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UNIVERSITY OF CALIFORNIA SAN DIEGO

Spatiotemporal trends and environmental drivers of larval rockfish species richness and
community assemblages in the Southern California Bight

A thesis submitted in partial satisfaction of the requirements for the degree Master of Science

in

Marine Biology

by

Jessica Breann Freeman

Committee in charge:

Brice X. Semmens, Chair
Andrew R. Thompson
Philip Hastings
Dovi Kacev

2021

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University of California San Diego

2021

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ABSTRACT OF THE THESIS

Spatiotemporal trends and environmental drivers of larval rockfish species richness and community assemblages in the Southern California Bight

by

Jessica Breann Freeman

Master of Science in Marine Biology

University of California San Diego, 2021

Professor Brice X. Semmens, Chair

Although it is well established that Marine Protected Areas (MPAs) are effective tools for augmenting the abundance of fished species, effects on biodiversity and community assembly are less clear. Many rockfish species were overfished in the California Current Ecosystem at the turn of the 21st century, and establishment of two large MPAs in the Southern California Bight, the Cowcod Conservation Areas (CCAs), alongside favorable environmental conditions helped rebuild overfished rockfish stock by 2020. Here, we evaluate the impacts of the CCAs and environment on rockfish diversity and assemblage structure using a 16-year time series (1998-2013) of genetically-identified rockfish larvae. We demonstrate that while rockfish richness generically increased across the time series, the greatest increases occurred inside CCAs

when temperature was low and dissolved oxygen high. Using multivariate methods (ordination and generalized linear latent variable models), we also find a clear species assemblage shift after the 2001 CCA implementations, driven largely by increased presence/abundance of rockfishes targeted by fisheries. Our results suggest that the large and sustained MPAs along the southern California coast have induced increases in the diversity of rockfish reproductive output, driven largely by the direct effects of fishing cessation on targeted species.

INTRODUCTION

Marine protected areas (MPAs) are widely implemented conservation tools worldwide (Lester et al. 2009). Concerns of overfishing drive one common goal of MPAs: to protect and restore depleted fisheries stocks (Takashina & Mougi 2014). MPAs are effective in increasing the abundance, biomass, and spillover of targeted fish species, and can benefit fisheries and the communities that rely on them (Barrett et al. 2007, Aburto-Oropeza et al. 2011, Lorenzo et al. 2020). While the effects of MPAs on fisheries-specific species are well studied, it is less clear how species diversity and community assembly respond to long-term protections. Given the growing favorability of MPAs in response to international goals to protect more of the ocean, filling in such knowledge gaps regarding the ecosystem consequences of MPAs will help managers establish expectations following implementation (UN-Oceans 2017).

Species diversity may either increase or decrease upon implementation of an MPA. The Intermediate Disturbance Hypothesis (IDH) postulates that species richness should be greatest when an ecosystem is subject to moderate disturbance, because if disturbance is very low, dominant predators or competitors will reduce diversity; conversely, if disturbance is very high, fewer species will survive or persist (Connell 1978). If we apply this framework to the biodiversity of fish assemblages, and view fishing as a primary source of disturbance, we can expect a range of responses of fish diversity to MPA implementation. First, if fishing intensity is great (high disturbance), then the abundance of apex predators is reduced, and small, short-lived species that are not targeted by fishing would dominate, and overall diversity will be low. Following the implementation of MPAs, diversity should increase as longer lived species recover from the decrease in fishing disturbances. However, if a species assemblage faces minimal pressure from fishing or other natural disturbances (low disturbance) after MPA implementation,

we might expect the community to shift to large, long-lived species that can outcompete, prey upon, or exclude smaller, short-lived fishes. Thus, the MPA might eventually lower diversity after fishing disturbances decline. Understanding how MPAs impact species diversity and community structure should more holistically provide insight on the MPA's function.

By the late 1990s it became apparent that many rockfish stocks off the west coast of the United States were severely depleted (Love et al. 1998). To augment rockfish recovery, the Pacific Fishery Management Council established two MPAs, termed Cowcod Conservation Areas (CCAs), in the Southern California Bight (SCB) in 2001 to assist the recovery of overfished Bocaccio (*Sebastes paucispinis*) and Cowcod rockfishes (*S. levis*). The CCAs are among the largest MPAs in the United States, and enclose a 10878 km² western and 260 km² eastern region (Thompson et al. 2017). The boundaries of the CCAs were chosen due to their historically high catch of Cowcod, and because they represent favorable habitat for many other rockfish species (Butler et al. 2003). Within CCAs, depth-based fishing restrictions protect the most depleted rockfish species. For Cowcod, all recreational and commercial take was prohibited, regardless of location (Federal Register 2003). The CCAs have shown promising results in restoring most of the overfished rockfish species. For example, larval abundances of six out of eight historically targeted species (along with some non-targeted species) showed significant increases in the years following CCA establishment, with the CCAs having a greater rate of increase for targeted species (Thompson et al. 2017). Additionally, hook and line surveys from 2014-2016 revealed CCAs had significantly higher catch per unit effort (CPUE), abundance, species richness, and sizes for many rockfishes compared to unprotected sites (Keller et al. 2019). As a result of increasing population size, the Pacific Fishery Management Council declared that Bocaccio and Cowcod were rebuilt in 2017 and 2019, respectively (Pacific

Fishery Management Council 2020). While the CCAs likely assisted recovery of these species, the impact of CCAs on overall rockfish species diversity and community structure is still not fully understood (Thompson et al. 2017, Schroeder et al. 2019).

Rockfish life history characteristics are highly variable. For example, life spans of rockfishes vary from just over a decade to over 200 years, and maximum lengths from 18cm to a meter (Love et al. 1990). With these age and size differences come varying growth rates, ages at first maturity, and fecundity (Love et al. 1990). Additionally, rockfishes occupy a diverse range of habitats, with depths ranging from the intertidal zone to over 7000m, and use a multitude of benthic substrate types (Love et al. 2002). They are important components of the marine ecosystem, serving as both predators and prey for a variety of species (Love et al. 1990). The SCB is approximately the world's center of rockfish diversity and hosts over half of all known rockfish species (Love et al. 2002). The unique and variable oceanographic conditions and habitats within the SCB seem to facilitate this high diversity (Love et al. 2002; Checkley & Barth 2009).

Given the high diversity of rockfishes in the SCB, and that the cessation of take resulting from CCAs only acts directly on a small subset of this assemblage, expectations regarding assemblage responses to such protection are unclear. It may be that the release from fishing disturbance inside the CCAs is enough to increase diversity by allowing large rockfishes to recover within an otherwise unaltered community structure. Alternatively, the removal of fishing and return of large predatory rockfishes may lead to reduced diversity due changes in the presence and abundance of smaller rockfishes resulting from changes in community interactions (e.g. predation, competition). Given the inherent diversity of life histories for rockfishes, thorough community assessments of rockfishes can be difficult. Variable habitat affinities from

semi-pelagic to benthic, rocky substrates and fish sizes make most common sampling methods, such as bottom trawls, submersibles, or hook and line, impractical to simultaneously quantify the entire community, while deep depth distributions rule out diver surveys for most species (Love et al. 2002; Thompson et al. 2017). Fortunately, all species of rockfishes give birth (females internally brood eggs) to planktonic larvae that occupy the upper 100 m; therefore larval sampling can quantify the entire rockfish community. Larval abundances are well-known proxies for the spawning stock biomass of fishes (Moser & Watson 2006).

In this study, we use enumerated ichthyoplankton (larval fish) samples collected at specific stations to evaluate spatiotemporal trends and environmental drivers in the species richness and community composition of larval rockfishes inside and outside CCAs across a 16 year time series (1998-2013). In so doing, we treat larval rockfish diversity as a proxy for the diversity of local reproductive output for rockfish species, which in turn is assumed to integrate the abundance and size of reproductive aged individuals contributing to the sampled larval pool (Moser & Watson, 2006). Based on our findings, we infer the response of the rockfish community to CCA implementation in terms of both diversity and community composition, and discuss our findings in the context of MPA effects on fish assemblages and biodiversity.

METHODS

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has regularly sampled and preserved ichthyoplankton in ethanol from 66 set stations, four times per year throughout the SCB since 1998 (formalin-preserved samples have been collected since 1949) (Moser et al. 2001, McClatchie 2014, Thompson et al. 2017). Of these stations, 36 occur on the continental shelf in southern California, and 6 fall within the boundaries of CCAs. CalCOFI uses 505 micrometer mesh bongo nets with a 0.71m diameter towed obliquely from 210m to the

surface to collect ichthyoplankton samples, and CTDs to collect environmental data (temperature, dissolved oxygen concentration, salinity, and chlorophyll *a*) (McClatchie 2014). This study analyzes ethanol-preserved larval rockfish collected during Winter (peak spawning season for most rockfishes) from 1998 to 2013 (Love et al. 1990, Moser et al. 2001).

Ichthyoplankton that were visually identified as rockfishes were removed from plankton samples (Thompson et al. 2017). Most rockfishes are indistinguishable to species based on morphology as larvae. However, those unambiguously identified as shortbelly rockfish (*S. jordani*) were recorded during initial visual identification. All other rockfish larvae were identified through genetic sequencing of the mitochondrial cytochrome *b* gene (Thompson et al. 2017). This gene can discriminate between almost all rockfish species in the southern California (pygmy rockfish, *S. wilsoni* genetic identification falls into a complex of five species but only pygmy rockfish is common in southern California; Taylor et al. 2004, Stierhoff et al. 2013). The larval sequences were then matched to the genetic library developed by Hyde & Vetter (2007). Samples from 2003 were poorly preserved, mostly failed to sequence, and are excluded from this study. To account for subtle disparities in tow length and depth, larval abundances were multiplied by the standard haul factor (volume of water filtered divided by the tow depth) and are expressed as larvae under 10m² of sea surface area to the tow depth (Smith & Richardson 1977).

Throughout this paper, we compare rockfish dynamics inside versus outside the CCAs using a paired design; that is, for each of the 6 CalCOFI stations inside of CCAs, we identified a non-CCA paired site that was most environmentally similar to it (Figure 1). To do so, we ran a cluster analysis based on Bray-Curtis dissimilarity matrix of the means of the environmental variables (temperature, dissolved oxygen content, salinity, and chlorophyll *a*) over the 13 year time series, as well as station depth and percent cover of hard substrate. This paired design

approach was first used, and thoroughly described in Thompson et al. (2017) (see methods in Thompson et al. 2017).

We used environmental covariates (temperature, dissolved oxygen content, salinity, and chlorophyll *a*) averaged over the top 100 m for each site measured at the time of larval sampling, so that each station has its own values for each year. We chose these covariates as they are known to affect larval rockfish distribution and abundance, and are reasonably independent of each other (uncorrelated) (Thompson et al. 2016, Schroeder et al. 2019). For the statistical analyses, we scaled the years and environmental covariates by subtracting each value by the mean and dividing by the standard deviation.

To assess spatiotemporal trends in species richness, and the effects of environmental covariates on such trends, we ran a series of Generalized Linear Mixed-effect Models (GLMMs) where richness was assumed to be Poisson distributed (log link function). We created a set of candidate baseline models in which species richness was dependent on different combinations of fixed effects for year (continuous), CCA inclusion (categorical), the interaction of year and CCA (allowing differing richness trends inside versus outside CCAs), and random effects of site pairs on the slope and intercept (Table 1). We compared baseline model parsimony based on AICc (Akaike information criterion corrected for small sample sizes). In the selected baseline model, species richness was dependent on the fixed effects of year, CCA inclusion, the interaction of year and CCA, and a random effect of site pairings on the intercept and slope (Table 1). Subsequently, to evaluate evidence for environmental drivers beyond the identified baseline model, we created a set of 15 candidate models with every combination of environmental covariates (temperature, dissolved oxygen content, salinity, and chlorophyll *a*) as added fixed

effects to the baseline model with the lowest AICc (Table 2). We compared model parsimony based on AICc.

To visualize changes in the larval rockfish species assemblage over time, we created a Non-metric Multidimensional Scaling (NMDS) plot using ordination based on the Bray-Curtis dissimilarity index over two dimensions. We averaged the species abundances across all 12 sites in each Winter, without discerning by site pairs or CCA. We grouped the NMDS by years (unscaled) prior to and after CCA implementation to assess changes in the community structure after protections.

To assess the effects of the environmental covariates on assemblage structure, we ran a set of Generalized Linear Latent Variable Models (GLLVMs) with a negative binomial distribution and log link function. We took the average of species abundances and environmental covariates by year inside and outside CCAs, and removed rare species (sum of yearly means < 20) from the analysis. After averaging by year for inside and outside CCAs, we scaled the environmental covariates by subtracting by their mean values and dividing by their standard deviations. In the baseline model, the species abundance matrix is dependent only on CCA inclusion, and is not dependent on any of the environmental covariates. In the 15 candidate models, the species abundance matrix is dependent on CCA inclusion and the environmental covariates, with every combination of the environmental variables included in the candidate set (Table 3). We compared model parsimony based on the lowest AICc (Akaike information criterion corrected for small sample sizes).

RESULTS

For the baseline models (Table 1), the preferred GLMM based on the lowest AICc included fixed effects for year (continuous), CCA inclusion (categorical), the interaction of year and CCA (allowing differing richness trends inside versus outside CCAs), and random effects of site pairs on the slope and intercept. Of those model variants that added environmental covariates to this baseline model, the one with the lowest AICc included both temperature and oxygen as fixed effects (Table 2). Across all environmental covariate candidate models, temperature showed a negative correlation with species richness, and oxygen, year, and CCA inclusion showed positive effects on species richness (Figure 2). The predicted richness based on the preferred model for each of the site pairings was consistently higher inside compared to outside the CCAs, and appeared to increase at a higher rate inside CCAs (positive year*CCA interaction; Figure 3). Counterfactual plots from the preferred model show predicted species richness is highest inside CCAs at the lowest and highest observed temperature and oxygen levels, respectively (Figure 4). Furthermore, predicted species richness is lowest outside CCAs at the highest and lowest observed temperature and oxygen levels, respectively (Figure 4).

The NMDS plot shows a distinct separation between the year groupings (Figure 5). Vector loadings of historically targeted rockfishes (*Sebastes goodei*, *levis*, *mystinus*, *ovalis*, *paucispinis*, *rufus*, and *serranoides*) are all directed towards the years following CCA implementation. NMDS stress was 0.0926.

The GLLVM model with the lowest AICc included all environmental covariates and CCA distinction (Table 3). All other models had a delta AICc greater than 10 AICc points above the selected model (Table 3). In the selected model, all species abundance point estimates and their respective 95% confidence intervals overlapped with zero for temperature correlations

(Figure 6). Some species abundances were negatively related to oxygen (*S. diploproa*) and salinity (6/13 species), while the rest overlapped with zero. One species (*S. mystinus*) was positively related to chlorophyll a, and the rest of the species overlapped with zero. Eight out of the 13 species abundances were positively related to CCA association; the other 5/13 species overlapped with zero (Figure 6).

DISCUSSION

We found increasing species richness driven by low temperature and high oxygen and the return of larvae from targeted rockfish species following the implementation of the CCAs. The rate of increase for species richness was consistently higher inside CCAs compared to paired sites outside CCAs, supporting the notion that mitigating fisheries disturbances with MPAs yields higher diversity. In addition to our work, studies have connected shifts in biodiversity and community structures to both ecosystem protections and disturbance levels. For example, MPAs within the Great Barrier Reef are positively correlated with increased fisheries diversity compared to their surrounding unprotected regions (Raymundo et al. 2009). Additionally, study areas further from MPAs are associated with less diversity and ecological redundancy in the northwestern Mediterranean Sea, partially due to fisheries related disturbances (Stelzenmüller et al. 2009). Nevertheless, studies directly linking protections to long term changes in fisheries biodiversity remain scarce, and more research is needed to conclude MPA effects on biodiversity (García-Charton et al. 2008).

We found increasing richness through time throughout the SCB, with higher rates of increase inside the CCAs compared to outside. Following the implementation of the CCAs in 2001, the species assemblage shifted towards the large, slow growing, historically targeted rockfishes (Figure 5). This community shift also included increased representation from some of

the more rare, un-targeted rockfishes (*Sebastes rosaceus*, *rufianus*, *diploproa*), suggesting that the return of the larger rockfishes has not resulted in a decrease in diminutive species. We found that some rockfish species abundances correlated negatively with salinity and oxygen, and positively with chlorophyll a and CCA inclusion (Figure 6), indicating that the environmental covariates and CCAs play a role in the abundances of many rockfishes. Because the assemblage hosts diverse life histories amongst species, it is not surprising that not all species were strongly related to each environmental covariate (Figure 6).

While MPAs may increase biodiversity and ecosystem functioning, they are often placed in areas that are politically favorable rather than ecologically favorable, consequently limiting the MPAs ability to mitigate direct anthropogenic pressures (Topor et al. 2019, Stevenson et al. 2020). This is particularly concerning for fisheries conservation given the widespread threat of overfishing (Link & Watson 2019). In the CCAs, however, locations were determined based on high historical Cowcod catch rates, in the best fishing waters for rockfish (Butler et al. 2003). Furthermore, MPAs with a combination of specific features (no take, well enforced, older than 10 years, larger than 100 km², and isolated) yield the most conservation success (Edgar et al. 2014). The CCAs have protected over 11000 km² for the last 20 years, prohibiting the take of numerous rockfish species. Isolation by sand and depth certainly varies throughout the CCAs due to the unique features within the SCB, but given their large sizes, it is likely that the centers of the CCAs are largely isolated in terms of fishing pressure near the boundaries. The CCAs are likely well enforced based on the successes in rebuilding previously depleted stocks (something not seen in other rockfish conservation areas with poor enforcement; Thompson et al. 2017). Our results not only serve as a success story for the southern California rockfish assemblage, but also for MPA efficacy when science based management is the highest priority.

In addition to the CCAs, the increase in larval rockfish species richness was likely driven by favorable environmental conditions in Southern California. The model findings suggest that richness is highest in years with colder and more oxygenated water (Figure 4). Additionally, of the four environmental covariates we analyzed, temperature was the strongest driver of rockfish richness, and was included in every model that had weight (Table 1). Considering eleven of the fifteen years in our time series were cooler than average, consistently favorable water temperatures in the SCB was a key factor in increasing rockfish species richness (Thompson et al. 2017). In general, cooler temperatures are associated with favorable spawning conditions for rockfishes and are favorable for larval survival and recruitment after spawning (Moser et al. 2001, Schroeder et al. 2019). Our results are also consistent with those of previous studies, concluding that “minty” water (cooler, oxygenated, fresher water) corresponds not only with higher abundance and recruitment levels of rockfishes, but also with higher species richness (Ralston et al. 2013, Schroeder et al. 2019).

Although rockfish richness is greatly influenced by environmental conditions, the CCAs apparently had added positive effects on richness through time. Species richness was consistently higher inside compared to outside CCAs (Figure 3). Additionally, across the time period, richness inside CCAs increased at a faster rate (Figure 4). The higher richness inside CCAs is likely due to the fact that CCAs were placed in habitats that are more favorable to rockfishes. This effect held within our model, despite accounting for environmental similarity through the site pairings. The fact that richness increased at a faster rate inside versus outside CCAs is most likely attributable to fishing restrictions and regulations inside the CCAs. With old, large females being protected from fishing in the CCAs, larvae will have higher survival rates, as maternal age and size are key factors in larval success (Berkeley et al. 2004, Sogard et al. 2008, Stafford et al.

2014). Protections of these large, fecund females are likely the reason richness is increasing at a faster rate inside the CCAs, while potential spillover of larvae to unprotected areas may be a supplemental driver (alongside favorable environmental conditions) of increased richness outside the CCAs, though more research is needed to confirm spillover effects for rockfishes in the SCB.

Because the SCB is a historical hotspot for rockfish diversity and high species richness (Love et al. 2002), it is promising that rockfish richness has increased following CCA protections and favorable environmental conditions. Additionally, two of three rockfishes (*S. goodei* and *S. ensifer*) previously noted as absent from the assemblage have returned to the SCB in the CalCOFI time series (Love et al. 1998, Thompson et al. 2017). The significantly higher increases in abundance of many of the heavily targeted rockfishes inside compared to outside CCAs indicates the CCAs are driving changes in richness by rebuilding previously depleted stocks (Thompson et al. 2017). These changes are likely the reason the community structure of rockfishes shifted toward the larger, historically targeted species following the implementation of the CCAs (Figure 5). This is further evidenced by the positive correlation between CCAs and abundances of historically targeted rockfishes (Figure 6). This shift also encompasses some of the rarer rockfishes (*S. rosaceus*, *rufianus*, *diploproa*), which are also likely benefitting from favorable spawning and recruitment conditions (Figure 5); however, they may also be benefitting from the resurgence of larger predatory rockfishes, as predators may enable rarer species via species interactions (Paine, 1966).

The time window for our study precedes the recent marine heat waves in the region. The SCB endured three heat waves from 2014 to 2019: “The Blob” from 2014-2016, a heatwave centered in the SCB and Baja in 2018, and “The Blob 2.0” in 2019 (Di Lorenzo & Mantua 2016, Amaya et al. 2020, Fumo et al. 2020). Notably, the Blob in 2014-2016 was the hottest marine

heat wave on record in the Pacific northeast (Di Lorenzo & Mantua 2016). Given our results that cooler temperatures drive increased richness (Figure 4), and given the importance of cooler temperatures for maternal investment, larval abundances, and larval recruitment, it is possible that the trends we detail here have changed since 2013 (Berkeley et al. 2004, Sogard et al. 2008, Stafford et al. 2014). However, cooler water pockets may have lingered in the SCB during such marine heat waves, and may have provided partial shelter from the temperature stress for maternal and larval rockfishes in those areas (Schroeder et al. 2019). Additionally, the oxygen content in the SCB may be declining with increases in temperature. For instance, predictive models suggest subarctic water mass in the California Current Ecosystem (CCE) will become warmer and less oxygenated due to climate change (Rykaczewski & Dunne 2010). As oxygen is a supplemental driver of larval rockfish species richness (Figure 4), these predictions hint at a potential reverse in richness trends alongside increasing temperatures. However, certain species of rockfishes may respond differently to climate changes in the CCE. Smaller and shorter lived species may adapt faster to environmental shifts, as size-dependent responses to such changes are documented for other assemblages (Genner et al. 2010). Further analyses of CalCOFI larval samples and environmental covariates are needed to confirm how recent conditions in the SCB have affected larval rockfishes.

Regardless of environmental changes, preservation of the CCAs may serve as an effective tool in helping maintain rockfish diversity in the SCB. In California waters north of the SCB, Rockfish Conservation Areas (RCAs) have been shown to have higher species richness, abundance, and mean lengths of rockfishes, as well as other demersal fishes (Keller et al. 2014). These results, alongside ours, suggest that MPAs are a sound resource for preserving rockfish biodiversity. With uncertainty surrounding environmental changes and subsequent effects on the

rockfish assemblage, continuing to mitigate the direct ecosystem disturbances under management control, such as overfishing and trawling, may help maintain community diversity.

TABLES & FIGURES

Table 1. Baseline model selection for Generalized Linear Mixed-Effects Models. Values are rounded to two decimals. Model formulations are specified for use in the R package lme4 (Bates et al. 2014).

Model	Formula	AICc	Δ_AICc	AICc_Weight
1	richness ~ year + cca + year*cca + (year pair)	896.7	0	0.52
2	richness ~ year + cca + (year pair)	896.87	0.17	0.48
3	richness ~ year + cca + year*cca + (1 pair)	906.95	10.25	0
4	richness ~ year + cca + (1 pair)	907.23	10.53	0
5	richness ~ year + (1 pair)	997.75	101.05	0

Table 2. Model selection table for Generalized Linear Mixed-Effects Models. Only models that added to the cumulative weight are included. Values are rounded to 2 decimals.

Model	Formula	AICc	Δ_AICc	AICc_Weight
1	richness ~ year + cca + year*cca + (year pair) + temperature + oxygen	879.39	0	0.36
2	richness ~ year + cca + year*cca + (year pair) + temperature + oxygen + salinity	880.47	1.08	0.21
3	richness ~ year + cca + year*cca + (year pair) + temperature + oxygen + chlorophyll α	881.15	1.77	0.15
4	richness ~ year + cca + year*cca + (year pair) + temperature + salinity	881.4	2.01	0.13
5	richness ~ year + cca + year*cca + (year pair) + temperature + oxygen + salinity + chlorophyll α	882.45	3.07	0.08
6	richness ~ year + cca + year*cca + (year pair) + temperature + salinity + chlorophyll α	883.64	4.26	0.04
7	richness ~ year + cca + year*cca + (year pair) + temperature	884.86	5.48	0.02
8	richness ~ year + cca + year*cca + (year pair) + temperature + chlorophyll α	887.03	7.64	0.01

Table 3. Model selection table for Generalized Linear Latent Variable Models. Only models with delta AICc < 100 are included. Formula is the species matrix by cca and listed environmental covariates. Values are rounded to 2 decimals.

Model	Formula	AICc	Δ_AICc
1	y ~ cca + temperature + oxygen + salinity + chlorophyll a	1384.82	0.00
2	y ~ cca + temperature + salinity + chlorophyll a	1394.98	10.16
3	y ~ cca + oxygen + salinity + chlorophyll a	1401.18	16.36
4	y ~ cca + temperature + oxygen + salinity	1401.76	16.94
5	y ~ cca + temperature + oxygen + chlorophyll a	1403.11	18.29
6	y ~ cca + temperature + salinity	1410.57	25.75

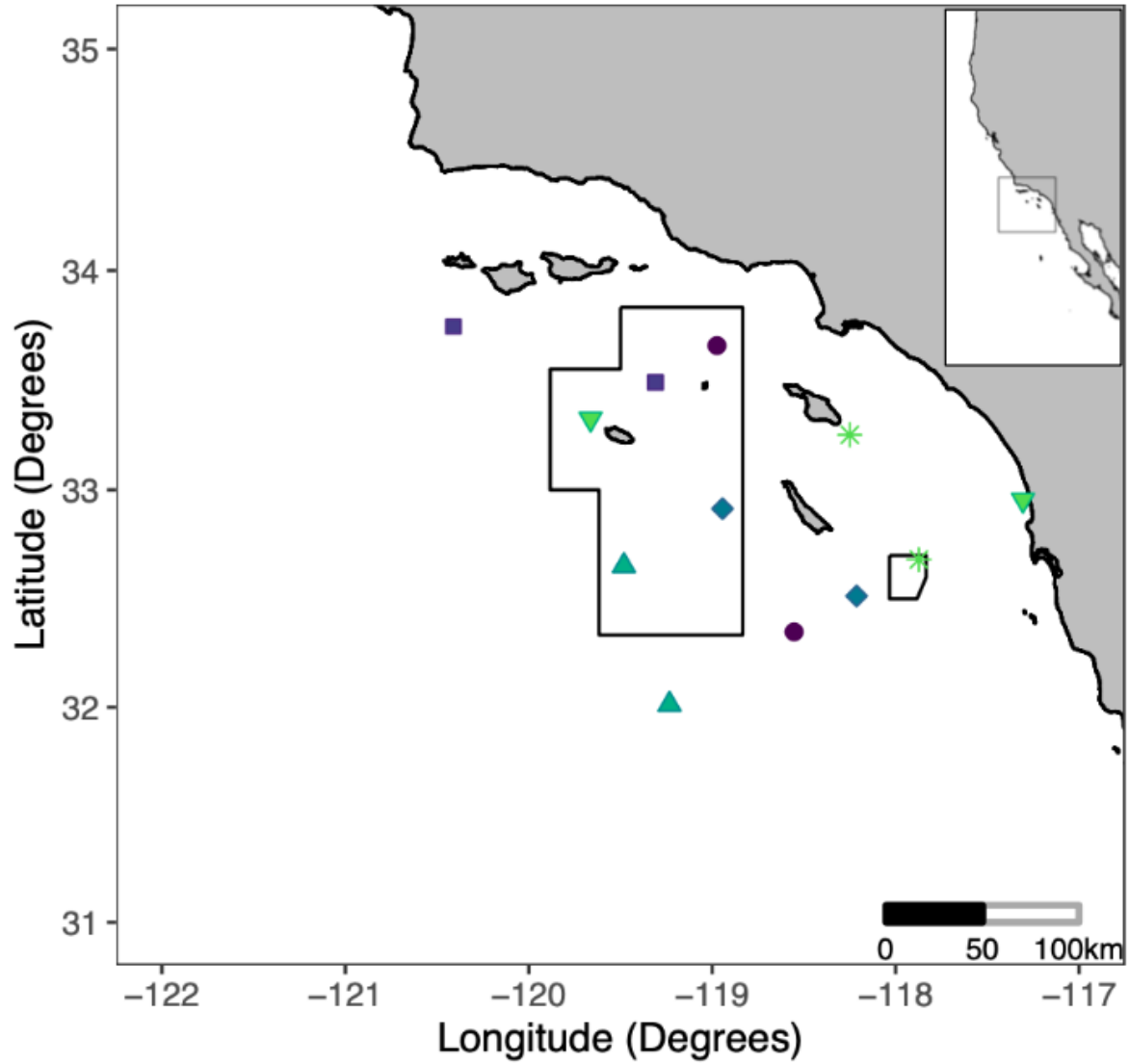


Figure 1. Paired California Cooperative Oceanic Fisheries Investigations (CalCOFI) sample sites in the Southern California Bight. The Cowcod Conservation Areas (CCAs) are outlined in black. Paired sites are shown by shape and color.

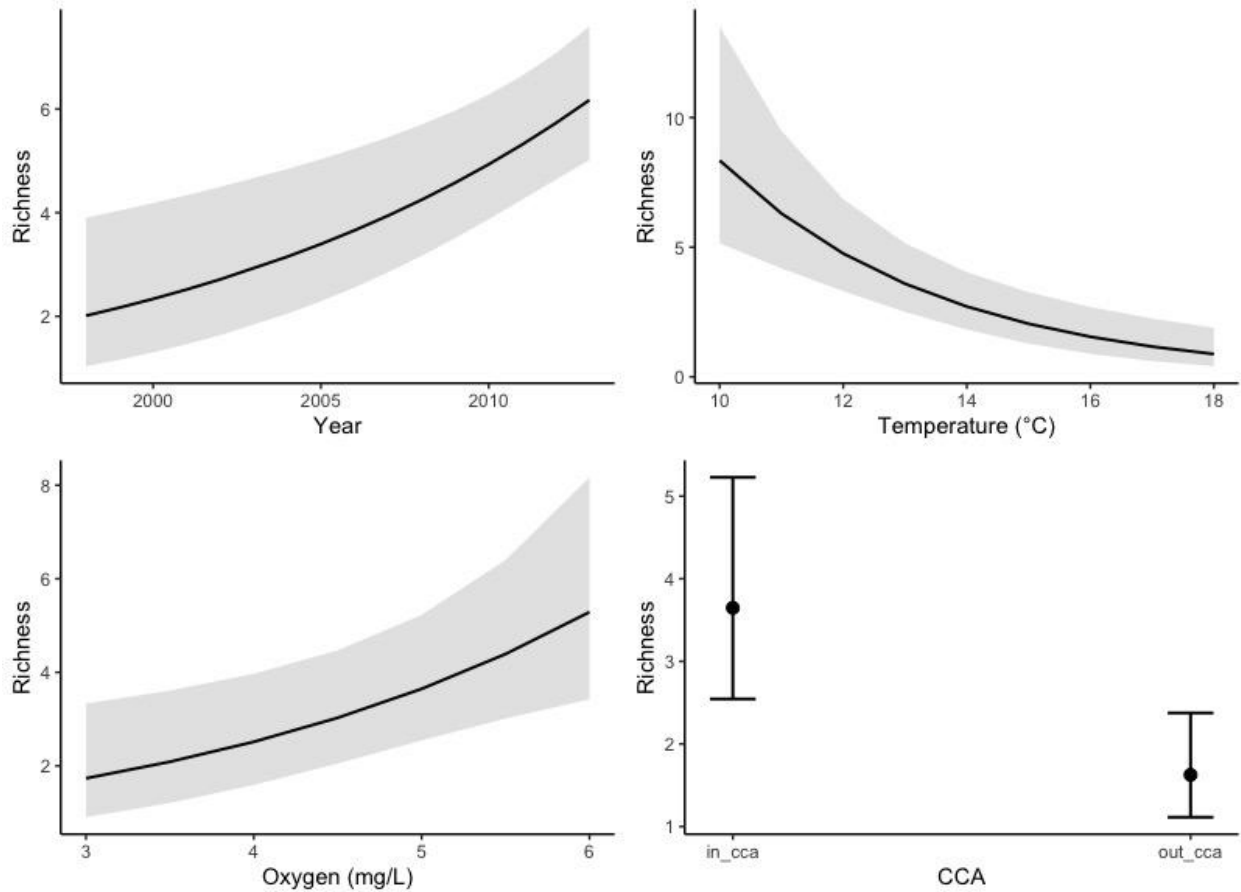


Figure 2. Breakdowns of predicted richness values for the fixed effects of the preferred Generalized Linear Mixed-effect Model. Predictions (black line) are shown with 95% confidence intervals (grey shading) for continuous variables (year, temperature, and oxygen). Predictions (black point) and 95% confidence interval (error bars) are shown for discrete variables (CCA).

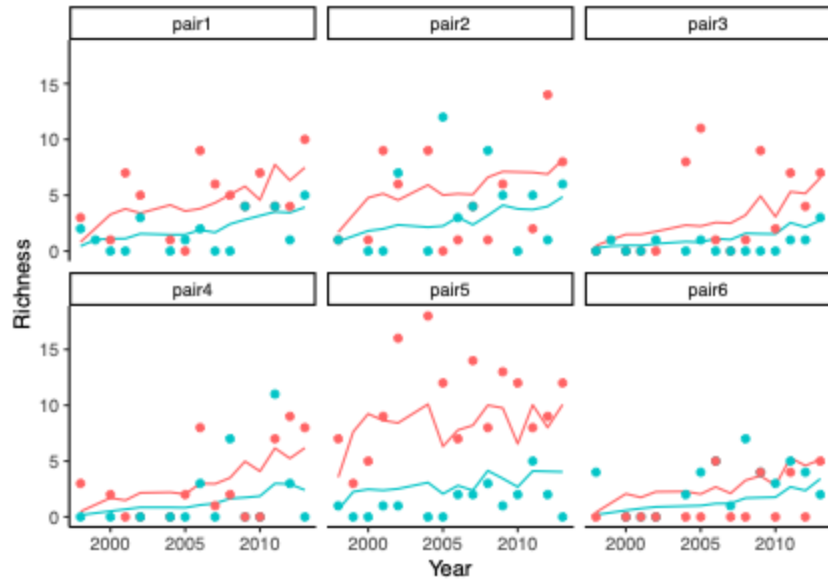


Figure 3. Predicted richness (lines) alongside observed richness (points) for each site pair of the preferred Generalized Linear Mixed-effect Model. Lines and points show predicted and observed richness inside (red) and outside (blue) Cowcod Conservation Areas.

Figure 4. Counterfactual plots of predicted richness for the preferred Generalized Linear Mixed-effect Model. Predicted richness is shown for varying temperatures and oxygen levels inside and outside Cowcod Conservation Areas. Temperature and oxygen levels range from the minimum to maximum values found in the data set.

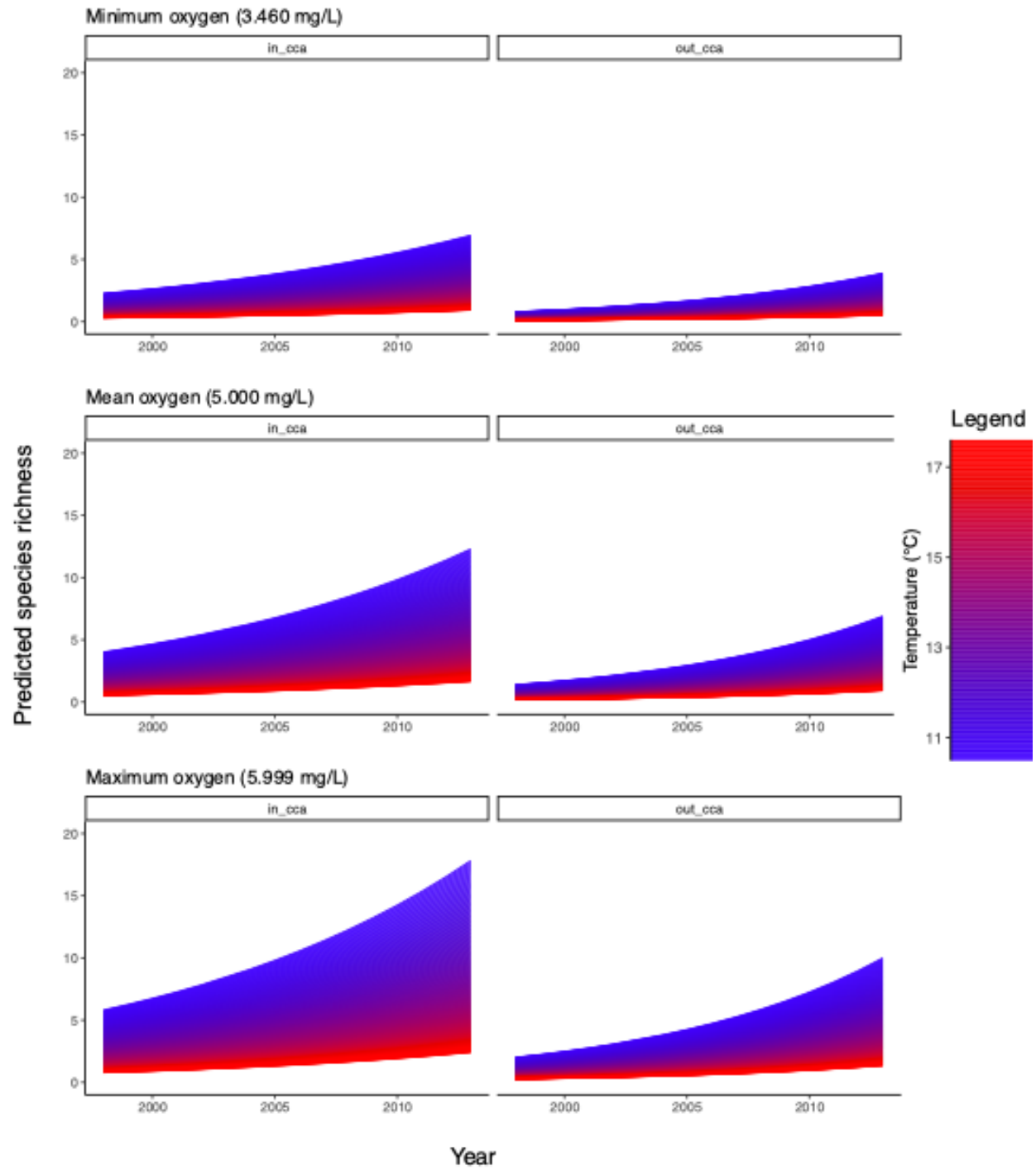


Figure 5. Non-metric Multidimensional Scaling (NMDS) plot of larval rockfish abundances. Years are grouped before and after Cowcod Conservation Area implementation in blue and red, respectively. Species loadings are shown for historically targeted rockfishes (purple vectors). Untargeted and targeted species are labeled in grey and purple, respectively. We eliminated rare species (sum of yearly means < 5) from the plot for visual clarity. NMDS stress = 0.0926.

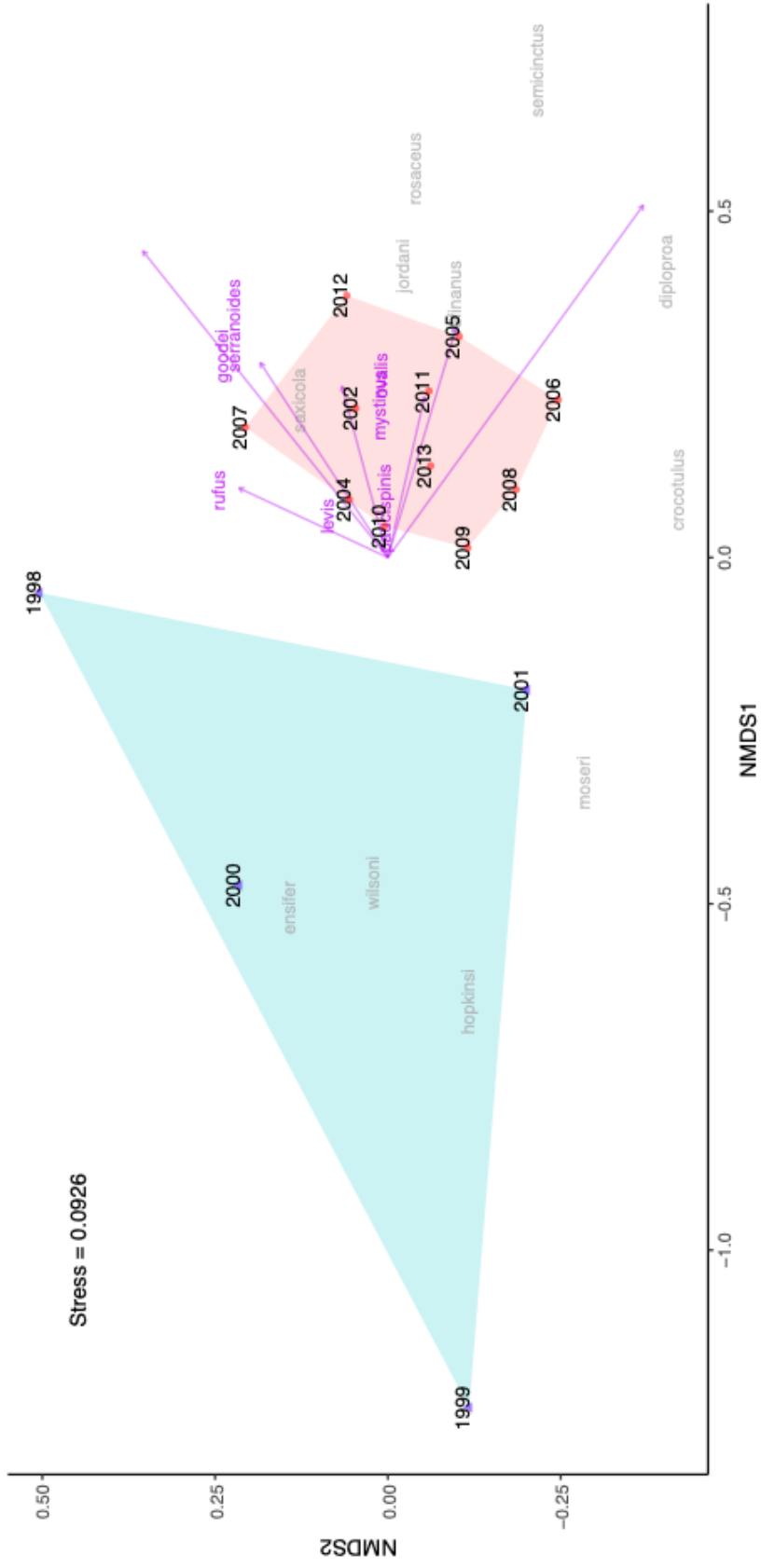
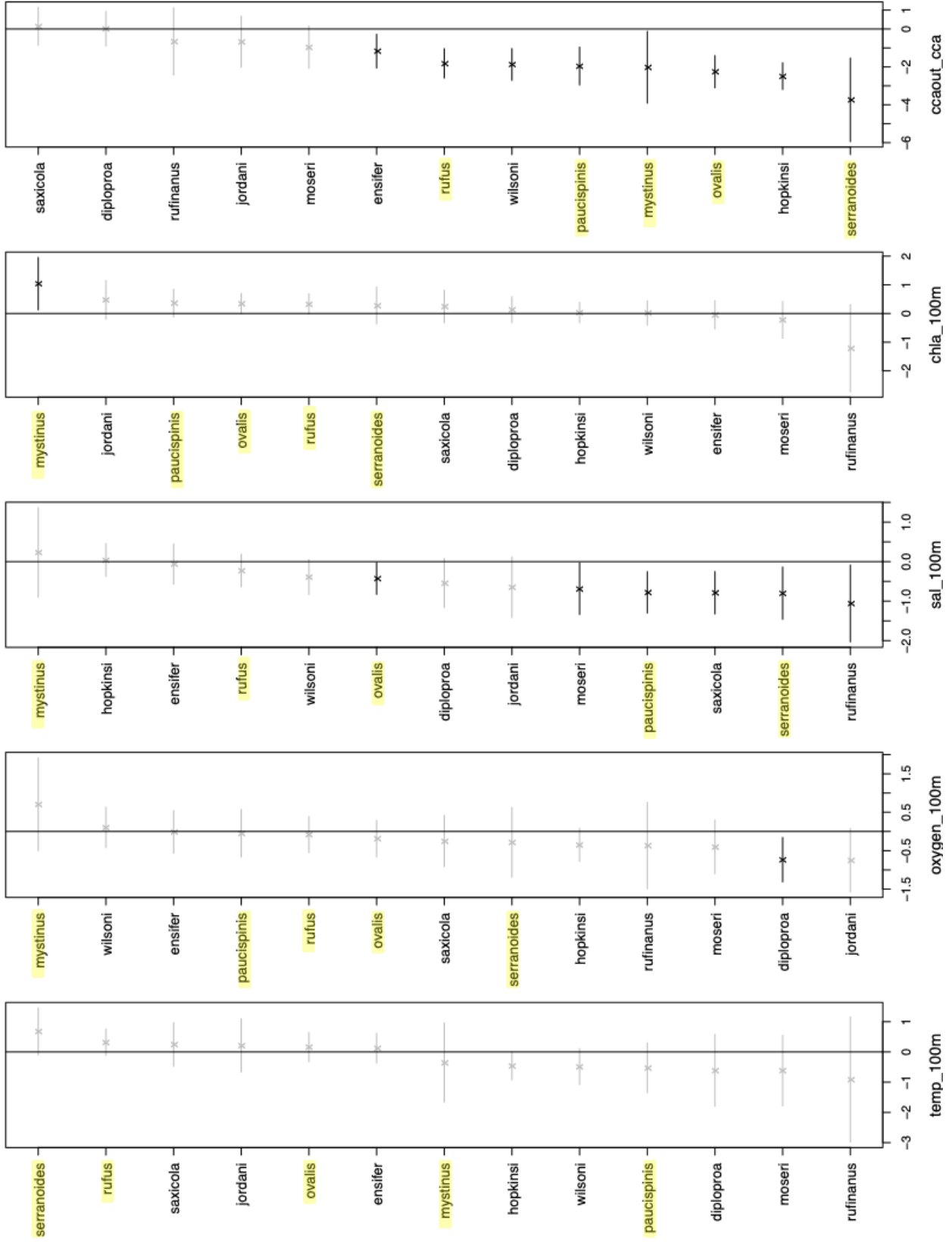


Figure 6. Point estimates and 95% confidence intervals of the covariate coefficients (temperature, oxygen, salinity, chlorophyll *a*, and CCA exclusion) for the preferred Generalized Linear Latent Variable Model. Estimates with confidence intervals not overlapping zero are shown in black. Labels of historically targeted rockfish species are highlighted in yellow.



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