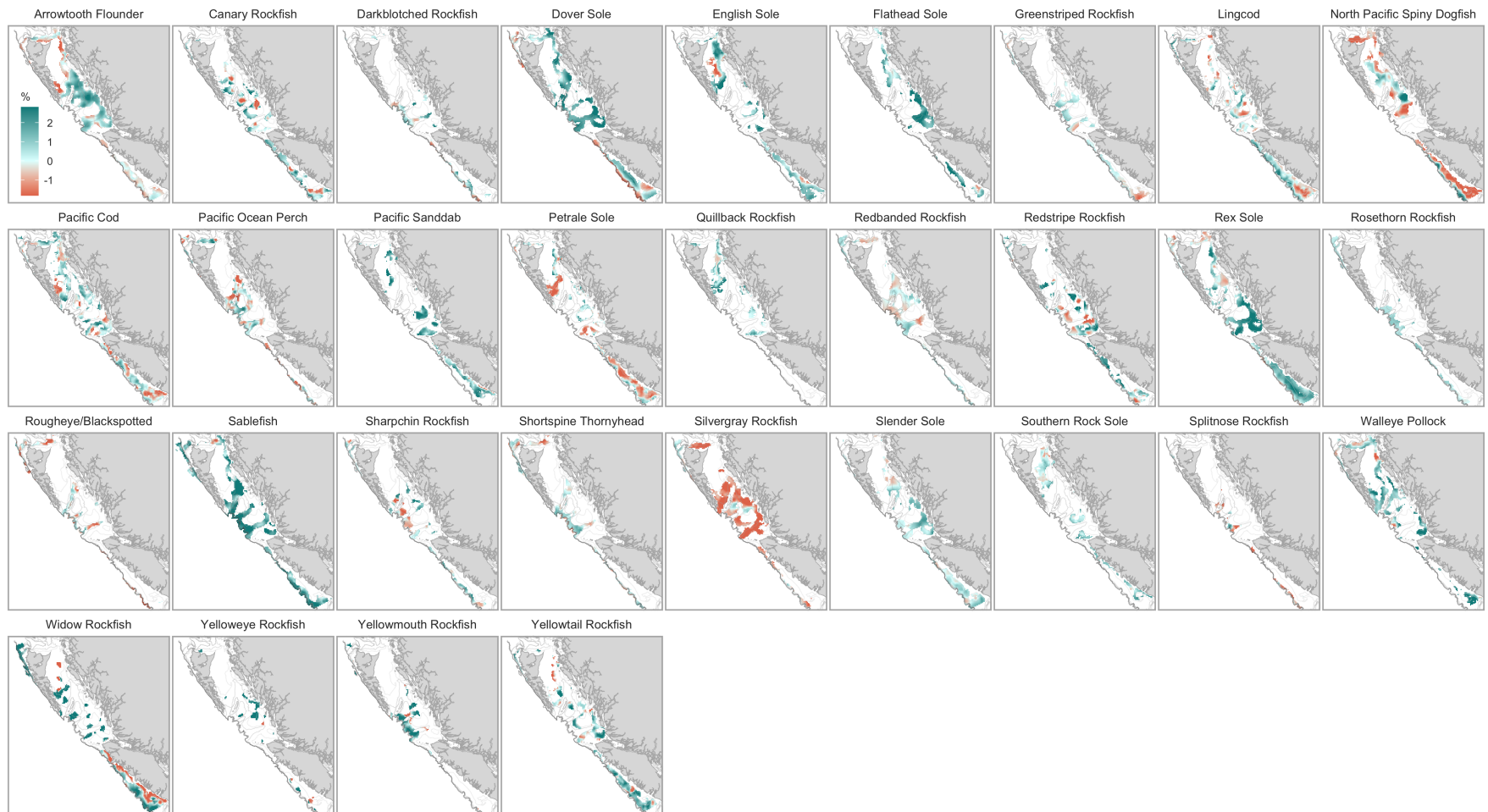


Figure S18: Biomass trends for immature fish populations on same scale as Figure S17.





Figure S19: Biotic velocities for mature fish populations.

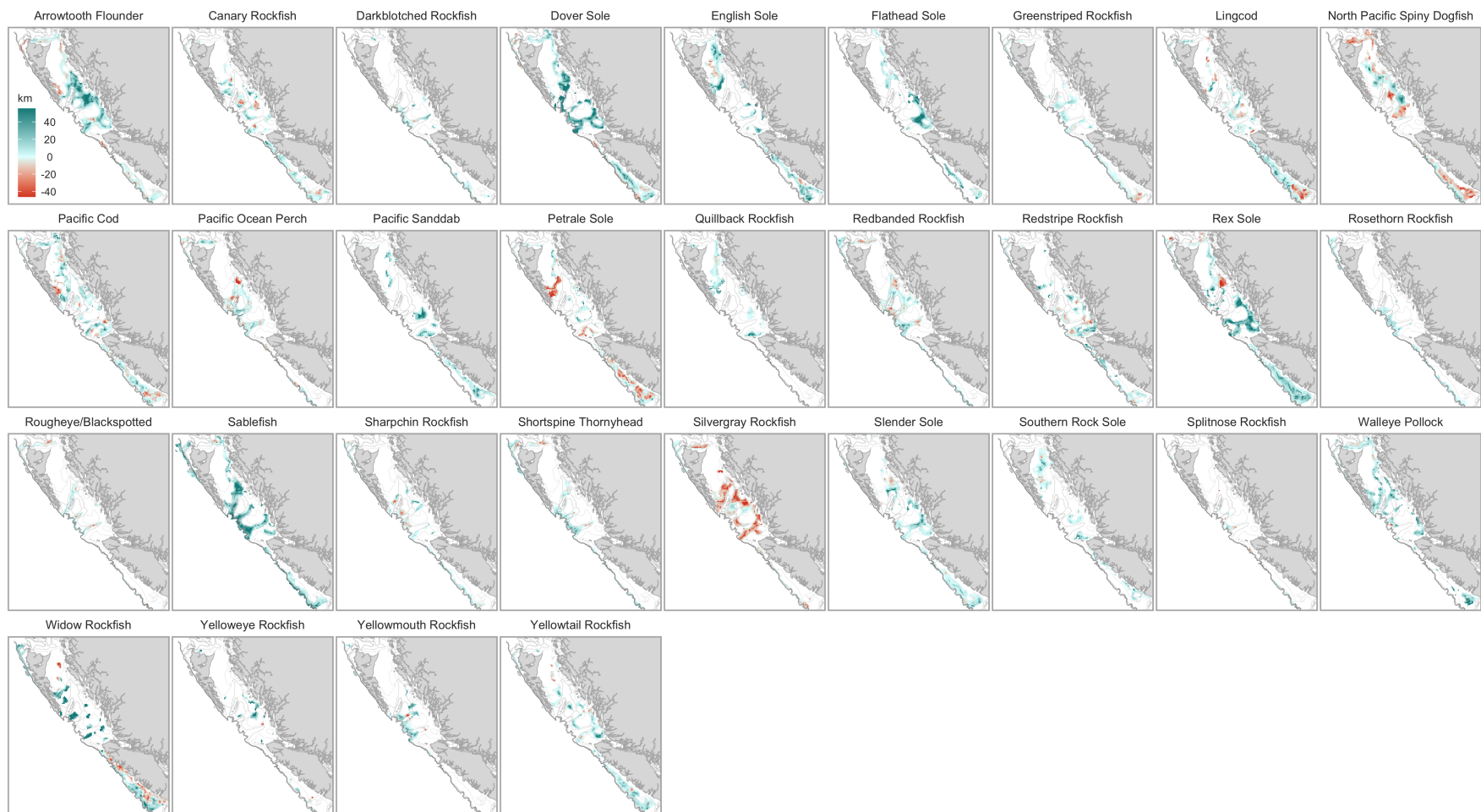


Figure S20: Biotic velocities for immature fish populations.

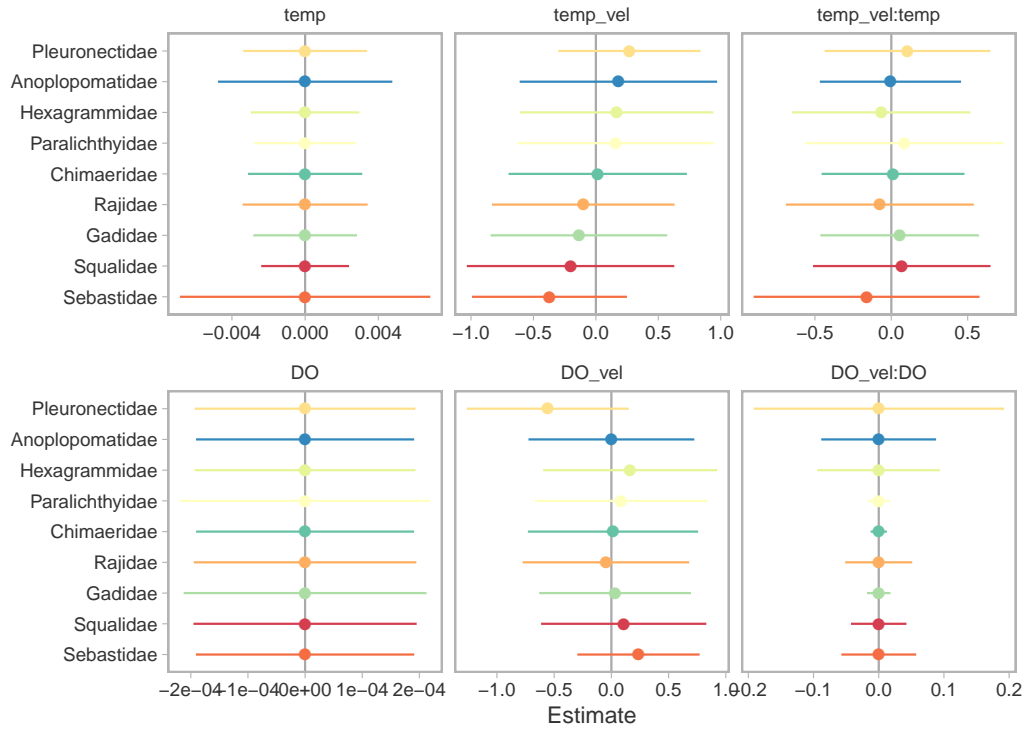


Figure S21: Family-level coefficient estimates for climate variables all have confidence intervals overlapping zero. Families are ordered by decreasing biotic velocity with increasing temperature velocity. This model includes the same climate variables as the “Velocity” models in Figures 2b and S23.

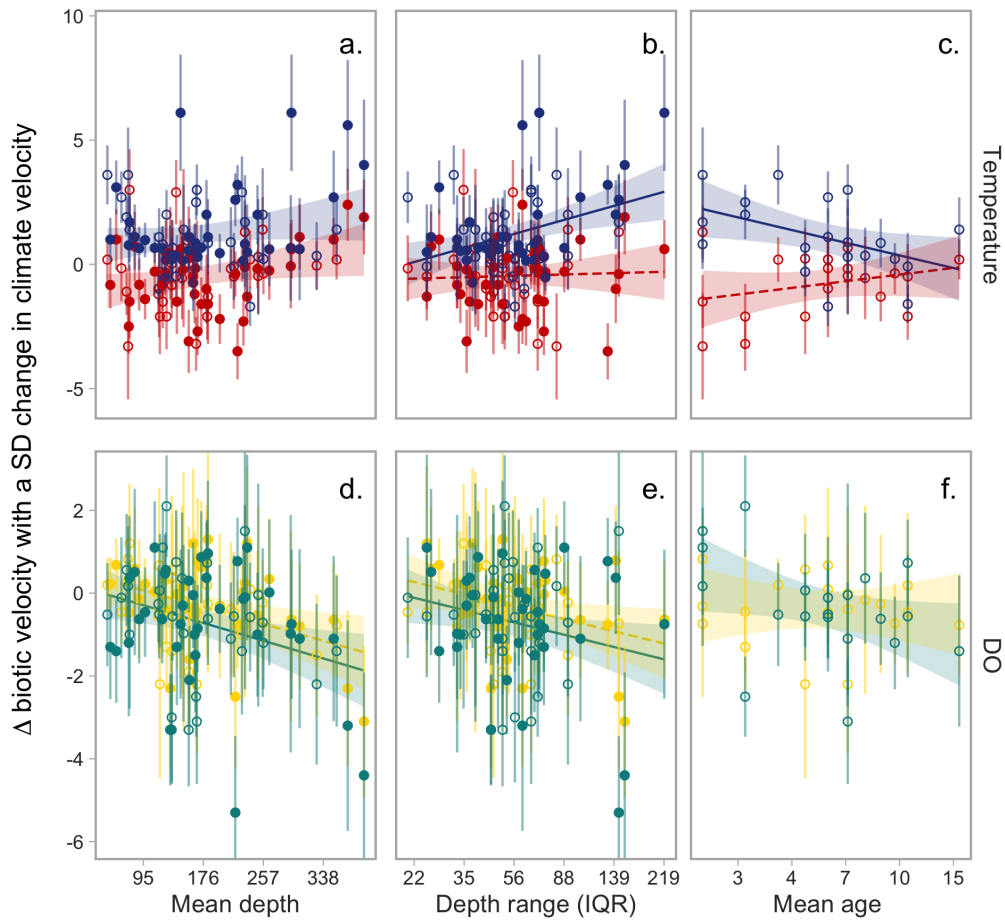


Figure S22: Occupied range of depths and immature population age correlate with the effect of warming temperature velocities on biotic velocities at low temperatures (a-c) and/or DO levels (e). Mean depth occupied only correlated with effects of DO (d). Each panel illustrates a separate model with a 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.



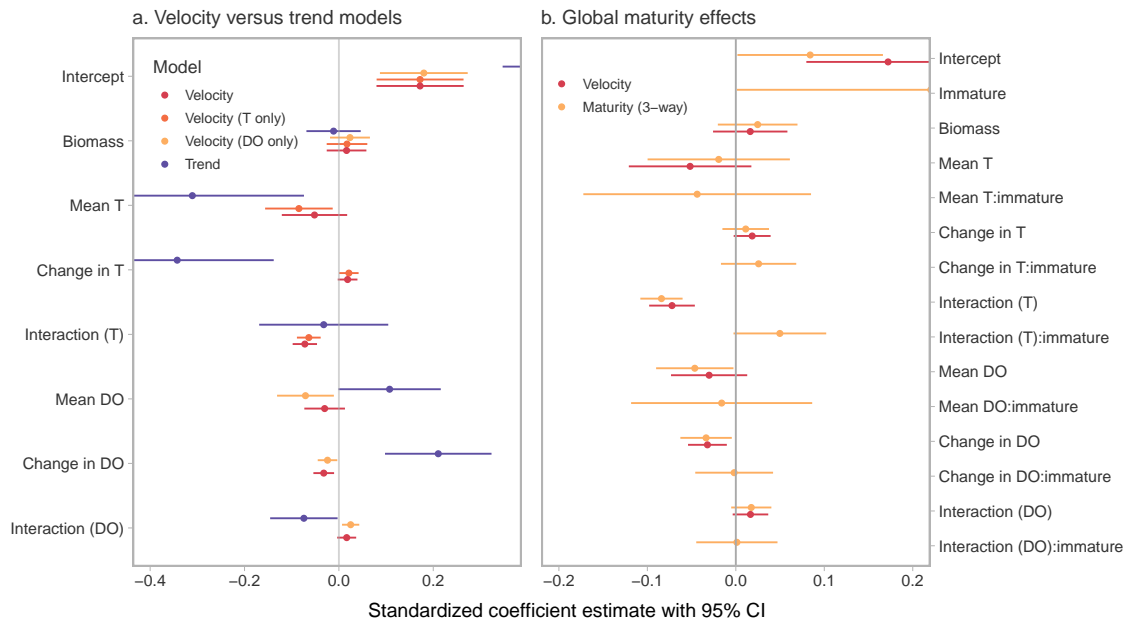


Figure S23: Global coefficient estimates for all fixed effects in a range of model configurations. All ‘velocity’ models predicted biotic velocity in response to climate changes calculated as gradient-based velocities (trend/spatial gradient). ‘Trend’ model predicts % change in biomass in response to 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.

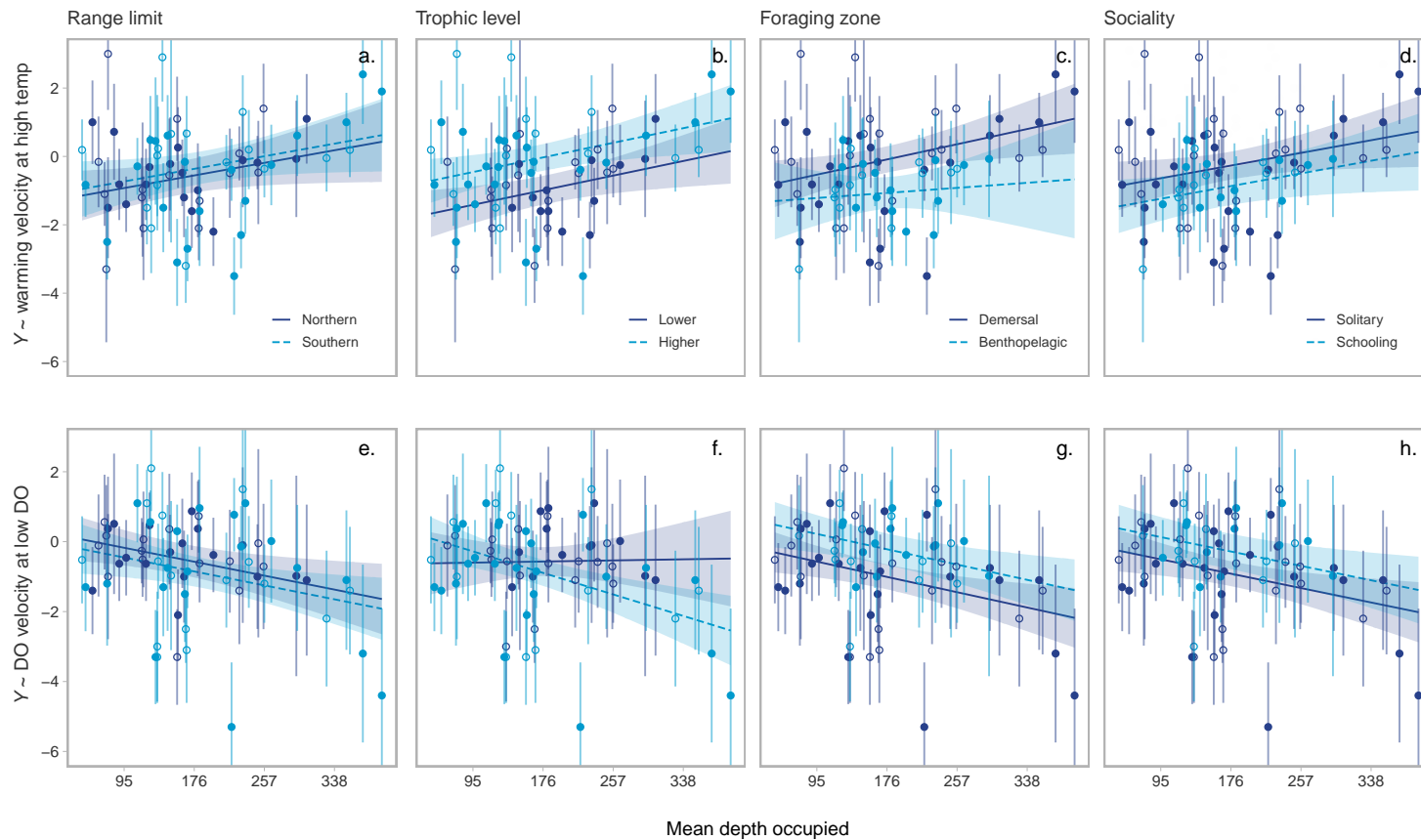


Figure S24: Ecological traits overlaid on responses to climate velocities, while controlling for the mean depth occupied by different maturity classes of each species. Points represent each species' raw slope estimates and their CI from the velocity model each coloured based on species and maturity-class 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.

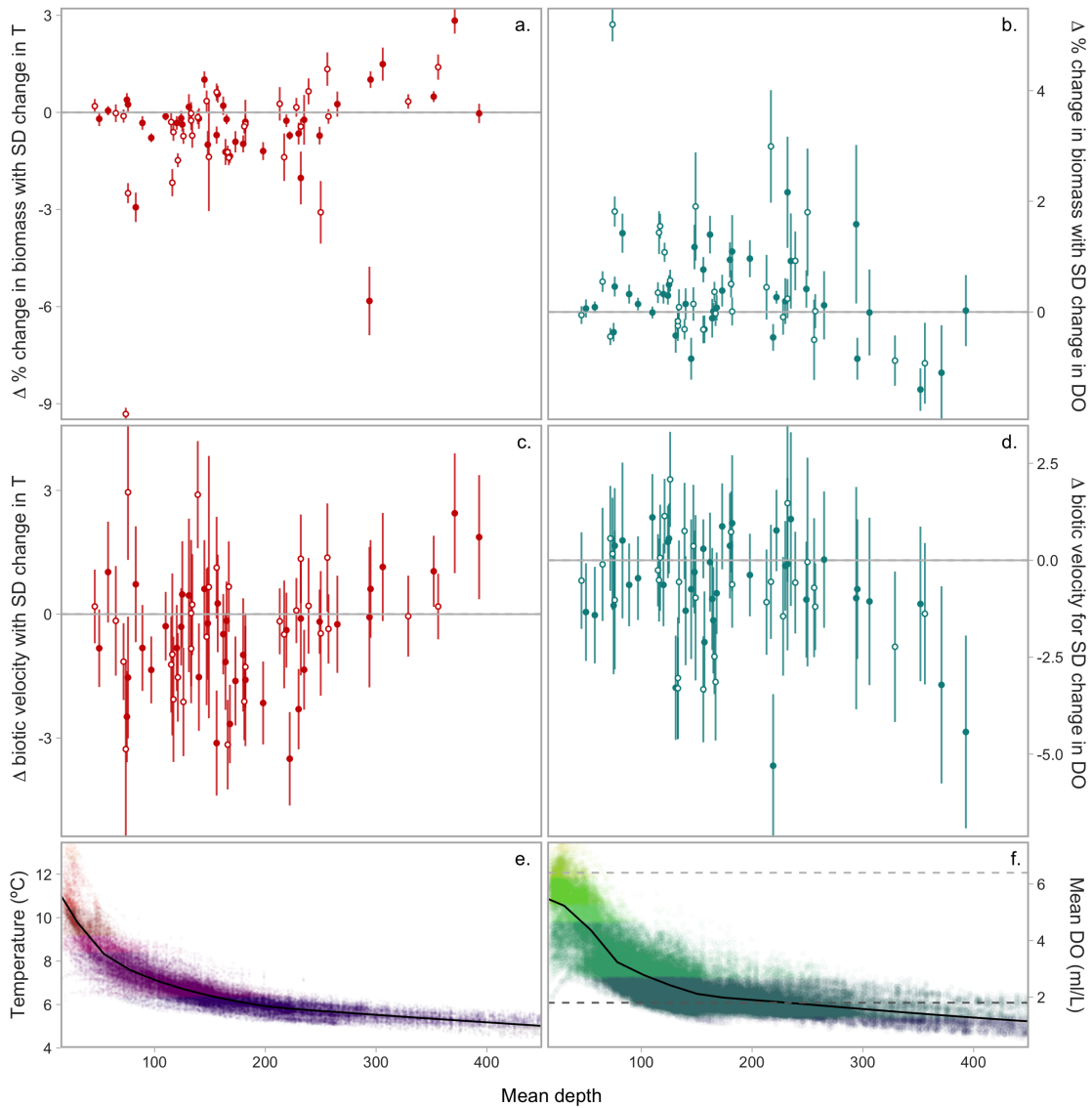


Figure S25: The slopes of the relationship between changes in biomass and climate, when calculated for the environmental extremes expected to have the greatest physiological impact—(b) highest temperature locations and (c) lowest DO locations—do not change predictably with mean occupied depth. Line segments 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).

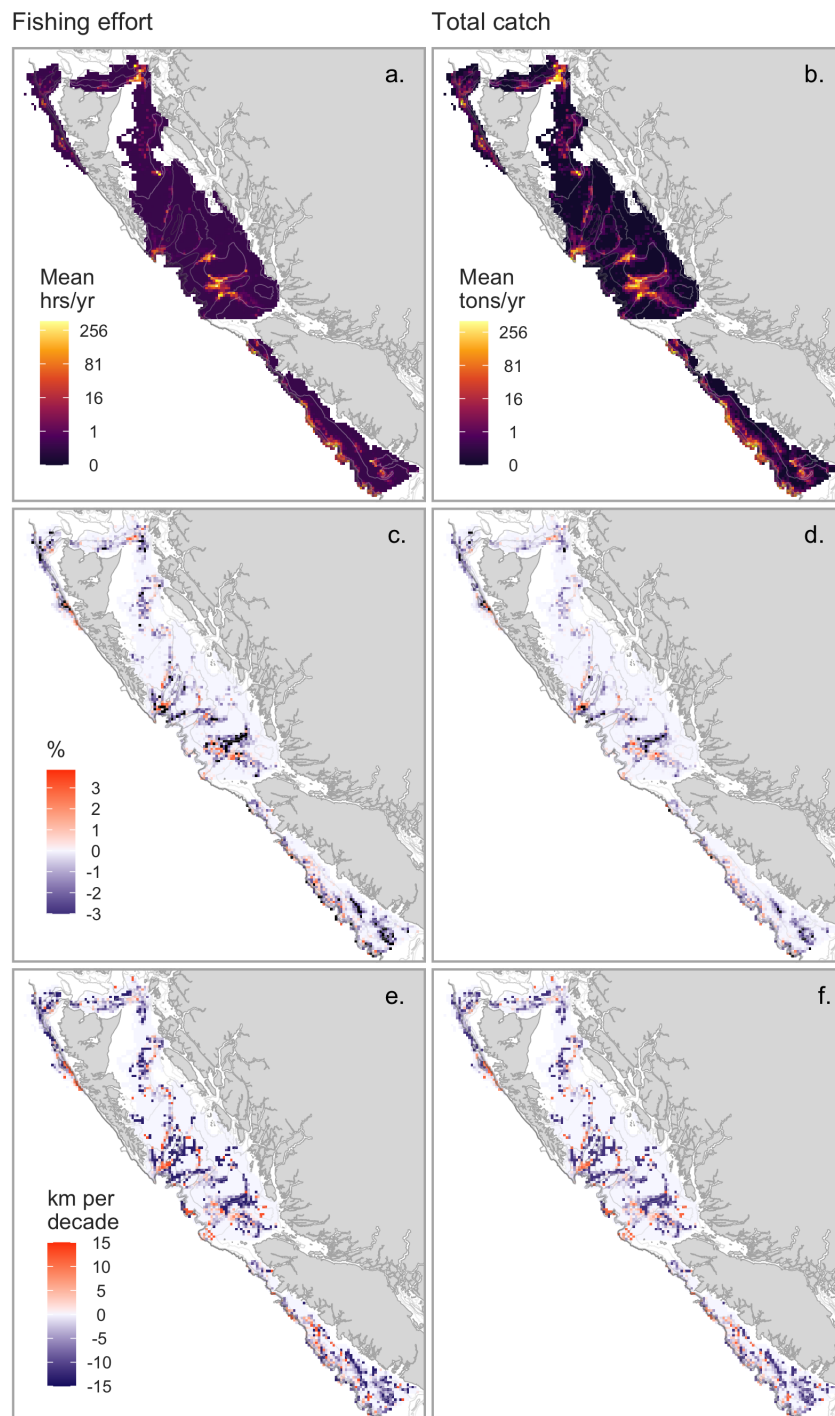


Figure S26: Variables capturing cell-specific commercial trawl fishing intensity: mean hours of commercial trawl fishing conducted (a) and mean tons of fish caught (b) per year, the % change in each estimate of fishing pressure (c, d), and the velocity of change in fishing pressure (e, f) between 2008 and 2018 for each  $4 \times 4$  km cell within the survey footprint.

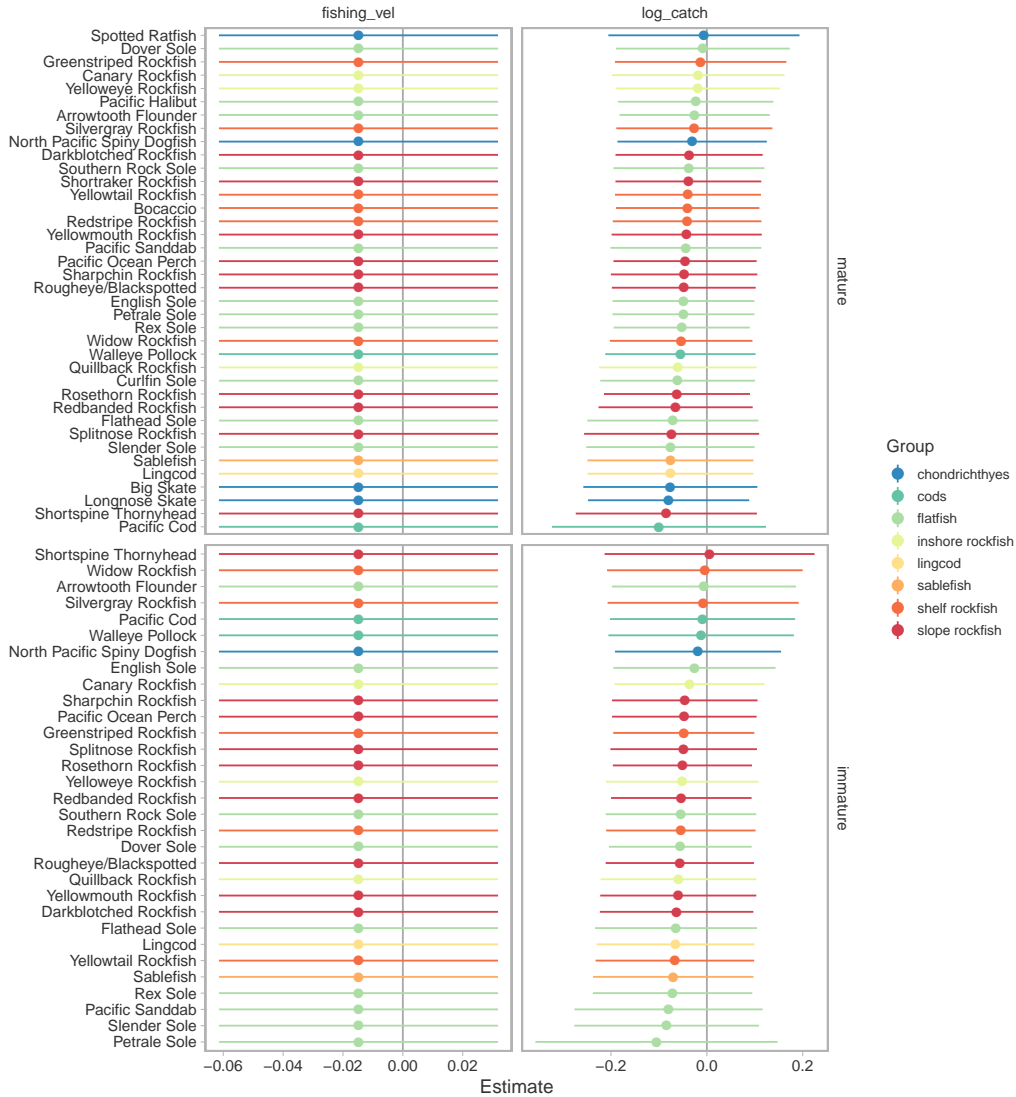


Figure S27: Species-specific coefficient estimates for variables accounting for fishing effort. This model includes the same climate variables as the “Velocity” models in Figures 2b and S23, as well as two variables capturing cell-specific commercial trawl fishing intensity: the velocity of change in 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 S26 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.

## Reviews

### Editor Comments to Author:

I have chosen to go for major revision, despite only one of the three reviewers recommending this course of action, as I think this will give you greater scope for dealing with the issues that have been raised.

As you know Fish and Fisheries asks authors to submit papers with wide geographical scope. Your study is limited to a relatively small area off the west coast of Canada. You do mention the wider context in your discussion but it would good to see this made more explicit by making comparisons with other areas of the world where your work could be relevant. The papers you mention that deal with other areas must be based on results from other areas and it would be useful if you could be more specific about these so the reader can see more clearly the wider significance of your results.

We were pleased to learn of the three helpful and positive reviews of our manuscript. We have addressed all reviewer comments in our response below.

Regarding the above comment about making more specific comparisons with other areas of the world where the work could be relevant, we have added new text from line 489 to line 501 in the discussion.

### Reviewer: 1

Comments to the Author Comments on the manuscript, “Contrasting climate velocity impacts in warm and cool locations show that effects of marine warming are worst in already warmer temperate waters” (English et al.)

General Comments A1: The authors examined biotic velocity patterns (from biomass distributions of marine species) within the Canadian basin in response to local climate trends and velocities. Overall, the paper is well-written and the results were clearly presented. It was interesting to see the differences in species-specific responses to changes in local climate, depending on whether a region experiences warming or cooling trends over time. I also liked that the authors recognized potential caveats of their study in the discussion, which partly addressed my first concern on the use of predicted species-specific biomass in linking biological changes with the local climate. I would think that using the actual biomass estimates as a response to the GLMMs would be a more straightforward way of capturing the relationship between these variables. On this note, I wonder as to how the observed and predicted species biomass (for mature and immature classes) compared overall.

We understand the concern with using predicted biomass in our second-level model, as we note in the discussion. We used modelled biomass estimates as a response because we needed a biomass

estimate in each grid cell to calculate biotic velocities for comparison to equivalent climate velocities.

Regarding observed and predicted species biomass: we have added Figs S3 and S4 of predicted vs. observed plots for each species-maturity combination. Despite model convergence, a couple immature species have a relatively poor fit to the positive biomass component due to low numbers of positive samples, which we note in the caption. We note that the immature components for these two species (Widow Rockfish and Yelloweye Rockfish) either follow the same pattern as the mature component in the biotic-climate velocity models with greater uncertainty (Widow Rockfish, Fig. 4) or had insignificant effects (Yelloweye Rockfish, Fig. 4).

A2: Also, as to the computation of biotic and climatic velocities, were model spatial predictions done annually between 2008 and 2018 (I supposed they were to allow for the calculation of pixel-wise temporal trends)? This is quite unclear and it would help to briefly mention/clarify this in the text. In the computation of the spatial gradients, the authors used the last two sample periods (2015-2018) but I am not quite clear on which temporal trends were used to calculate the velocities? I see that in particular, temporal trends were computed for biennial time-steps depending on the location of the survey LL.241-245 (now line 247). I would suspect that depending on the temporal subset, the temporal trends would be different, which would also be reflected in the subsequent computed values of velocities. How were these differences in the temporal trend between time slices (and/or portions of the surveyed region) handled in the analyses?

Model spatial predictions were made biennially between 2008–2018 or 2007–2017, depending on the surveyed area. The temporal trends were for these same timesteps (stated on line 247), but how differences between survey area are addressed is now explained more clearly with sentences on line 249: “In order to compare between survey areas with different sampling years, we converted values for all cells to a rate of change, or trend, per decade” and line 254 “input information related to a cell and any cell near enough to share spatial information in a gradient or in the overall spatial models (this includes all response and predictor variables) all share the same sample years.” We have not attempted to interpolate for missing year-locations and instead to focus on the patterns detected in those that were sampled.

Specific comments

A3: L.97: Similarly should read Similar

Change made. See line 99.

A4: L.113: in should read from

Change made. See line 113.

A5: L.134: In this subsection, it is good to have the information on survey sites (number of sites sampled) and a map that will show the sampling stations, perhaps in the supplementary materials.

We have added Fig. S1, which shows the distribution of survey samples in both time and space, and the mean and range of sample numbers per year are now given on line ??.

A6: L.243: should it be 11 years between 2008 and 2018? And 9 years between 2009 and 2017?

The reviewer is correct, thanks. Change made. See line 247.

Figure 1a, please include the geographical coordinates on the map for reference.

Change made.

## **Reviewer: 2**

### Comments to the Author

B1: Thanks for the opportunity to review this work from English et al. This work presents an interesting evaluation and application of temporal trends of temperature and oxygen across several demersal marine fishes, using in some cases, climate velocity. My main concern within this this work is that the gap that this manuscript is trying to fill is a little bit unclear. For example, lines 79-92 is just justification/explanation of the different climate velocity metrics. The conclusion is that local velocity is better because analog velocity has a problem with the threshold (this is a problem of definition not the metric itself). Another is in lines 93-103, which introduces the concept of biotic velocity but unclear to me why should be included here. Same with lines 104-116. Totally disconnected from the previous paragraphs. I would have expected that you take the concepts mentioned before and bring the gap together of why groundfish...etc. Lines 111-116 IS the gap of this paper in my opinion and has been expressed in only 5 lines.

We describe the broad gap we are trying to fill from line 66 to line 80, preceding the explanations on line 81 through line 105 that introduce the concepts underpinning our approach to filling this gap. The gap identified by the reviewer (on line 113 to line 118) is more of a description of the case study on which we test our approach.

B2: Another major issue with this manuscript is related to climate velocity and Oxygen. Brito-Morales et al. 2018 provide a good example of why this could be not appropriate from an ecological point of view (at least in marine systems). Climate velocity, in ecological terms, indicates how much and in which direction a species distribution would need to move to remain in the same climatic environment. So, are species' distribution really "following" oxygen levels? What is the performance curve of preference for oxygen for species in general? (For example, Figure II in Brito-Morales et al. 2018) If oxygen declines, species' distributions will tend to shift to their "preference level" and, more importantly, if the conditions are restored species would tend to shift back to their original condition? There is a reason why climate velocity in marine systems has been used mainly with temperature and in terrestrial systems with temperature and rainfall. The answer is in Box 3 (Methodological Considerations When Applying Climate Velocity, Which Environmental Variables?) in Brito-Morales et al. 2018. I'm not saying that the authors' approach is wrong, it is just that I do not understand the ecological reason why oxygen is a good predictor of species range shifts. The authors have not provided any fundamental analyses to justify this inclusion in the paper.



We agree that our justification for considering an effect of DO on fish distributions was omitted from the this manuscript and thank the reviewer for pointing this out. We have add this to line 118 where we now note that “a warmer ocean is expected to hold less oxygen, while becoming more stratified (Levin and Le Bris 2015), and some groundfish species in the Eastern Pacific have been shown to respond to these changes (Keller *et al.* 2017)”. While a climate-analog approach using a hypoxia threshold would be interesting to explore, we think it is beyond the scope of this paper. Instead, we use this analysis to test whether including evidence of any local changes (trends or velocity) in DO are correlated with the change in species biomass, after accounting for changes in temperature. Further analyses that explore potential thresholds of response are planned; however, relatively few locations in this analysis actually drop below expected hypoxia thresholds. What we are testing for here is actually whether a reduction in DO might also be correlated with habitat selection or population growth rates through non-lethal or indirect mechanisms (e.g., slower metabolic rates, predator avoidance, changes in decomposition rates). We note aspects of this in the discussion on line 483, line 563, and line 566.

We have added a supplemental figure depicting the species-level predictions in response to temperature from a model with just temperature and from one with both variables Figure S16 and refer to it on line 427 where we now say “Including DO in the model along with temperature did not substantially alter the effects of temperature for any species”.

More details comments:

B3: 79-81. That’s not totally true. Local climate velocity has been more used in medium-coarse resolution because its tends to be much variable at finer scales due to the temporal component (denominator).

We have clarified on line 81 that population-wide indices refers to single value for a whole population, such as centre of gravity, which is a much coarser scale than a “medium-coarse resolution”. We address issues with variability in the denominator (the spatial component) in the paragraph starting on line 257.

B4: 118. (now line 122) It says “velocity” but should be “climate velocity”?

We think the current phrasing “shaped by local temperature and DO trends and velocities” is clearest because it refers specifically to temperature and DO and couldn’t be understood as meaning other climate variables not listed.

B5-6: 125, 130, n... Be consistent with terminology. Should be “climate velocity” instead of “velocity”

We think that because we are looking at both biotic and climatic velocities, “gradient-based velocities” is appropriate on line 129 and “velocities of biotic and climatic change” on line 133 is also most accurate.

B7: 217 (now line 221) “We predicted” but is it possible to use survey data to compare how well the predictions are with “real” information? I think this is an important step in using prediction. There

is a good free available dataset at finer resolution that could be used to compare the predictions and has been omitted by authors.

Agreed. We have added supplemental Figure S2 of predictions vs. observed data for climate variables. However, we are not sure what finer resolution free data is being referred to. Sea surface temperature data exists, but so far as we know, similar spatial and temporal resolution bottom temperature and DO layers are not freely available. In the discussion starting on line 587, we also acknowledge that “An alternative would be a ROMS (Regional Ocean Modeling System) model (Peña *et al.* 2019), which could extend 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 with survey data (e.g., primary production), and allow for forward projections. Preliminary investigations indicated a strong correlation between our CTD projections and recently updated ROMS bottom temperatures. With the greater spatial and temporal extent that ROMS data will provide, calculation of more geographically precise analog-based climate velocities could be used to further refine the identification of areas important for conservation (Brito-Morales *et al.* 2018).” The ROMS model output, however, was not yet available when this analysis was conducted.

B8: 237 (now line 242) gradient-based velocity or more commonly “Local climate velocity” in my opinion does not fit well at finer resolution. It is more for medium-coarse resolution (see Brito-Morales *et al.* 2018 SOM). Also, in terms of climatic variables local climate velocity “has been favoured by ecologists when gradients are smooth and where there is one main variable driving change” (Brito-Morales *et al.* 2018). This study is not that case. Another “climate-analog velocity has usually been used with multiple variables” (Brito-Morales *et al.* 2018). To me, this would be an adequate metric to applied in this paper. Also, check Garcia Molinos *et al.* 2017 GCB paper in Japan MPAs using climate-analog velocity.

We discuss climate-analog velocity and explain why we do not use it on line 92 “the choice of thresholds and other statistical properties (e.g., clumpiness) make them less useful than gradient-based local velocities for meta-analysis (Ordonez and Williams 2013)”. Indeed we did explore their application in this context and identified these two primary obstacles: 1. without a much longer time series of environmental variables from which to identify relevant thresholds of environmental change, any threshold choice becomes quite arbitrary, and 2. statistical meta analyses that control for spatial autocorrelation worked well on the gradient-based velocities by employing a Student-t observation distribution, but the analog climate velocities produced bizarre statistical distributions (“clumpy” and extremely heavy tailed) that we couldn’t adequately fit models to.

B10: 260 (now line 269) “We calculated spatial gradients using the vocc R package (Brown and Shoeman)”. The authors should not be using this package as it has been replaced by “García Molinos, J., Schoeman, D. S., Brown, C. J. and Burrows, M. T. (2019). VoCC: The Velocity of Climate Change and related climatic metrics. R package version 1.0.0. ”. I strongly recommend performing new update calculations based on the previous paper/Github repository.

This update came out after we had invested effort writing custom functions that were tightly integrated with the data formats accepted and produced by the older version. Therefore, we opted to use a subset of the data used in the VoCC vignette to test that both sets of functions produce

identical results; fortunately, they do. We have added text to line 269 also directing the reader to the newer package version and now state that we tested to ensure they produced the same results.

B11: 294 (now line 305) Simulation study section. I would move this section to Supplemental as it is disconnected from the others and was difficult to follow up.

We feel that the simulation study is critical to justifying the validity of our analysis, only takes two paragraphs to explain the method and results, and is illustrated in a key figure ( 2). Therefore, we would prefer to leave it in the main text. However, if the editor feels differently, we would be happy to move this section to the supplement.

B12: 356-359 (now line 427) Local climate velocity is a vector so it is important to know also the direction (not just how much but also where!). This is why using O<sub>2</sub> is not so good idea in terms of having 2 different local climatic variables in climate velocity estimates (see main comment). For instance, are vectors from both variables in opposite directions? how do they cancel each other if that it's true? Does the same direction mean you added those vectors (and magnitudes) together? What would that mean for species/fish context? (which is the more relevant aspect for the paper) Perhaps using analog climate velocity for multivariate purposes (Garcia Molinos et al. 2017 GCB is a good place to start). To me, these results do not mean too much if the context is just to describe climate velocity estimates. Please check also Hamann et al. 2015 for more context and Brito-Morales et al. 2018 Box 3 Combining Environmental Variables section.

We considered this, but if temperature and DO levels both go into the same velocity calculation, it won't help us understand which factor is more likely to be driving the observed patterns. We think a combined analogue velocity would be interesting, but outside the scope of this paper. We did, however, test to see if including DO was impacting our conclusions regarding the effects of temperature, and it does not. We have added a supplemental figure depicting the species-level predictions in a model with just temperature and one with both variables Figure S16 and refer to it on line 427.

B14: 493-498 (now line 514) This just confirm what I've been suggesting in previous comments: I do not think that local climate velocity is a good estimate metric at finer resolutions or even with multiple environmental variables. I strongly recommend authors to climate-analog velocity and a proper, perhaps structured and well cited, framework about why Oxygen is a variable than can be used with climate velocity to predict species' range shifts.

Please see our responses to B2, B3 and B12 above.

B15: 538 The authors constantly through the ms refers to "individual movement", which is not appropriate for climate velocity in my opinion. Climate velocity is a metric that is related with population movement and NOT individual movement. Seems to me that authors have not realised that this is a major ecological point of view and should be noted and corrected in the actual version of the ms.

We have modified all references to "individual", "organism", and "fish" movement to refer to population or fish-population movement.

## Reviewer: 3

### Comments to the Author

C1: This is a complicated paper. It presents some important results that will help to refine current ideas about the spatial adjustments of fish communities in response to climate shifts. The manuscript is a little hard to read in places where the authors use jargon. An example is l.52 where they refer to “climate-induced hyperstability-catch rates”. I suspect that many readers will have no idea what this is. Line 73 uses the term “depredation”, which is correct, but I had to look it up: [URL](#).

“Climate-induced hyperstability-catch rates” has been replaced by “such changes can cause the efficiency of fishing to increase if population density increases faster than range expansion during population growth, or temporarily maintain catch rates despite population decline if organisms move towards preferred habitat as it becomes available” on line 53. We replaced “depredation” by “predator-prey interactions” on line 71. We have tried to reduce jargon wherever possible throughout the manuscript.

C2: In an effort to be specific, yet brief, about their results, the authors resort to complex sentences. One example is the repeated use of this phrasing: “result in smaller negative or larger positive biotic velocities.” Another example is on l.399 (now line 411): “the expected biotic velocity was strongly negative for 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 high climate velocity”. These sentence constructions are hard to digest because the point is lost in their complex structure.

In the results line 387 now reads “local biomass was more likely to increase and to result in larger positive biotic velocities (or to decrease less and result in less negative biotic velocities)” The sentence on line 411 now reads “in the warmest locations experiencing maximum climate velocity the expected biotic velocity was strongly negative for 19 of 69 species-maturity combinations (Figure 5b). Meanwhile, in cooler locations experiencing the same high climate velocity, biotic velocities were often positive”

We acknowledge that these are still somewhat complex statements (although hopefully in easier to digest now), but we are trying to balance simplicity with specificity and accuracy in the results section. We do interpret these results using more general language in the abstract and in the discussion (e.g., line 474).

C3: A surprising result is the very small distances that fish would need to move to maintain their starting thermal or oxygen conditions. l.356-359 (now line 366). “...an organism would have to move an 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.” I’m surprised that such small shifts are measurable given the imprecision of trawl surveys. The reported shifts are about 1km per year ... I can’t help wondering whether simply repeating a trawl survey might yield movements of this magnitude, without needing to invoke community adjustment to environmental shifts. The authors are detecting a very small effect using sophisticated statistics operating on

imprecise data. The analyses are impressive, but are these very small spatial shifts a real effect of climate? And what are the implications of such small shifts. The authors miss the opportunity to point this out in the Discussion (see below).

It's important to note that the 10.5 km/decade value is an *average* amount of climate velocity across the whole coast. Some locations experience much more extreme temperature climate velocities (up to ~ 80 km per decade; Figure 1f). When it comes to animal abundances (as opposed to the temperature measurements underlying the above), we agree that there is a large amount of observation error in this or any trawl survey and this error is a very valid concern. The fact that "simply repeating a trawl survey might yield movements of this magnitude" is partly the reason for (1) the hierarchical approach across many species and (2) the simulation study. By simulating similar magnitudes of biotic change (with similar spatial correlations), we showed on line 322 that "Null models based on simulated biotic trends and observed climate trends showed fewer significant relationships at the species level than would be expected by chance (Figures S5, S6, and S7)."

C4: In the Discussion, l.575 (now line 606) states: "Climate change is expected to have large impacts on fish stocks and their management, particularly with respect to changes in species distribution (e.g., Tommasi et al. 2017, Karp et al. 2019, Free et al. 2019)". l.588 (states that "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)." I think given the very small spatial shifts that this study demonstrates, the authors should really turn this discussion focus around. Specifically, while large spatial shifts are expected, what this fine scale study demonstrates is that small, spatial shifts may occur due to complex interactions between species-specific fish distributions and both climate trends and climate velocities. Whereas large shifts in distributions would demand adjustment of management strategies, the small shifts detected in this study indicate no such adjustment is needed in the near-term, while providing a sophisticated set of analytical tools for sensitive detection of larger shifts if and when they occur.

We agree with the statement that "small, spatial shifts may occur due to complex interactions between species-specific fish distributions and both climate trends and climate velocities" and think that our discussion gets at this point. We do not necessarily agree that "the small shifts detected in this study indicate no such adjustment [of management strategies] is needed." We note that:

- We are only examining a single decade and such changes will compound over time.
- A redistribution of species can have major consequences for fishing opportunities and conservation of rarer species when "choke" species (species with limited quota that co-occur with species of fishing interest) limit fishing opportunities. For example, on the British Columbia coast, Bocaccio and Yelloweye Rockfish have limited fishing opportunities for more desired species with higher quotas (e.g., Halibut).
- A redistribution of species can have major consequences when fishing is geographically fixed, such as for small nations or Indigenous peoples with defined spatial fishing regions.

- A redistribution of species can have major consequences for marine spatial planning. For example, a marine reserve designed to protect a particular at-risk population may no longer be as effective after a local redistribution of abundance.

We now include these points in a new paragraph starting on line 596 in the discussion.

I think the paper should be published. Papers that are true to the data, even in the face of dominant paradigms, are good for science. But the authors should not shy away from conclusions supported by their data, in preference to what might have been expected prior to analysis.

Thank you, we agree.