Spatio-temporal modeling of oxygen on fish distributions: Results from trawl-based measurements

Contents

1 Introduction blah blah

Species distribution modeling attempts to predict local abundance from environmental attributes. One key challenge is that a number of these environmental variables co-vary, and have strong spatial structure. Contemporary spatial models allow us to ask whether the addition of an environmental covariate leads to better predictions than modeling spatial structure alone. However, the choice of environmental variables, and the functional form linking environment to species local density needs to be informed by physiological and ecological mechanisms.

The effect of oxygen on species distributions is a prime example. Basic organismal biology tells us that oxygen acts as a limiting factor on organisms, meaning that we expect to see effects when ability to acquire oxygen exceeds the demand for oxygen. Recently, the development of the "metabolic index" explicitly measures the ratio of oxygen supply and demand. The metabolic index is parameterized from species - specific laboratory studies that identify when the supply is less than demand, and how that depends on ambient temperature. Thus, metabolic index is rooted in specific mechanism of how oxygen affects organisms, and accounts for the effect of temperature on oxygen needs. Consequently, the metabolic index is now commonly used to evaluate changes in habitat volume under projections of future environmtnal conditions.

One challenge in using the metabolic index is that the data needed to parameterize the index is often lacking. At present, there is a paucity of studies that have conducted the laboratory experiments that allow for precise measurement of the allometry of the metabolic index, and the effect of temperature.

One alternative to the specific parametric model derivation of the metabolic index is to use statistical models to survey data, and ask whether the models can reveal species sensitivites to oxygen conditions *in situ*. Yet, doing so requires careful thought as to how oxygen can be expressed in a statistical model to preserve the underlying mechanism. For instance, a simple approach of including dissolved oxygen of partial pressure of oxygen as a linear predictor is not consistent with physiological theory or experience. An alternative approach is statistical breakpoint models, whereby models assume that there is no effect of oxygen above some estimated concentration or pressure, but depends in a linear or log-linear manner below that level. Further, the dependence of oxygen sensitivity on temperature might be incorporated as a standard interactive effect.

Here we fit distribution models to bottom trawl survey of Sablefish, to ask: 1. Is it possible to distinguish among effects of depth, space, and environmental conditions such as temperature and oxygen, given the strong covariance among these 2. Do models with breakpoint models perform better than those the model oxygen in linear fashion 3. Do statistical models fit to estimated metabolic index perform better than those fit to just dissolved oxygen or partial pressure (i.e. does the dependence of temperature on oxygen needs matter when predicting species distributions, especially given the covariance in temperature, oxygen)

2 Methods

2.1 estimating metabolic index parameters for sablefish

2.2 trawl survey data

2.3 spatio-temporal modeling

2.4 Alternative Models

All models include space, year effects, and depth (modeled as a quadratic function), and that the spatial effects were constant across years. This was necessary so that we could then ask whether inter-annual changes in temperature and dissolved oxygen led to differences in local density. We then added addional fixed effects predictors in various combinations to consider effects of temperature, pO_2 with and without a breakpoint function, and the metabolic index. A total of 9 different models were compared (Table 1). We used AIC to judge the degree of support for each model.

3 Results

3.1 Estimating metabolic index parameters

Sablefish exhibit exceptionally high tolerance for low dissolved oxygen compared to the other marine fish species included in the analysis (Figure 1). Moreover, the relationship between body-mass adjusted critical pO_2 and temperature (expressed as the inverse of k_bT appeared to be similar among those species for which data were available at multiple temperatures, once data were corrected for body size. Thus, the estimated value for $E_o = 0.4525$ was deemed suitable to use for sablefish. The body size scaling of the metabolic index, n was estimated to be -0.30 i.e., metabolic demands scales more strongly with body size than does metabolic supply.

3.2 Summary of Environmental Conditions

Unexpectedly, oxygen levels were greatest in shallow (< 150 m) and nearshore areas compared to deeper areas (Figure 2). This offshore gradients was strongest in southern California, south of San Francisco Bay. This spatial pattern of bottom oxygen was relatively similar across years, with some annual events. Most notably, oxygen levels, particularly in shallow nearshore areas, were highest in 2015 compared to other years.

Bottom temperatures were greatest in the middle of the spatial domain (Figure 3). North of this region, upwelling likely contributed to cooler bottom temperatures, even in shallower (<200 m) habitats). The 2014 - 2015 anomalous temperature event was evident throughout the coast in shallower habitats.

The metabolic index was generally higher in the northern extent of the survey range, lowest in the deeper and southernmost regions, and exhibited moderate inter-annual variability (Figure 4). Despite the warm temperatures in 2015, the metabolic index was generally high in this year, particularly in the northern half of the survey domain. Overall, the metabolic index was, on average, lowest in 2011 and 2013, but the effect size

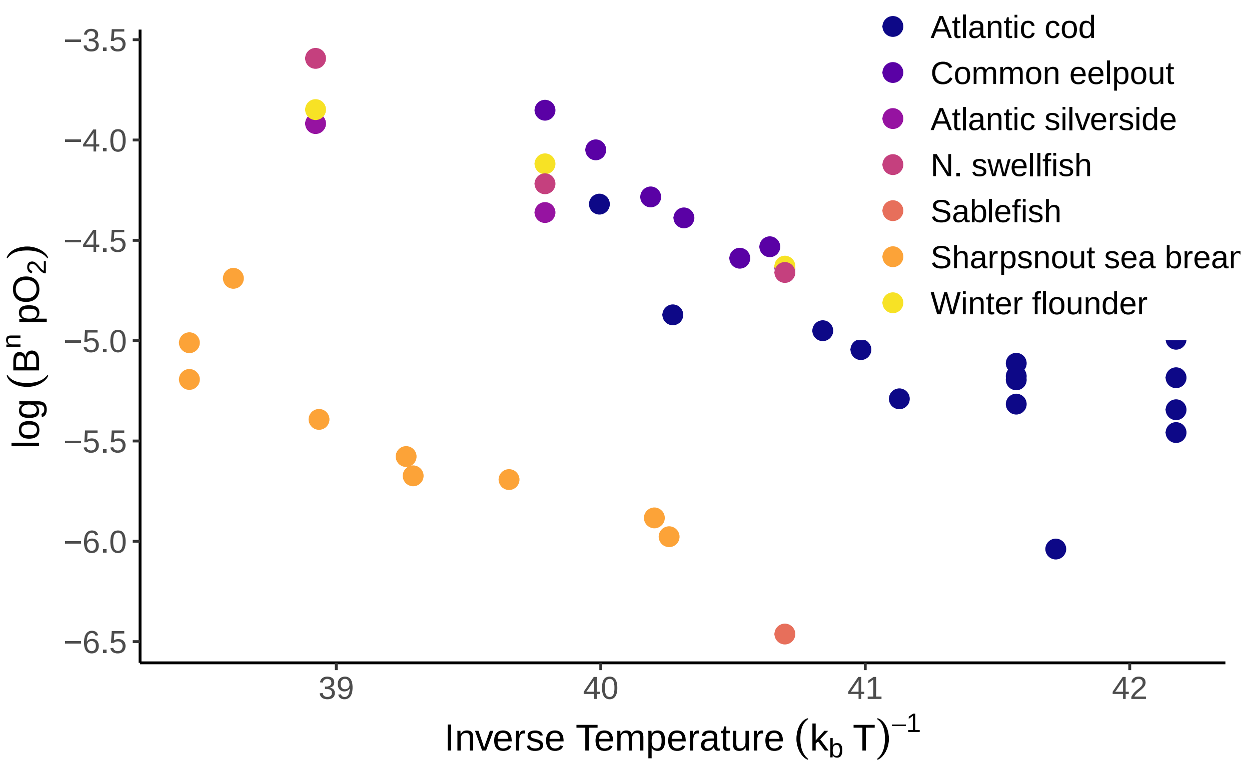

Figure 1: Fitted relationship between body-size adjusted critical pO_2 and temperature

was not particularly large. The spatial patterning of metabolic index was relatively similar across years, and most areas exceeded the estimated physiological limit of 1, although avoidance is expected at values of the index that exceed 1.

3.3 Summary of Sablefish Distributions

Sablefish were captured throughout the survey domain 5), Graphical representation of the trawl survey catch data did not reveal profound shifts in sablefish catch rates across the years (Figure 5).

3.4 Model Comparison, using full survey geographic range and trawl-based oxygen measurements

The best fitting models all contained oxygen-related predictor and a breakpoint model.The best fitting model used pO_2, combined with a linear temperature effect (Table 1). The metabolic index model, however, had much less support than the pO_2 models (with or without temperature as an additional predictor). Note that the metabolic index becomes a linear function of pO_2 when E_O approaches zero, so weakening the temperature dependence of the metabolic index would improve the fit of the metabolic index model, but not lead it to fit better than the breakpoint pO_2 model.

Model diagnostics indicated no spatial pattern in residuals (Figure 6). To simply representation, we calculated the vector $\mathbf{R}$ of residuals, and standardized by the standard deviation of the residuals. Extreme catch events (exceptionally high catches) were observed throughout the survey area, though were notable less rare in the southern-most portion of the survey domain.

3.5 Effect Sizes

The best fitting model indicated strong effects of pO_2, temperature, and depth, even when accounting for latent spatial effects (Figure 7). Generally, predicted mean sablefish catch rates declined by over one half at

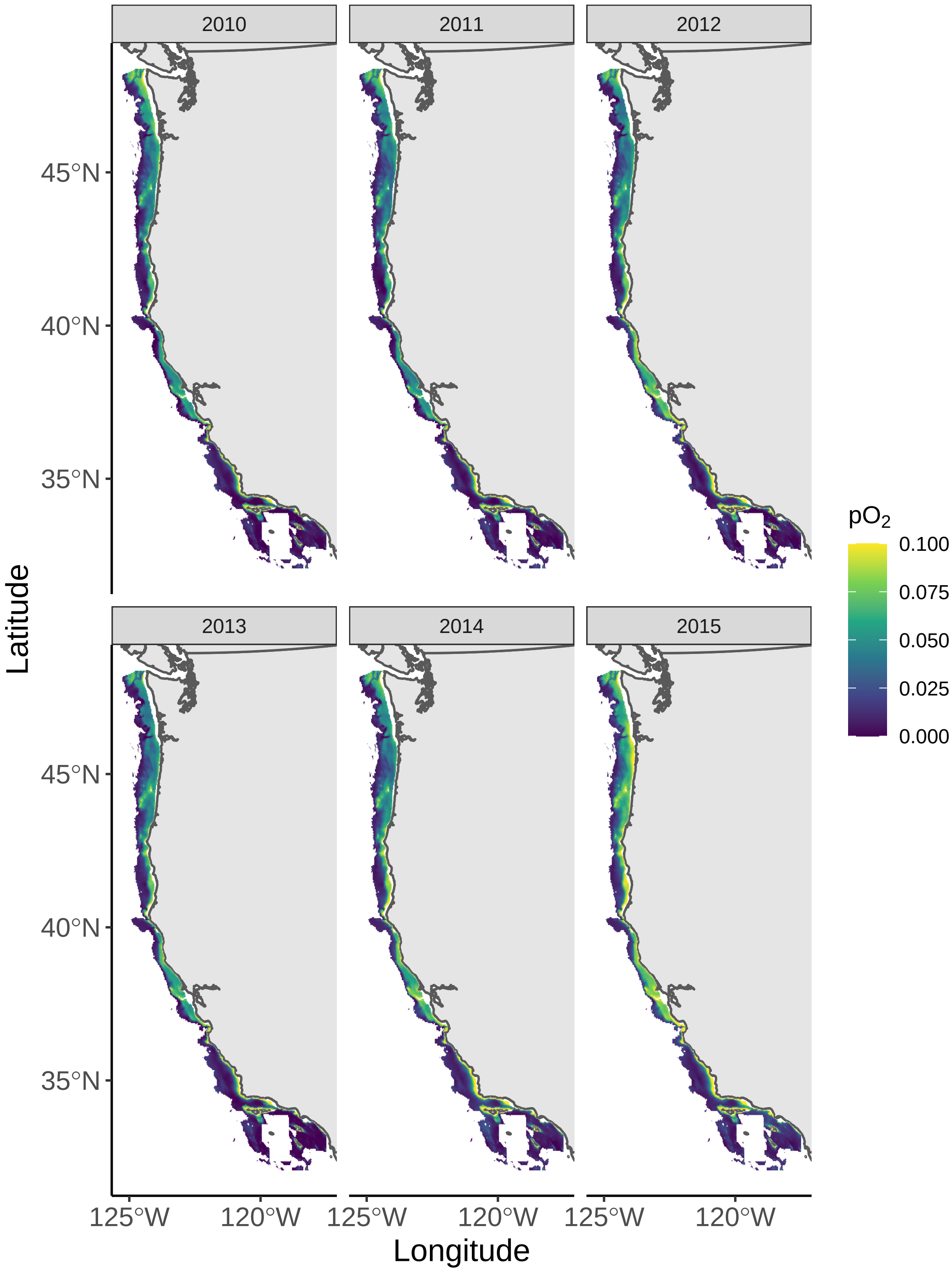

Figure 2: Spatio-temporal variation in bottom oxygen levels (atm)

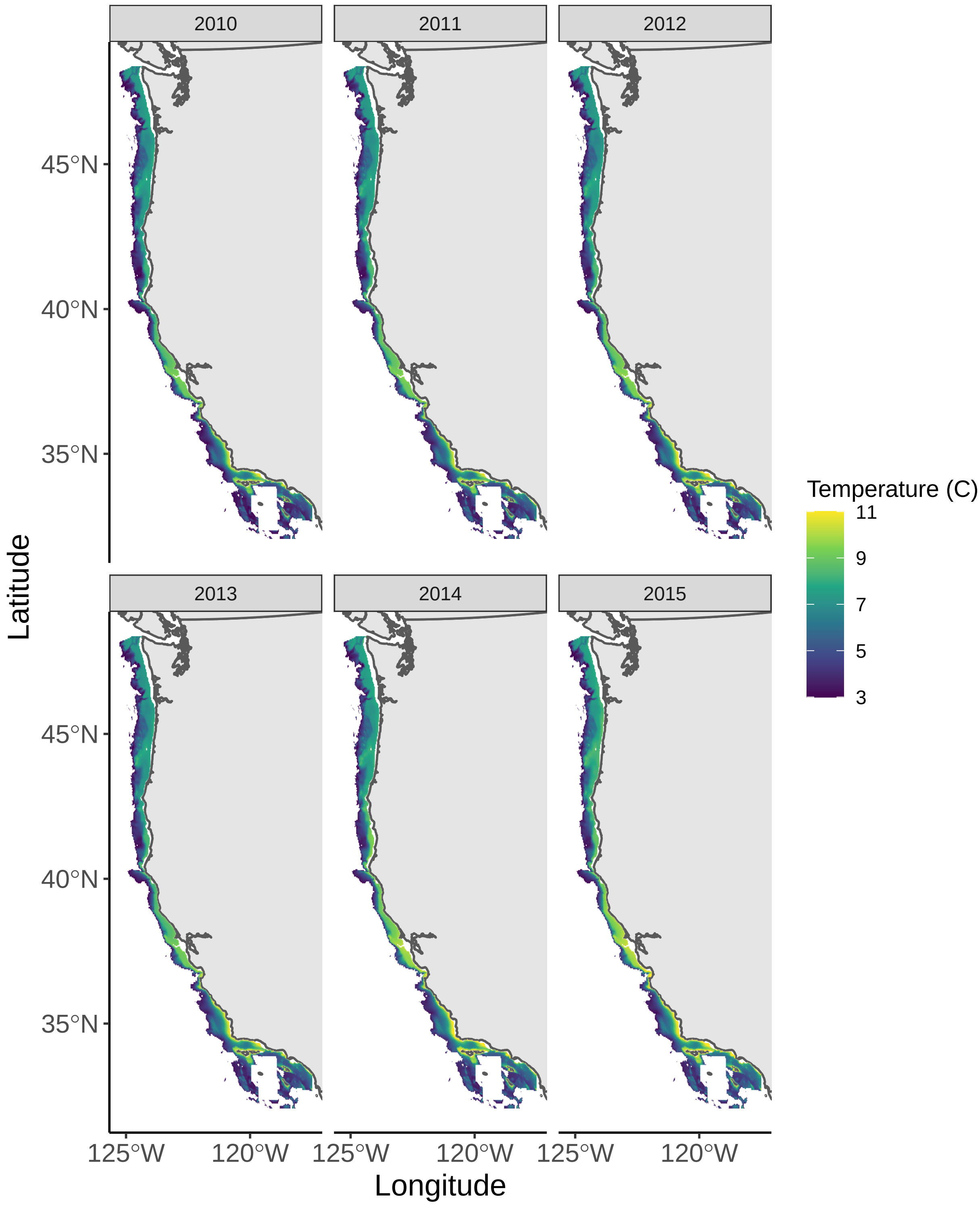

Figure 3: Spatio-temporal variation in bottom temperature

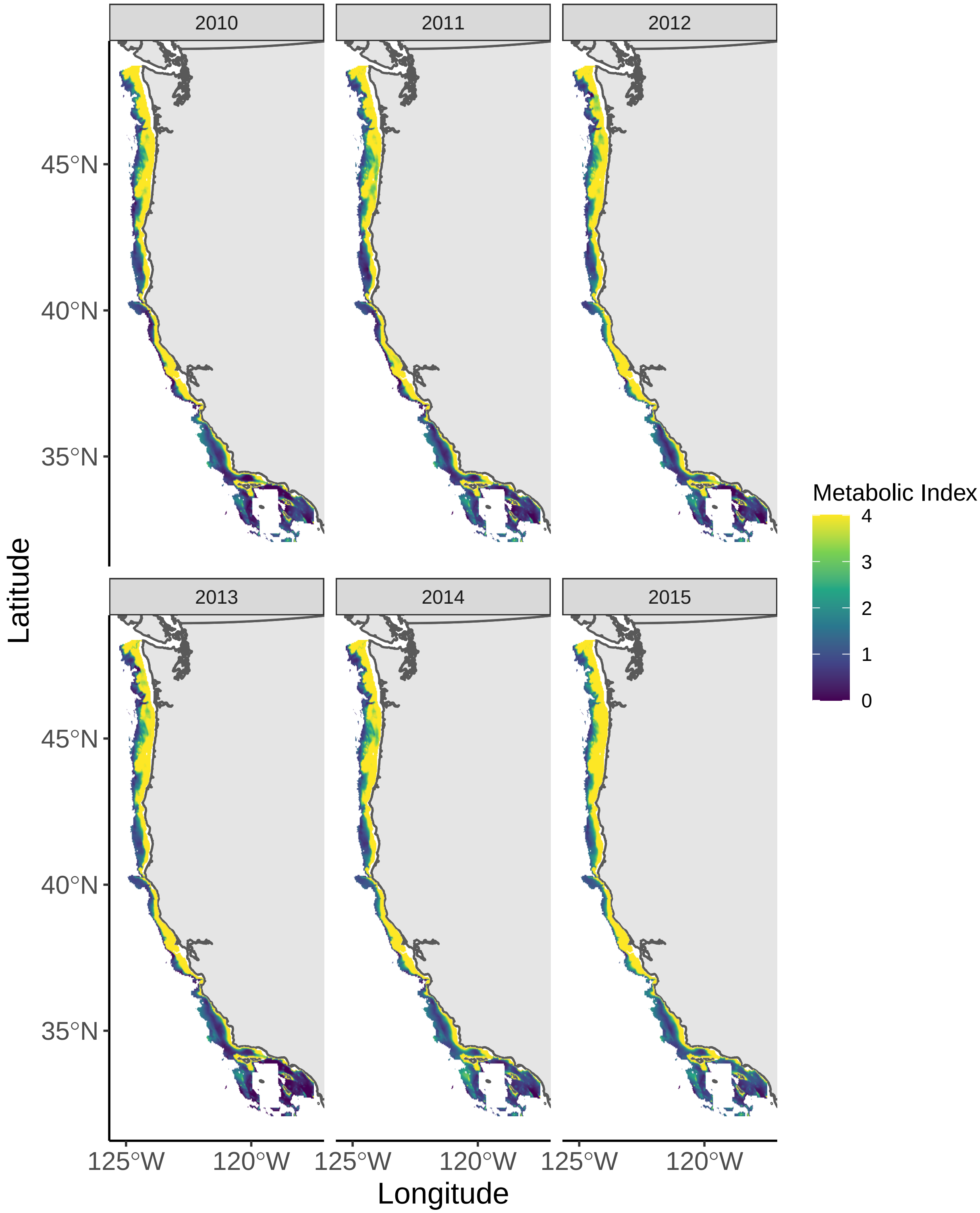

Figure 4: Spatio-temporal variation in the metabolic index

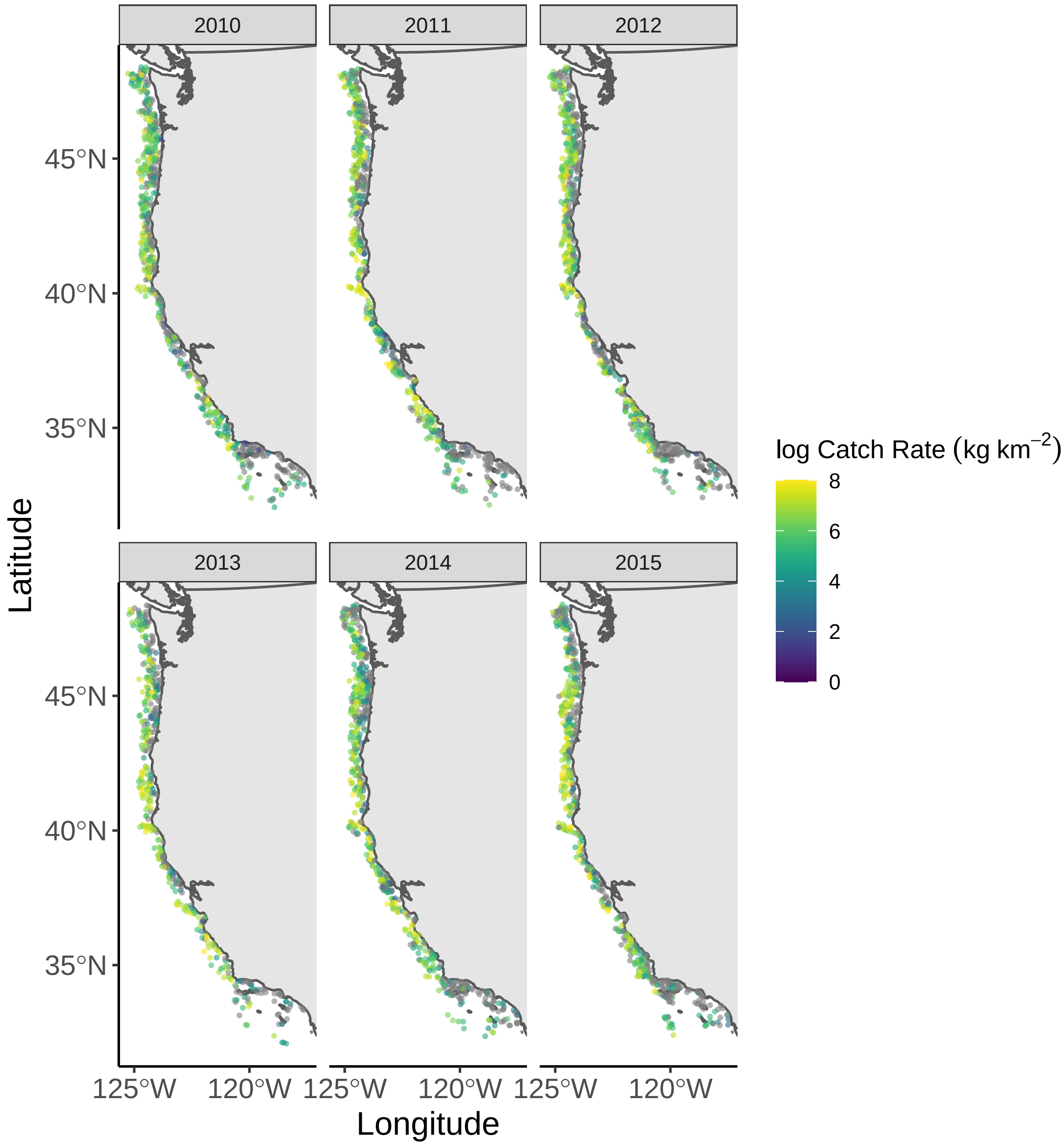

Figure 5: Spatial distribution of Sablefish. Each point is a trawl survey location, the color indicates catch rate. Gray circles indicate absence of sablefish in the sample

Table 1: Model selection using AIC

Additional Predictors	Delta AIC
none	41.440102
temp	42.857483
po2	44.829627
mi	42.008361
temp + po2	45.366746
temp + po2 + temp * po2	27.059544
breakpt(po2)	3.575794
breakpt(po2) + temp	0.000000
breakpt(mi)	8.054504

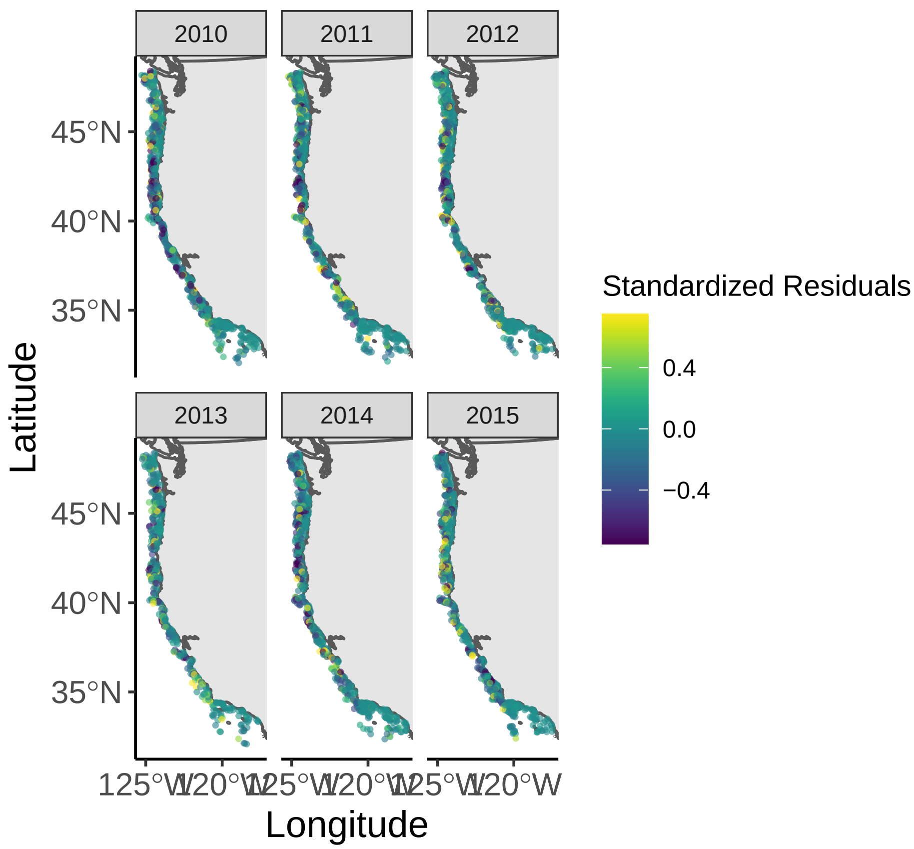

Figure 6: Standardized residuals of best fitting model

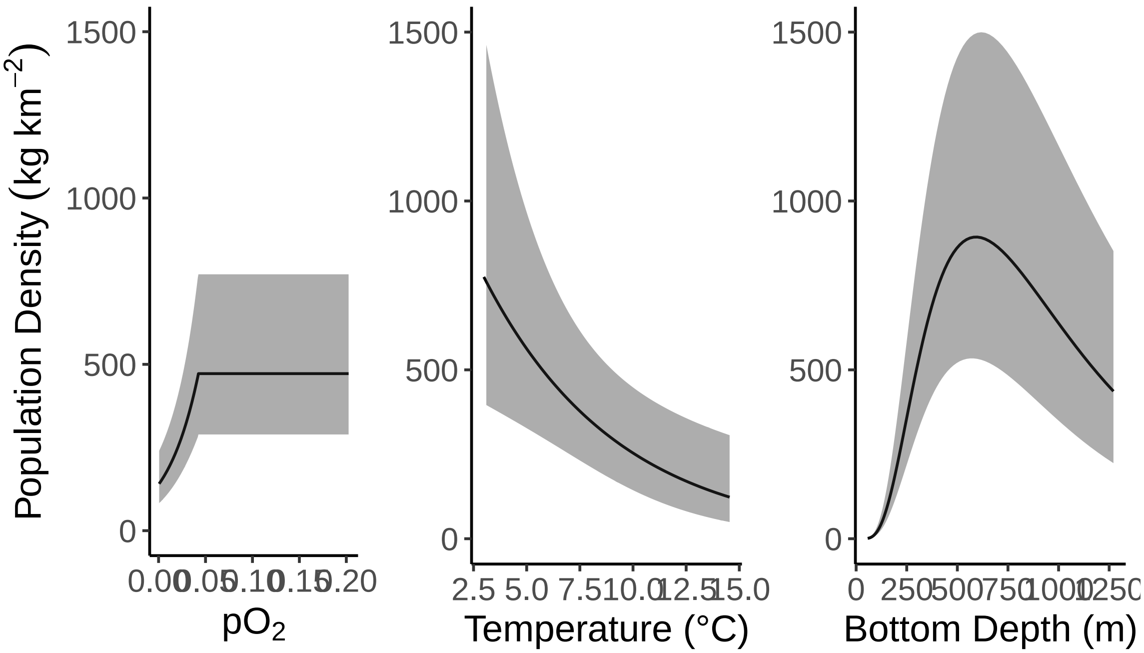

Figure 7: Marginal effects of oxygen, temperature and bottom depth

the lowest observed pO_2 compared to values above the estimated threshold of ca. 0.05 atm. Temperature was strongly and negatively related to temperature as well. Sablefish densities peaked at relatively deep (500 - 700 m) depths, and were predicted to be near 0 at depths shallower than 100m.

Finally, we mapped the effect of oxygen on sablefish by comparing predicted catches from the best-fitting model applied to fitted grid of pO_2, to predicted catches when all pO_2 were set above the estimated threshold (Figure 8). By far, the largest effects of oxygen were reflected in southern California, where catch rates were predicted have been reduced by. Moreover, the model predicts that at least some of the decline in catch rate at deep (>750 m) is attributable to the reduced pO_2 that is common in these areas.

Finally, we examined the relationship between survey catch rate and components of the metabolic index. For each survey sample taken at depths greater than 200 m, we calculated the temperature term in the Arrrhenius equation, and the remaining terms in the metabolic index. The critical oxygen threshold in eq X is defined by a line whose intercept and slope are set by the terms E_0 and A_0. Notably, there were many catch events at oxygen and temperature levels below the critical threshold line, indicating that the experimental work may now accurately predict species sensitivity to oxygen *in situ*. This does not necessarily affect the predictive ability of the fitted statistical model, which is simply relating variation in the catch rate to the input values of the metabolic index. There appears to be a combination of temperature and pO_2 below which sablefish are more commonly absent from the trawl tows. However, there was no apparent gradation in positive catch rates within the state space, which is likely why the metabolic index did not perform as well as the breakpoint model with separate pO_2 and temperature terms.

4 Discussion points

- Despite having a strong basis in physiological theory, the metabolic index did not provide strong explanatory power of local abundance, even when represented as a threshold, breakpoint function.
  - the metabolic index may perform better to define range boundaries i.e, the relationship between catch rate and metabolic index is extremely steep so that metabolic index does not improve prediction of sablefish catch rates in marginal oxygen conditions.
  - The fitted parameters of the model suggested high tolerance of sablefish to low oxygen, yet there

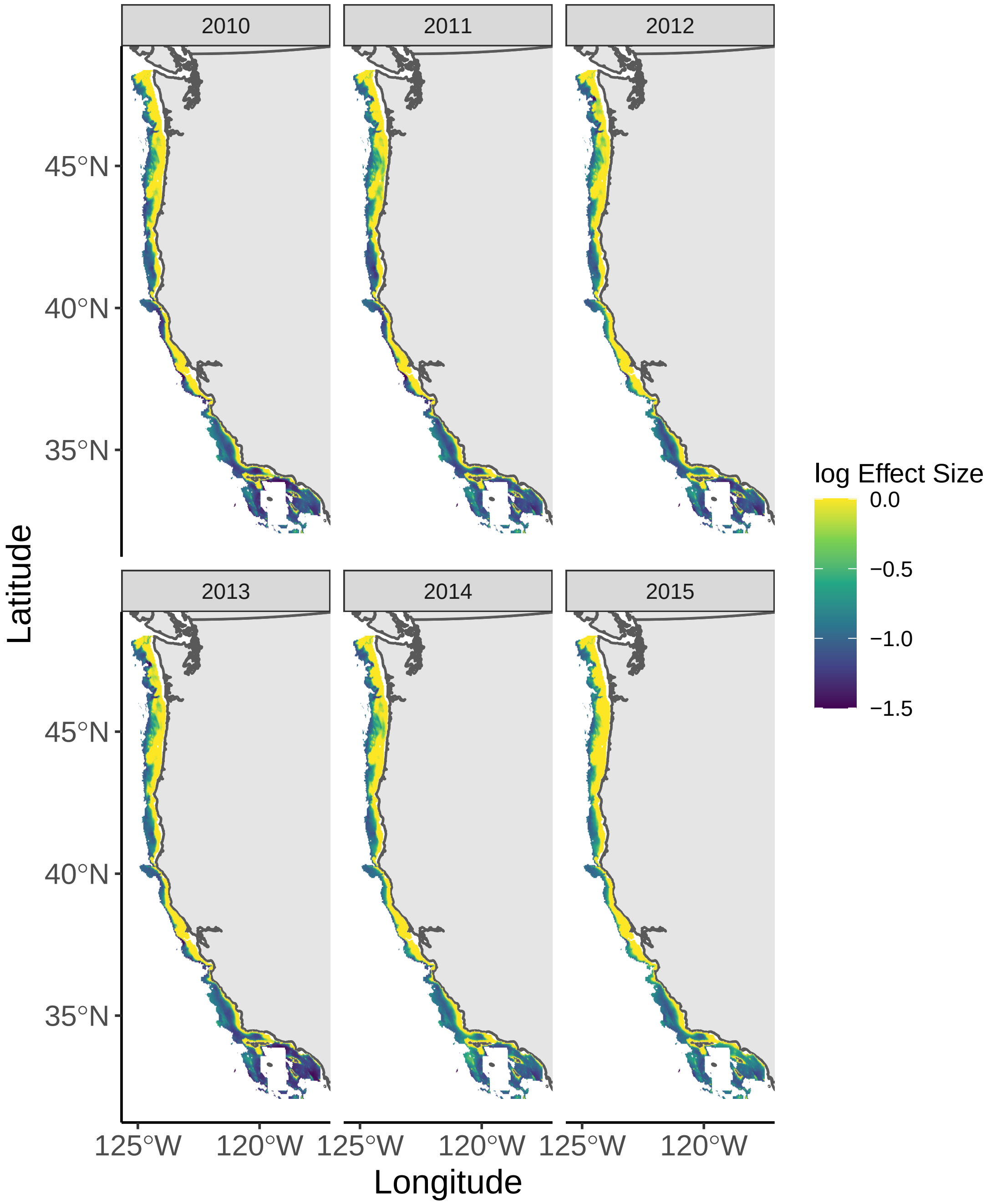

Figure 8: Predicted contribution of oxygen on spatial distribution of sablefish

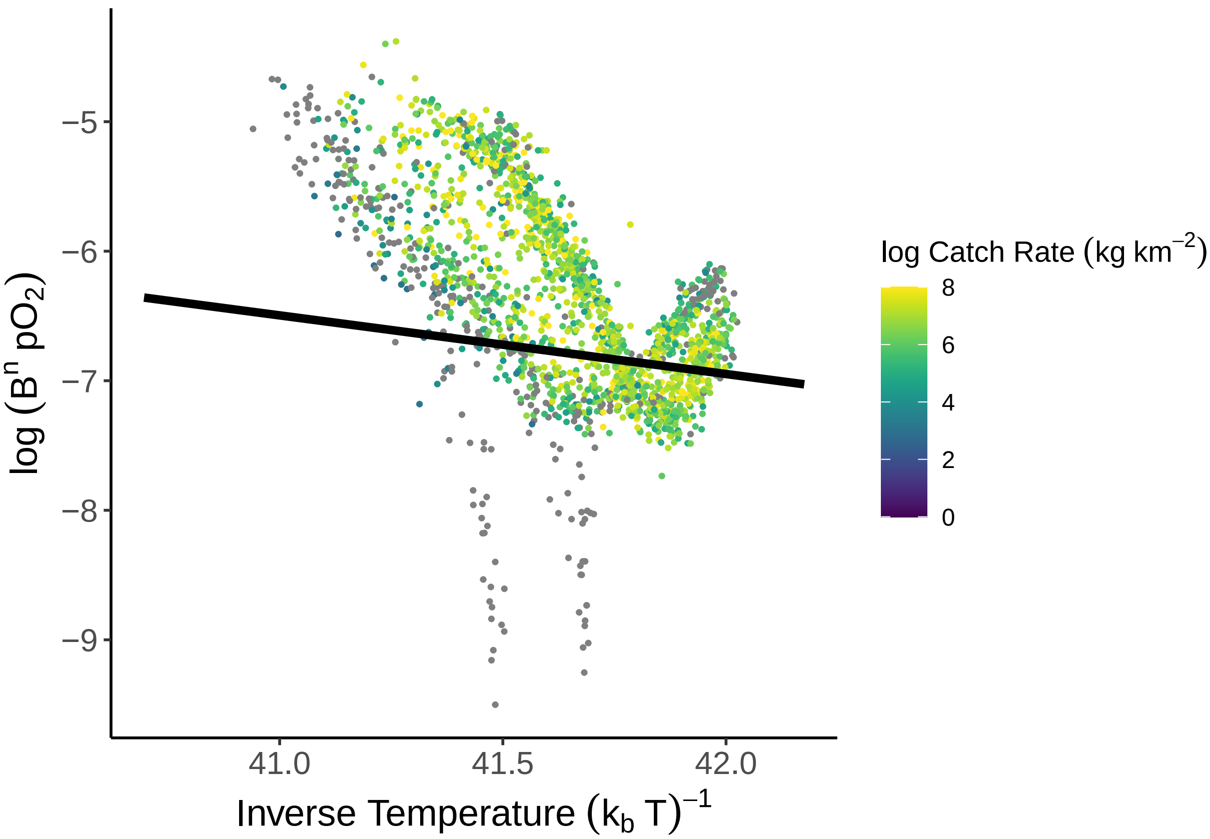

Figure 9: Sablefish catch rate as a function of temperature and body mass-scaled oxygen partial pressure. Each point is a trawl survey sample, and color denotes catch rate. Dark grau points indicate hauls where sablefish were absent. The solid black point indicates the estimated critical threshold (where metabolic index equals 1)

were many catch events captured at temperature and oxygen levels at which the metabolic index would predict are lethal. This suggests either imprecision in the parameter estimation, or that short-duration laboratory experiments do not predict oxygen sensitivity in situ. Similar conclusions were reached by Moriarty et al. to possible explain unexpected sensitivity of pelagic fish to reduced oxygen levels.
  - note that we assumed a constant body size, but more specific information on average body size per tow might improve the performance of metabolic index
- Breakpoint models provide a simple way of statistically modeling limiting factors to species distributions.
  - The estimated pO_2 threshold was generally consistent with the single laboratory experiment conducted on sablefish oxygen tolerance. To be consistent, the estimated breakpoint should exceed the lethal threshold and be near oxygen levels where non-lethal effects begin to be evident. We find that both of these are true: the estimated breakpoint threshold (0.04 atm) was higher than the lethal threshold value of 0.01 atm, and was nearly identical to the pO_2 at which oxygen consumption rate began to decline (0.039 atm. However, we note that this experiment was conducted at temperatures that were greater than those experienced by sablefish at typical depths, and used relatively small-sized adult sablefish (675 g).
- caveats, latent variables, habitat, confounding of depth and everything else
- note that the model predicts mean catch rate, but actual catch rate may vary (pull out statistics on percent deviance explained by model or some such thing).