



Impacts of marine protected areas and the environment on larval rockfish species richness and assemblage structure in the Southern California Bight

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ABSTRACT: Although it is well established that marine protected areas (MPAs) are effective tools for augmenting the abundance of fished species, effects on biodiversity and assemblage structure are less clear. Many rockfish (genus *Sebastes*) species were overfished in the California Current Ecosystem at the turn of the 21st century, leading to establishment of 2 large MPAs in the Southern California Bight, the Cowcod Conservation Areas (CCAs). The CCAs, alongside favorable environmental conditions, helped rebuild overfished rockfish stocks by 2019. Here we assessed the impacts of the CCAs and environment (temperature, oxygen, salinity, chlorophyll *a*) on rockfish diversity and assemblage structure using a 16 yr time series (1998–2013) of genetically identified rockfish larvae. Larval rockfish richness generally increased across the time series, with the greatest increases inside CCAs when temperature was low and dissolved oxygen was high. We also found a clear species assemblage shift after the implementations of the CCAs, driven largely by rockfishes targeted by fisheries. This shift was most likely initially driven by maturation of a strong 1999 year class, and sustained by protection from fishing and favorable environmental conditions. Our results suggest that the large and long-term MPAs along the southern California coast have induced increases in the diversity of larval rockfish, driven largely by the direct effects of fishing cessation on targeted species.

KEY WORDS: *Sebastes* · Cowcod Conservation Areas · Fisheries · Diversity

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1. INTRODUCTION

Marine protected areas (MPAs) are widely implemented conservation tools worldwide (Klein et al. 2008, Lester et al. 2009, Rojo et al. 2019). Concerns of overfishing drive one common goal of MPAs: to protect and restore depleted fisheries stocks (Shipp 2003, 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, Di Lorenzo et al. 2020). However, MPAs may take several years to decades to reach their conservation goals (Russ & Alcala 2004). Given the growing favorability of MPAs in response to international goals to protect more of the ocean, deepening the knowledge regarding the long-term ecosystem consequences of MPAs will help managers establish expectations following implementation (United Nations-Oceans 2017).

From a theoretical perspective, species diversity may either increase or decrease in response to MPA implementation. While the potential mechanisms

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driving these biodiversity changes remain a topic of debate, they provide a natural history context for discussing possible outcomes following MPA implementation. One potential mechanism can be derived from the intermediate disturbance hypothesis (IDH), which postulates that species richness should be greatest when an ecosystem is subject to moderate disturbance (Fig. 1; Connell 1978). If we apply this framework to the biodiversity of fisheries assemblages, and view fishing as a primary source of disturbance, we can expect a range of biodiversity responses to MPA implementation. The more severe the fishing pressure prior to MPA implementations, the more we might expect diversity to increase following protection, as ecosystem disturbances return to a moderate level. Another potential mechanism for biodiversity shifts is described by the 'big old fat fecund female fish' (BOFFFF) hypothesis, which asserts that certain fishes display increasing fecundity with increasing age and size (Marteinsdottir & Steinarsson 1998, Berkeley et al. 2004a,b, Berkeley 2006, Field et al. 2008, Hixon et al. 2013). If the BOFFFF hypothesis applies to species within an MPA that were previously the targets of fishing, we might expect increases in biodiversity as individuals are permitted to age and grow larger, thereby increasing their reproductive output within the MPA. There are likely several other possible means by which MPAs alter regional diversity, and the interaction of such mechanisms, the efficacy of the MPAs, and the life histories of the species within may dictate alternative biodiversity outcomes. Understanding how MPAs impact species diversity and assemblage structure should more holistically provide insight on the function of the MPAs.

In the late 1990s, the first stock assessment of rockfishes off the US west coast revealed that many rockfishes were severely depleted (Love et al. 1998). Many rockfishes targeted by fisheries showed de-

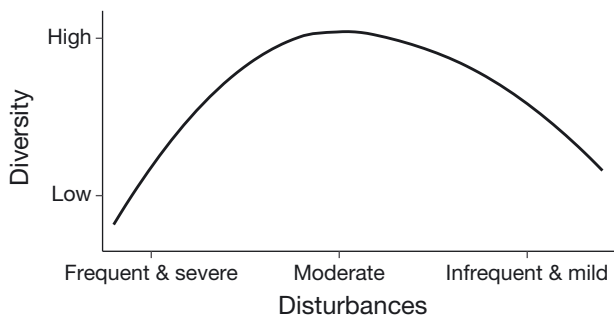


Fig. 1. Intermediate disturbance hypothesis (based on Connell 1978). Hypothetical change in ecosystem diversity (black curve) in response to varying disturbance levels

creasing catch per unit effort (CPUE) and decreasing mean length of adults, which are indicators of overfishing on fishery populations (Love et al. 1998). In response, the Pacific Fishery Management Council established 2 MPAs, termed the Cowcod Conservation Areas (CCAs), in the Southern California Bight (SCB) in 2001 to assist the recovery of overfished bocaccio *Sebastes paucispinis* and cowcod *S. levis* (Department of Commerce 2003). The CCAs are among the largest MPAs in the USA, and enclose a 10 878 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 the CCAs, depth-based fishing restrictions protect the most depleted rockfish species. For cowcod, all recreational and commercial take was prohibited, regardless of location (Department of Commerce 2003). The CCAs have shown promising results in restoring many overfished rockfish species. For example, larval abundances of 6 out of 8 historically targeted species (along with some non-targeted species) showed significant increases in the years following establishment of the CCAs, with the CCAs having a greater rate of increase for targeted than non-targeted species (Thompson et al. 2017). Additionally, hook and line surveys from 2014 to 2016 revealed that the CCAs had significantly higher CPUE, abundance, species richness, and sizes of 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 (populations at abundance levels that can sustain maximum sustainable yield) in 2017 and 2019, respectively (Pacific Fishery Management Council 2020). While the CCAs likely assisted recovery of these species, the impact of the CCAs on overall rockfish species diversity and assemblage structure is still not fully understood (Thompson et al. 2017, Schroeder et al. 2019).

Rockfishes are a relatively diverse genus (*Sebastes*) within the scorpionfish family (Scorpaenidae), with highly variable life history characteristics (Love et al. 2002). For example, life spans of rockfishes vary from just over a decade to over 200 yr, and maximum lengths span from 18 cm to 1 m (Love et al. 1990). With these age and size differences come varying growth rates, ages at first maturity, and fecundity (Love et al. 1990). Many rockfishes show an exponential increase in fecundity with increasing lengths, in that larger individuals produce more

eggs than their smaller counterparts (Love et al. 2002). All rockfishes give live birth, but the amount of energy the larvae receive from an egg yolk (ovoviviparity) or from maternal fluids (viviparity) varies across species (Love et al. 2002). Additionally, rockfishes occupy a diverse range of habitats, with depths ranging from the intertidal zone to over 2000 m, 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, including other rockfishes (Love et al. 1990). The SCB is approximately the global 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 subset of this assemblage (many smaller species altogether will not or only very rarely bite hooks, making them less vulnerable to overfishing, and rendering CPUE data ineffective for stock assessments), expectations regarding full-scale assemblage responses to such protection are unclear (Love et al. 2002, Thompson et al. 2016). It may be that the release from fishing disturbance inside the CCAs is enough to increase diversity by allowing large rockfishes to recover and increase spawning output (Love et al. 2002, Berkeley et al. 2004a,b, Sogard et al. 2008). Alternatively, the removal of fishing and return of large predatory rockfishes may lower diversity due to 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 assemblage 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 assemblage, 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 water column to depths of 100 m; therefore, larval sampling can quantify the entire rockfish assemblage (Love et al. 2002). Larval abundances are well-known proxies for the spawning stock biomass of fishes and are used as indices of spawning stock biomass for rockfish stock assess-

ment (Moser & Watson 2006, Field et al. 2009, Dick & MacCall 2014).

In this study, we used enumerated ichthyoplankton (larval fish) samples collected at fixed stations to evaluate spatiotemporal trends and environmental drivers in the species richness and assemblage composition of larval rockfishes inside and outside of the CCAs across a 16 yr 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 and that from previous research, we infer the response of the larval rockfish species diversity and assemblage structure to CCA implementation and oceanographic dynamics.

2. MATERIALS AND METHODS

2.1. Data collection

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has regularly sampled and preserved ichthyoplankton in ethanol from 66 set stations, 4 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 are on the continental shelf in southern California, and 6 fall within the boundaries of the CCAs. CalCOFI uses 505 μm mesh bongo nets with a 0.71 m diameter towed obliquely from 210 m to the surface to collect ichthyoplankton samples, and CTDs to collect environmental data (temperature, dissolved oxygen concentration, salinity, and chlorophyll *a* [chl *a*]) (McClatchie 2014). Here we analyzed 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 *Sebastes 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 southern California (pygmy rock-

fish *S. wilsoni* genetic identification falls into a complex of 5 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) using adult rockfishes. Samples from 2003 were poorly preserved, mostly failed to sequence, and were 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 10 m² of sea surface area to the tow depth (Smith & Richardson 1977).

We compared rockfish dynamics inside versus outside the CCAs using a paired design; that is, for each of the 6 CalCOFI stations inside of the CCAs, we identified a paired site with similar environmental characteristics outside of the CCAs (Fig. 2). We chose paired sites by running a cluster analysis based on a Bray-Curtis dissimilarity matrix of the means of the oceanographic variables (temperature, dissolved oxygen content, salinity, and chl *a*) over the 16 yr time series, as well as station depth and percent cover of hard substrate. This paired design approach was first used, and thoroughly described, by Thompson et al. (2017) (see their supplemental methods).

We used environmental covariates (temperature, dissolved oxygen content, salinity, and chl *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. These covariates were previously shown to affect rockfish distribution and abundance, and are reasonably independent of each other ($r < 0.57$) (Thompson et al. 2016, Schroeder et al. 2019). For the statistical analyses, we scaled the years and environmental covariates by subtracting each value from the mean of that variable and dividing by the standard deviation.

2.2. Diversity

To assess spatiotemporal trends in larval rockfish species richness (the total number of species present at each site), and the effects of environmental covariates on such trends, we ran a series of generalized linear mixed-effects models (GLMMs) where richness was assumed to be Poisson distributed (log link function). We created a set of candidate baseline models in which

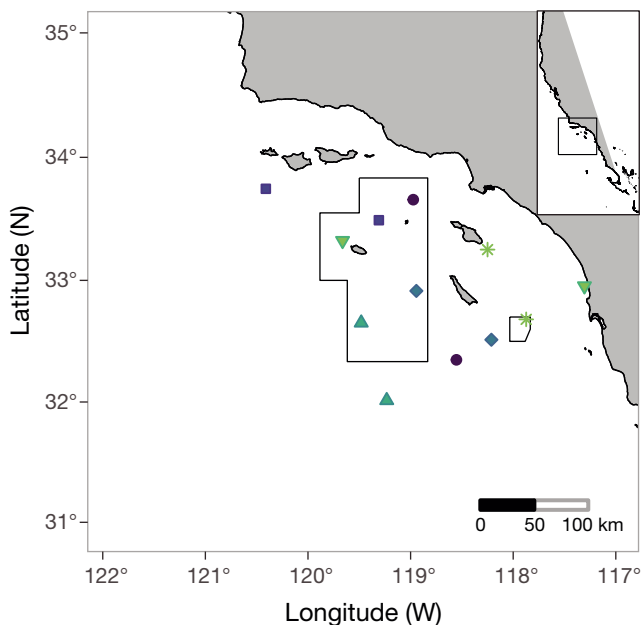


Fig. 2. Paired California Cooperative Oceanic Fisheries Investigations sample sites in the Southern California Bight. The Cowcod Conservation Areas are outlined in black. Paired sites match in shape and color

species richness was modeled against 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 model parsimony based on values of Akaike's information criterion corrected for small sample sizes (AICc). In the selected baseline model, larval 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 baseline model, we created a set of 15 candidate models with every combination of environmental covariates (temperature,

Table 1. Baseline model selection for generalized linear mixed-effects models. Values are rounded to 2 decimals; cca: Cowcod Conservation Area; AICc: Akaike's information criterion corrected for small sample size

Model	Formula	AICc	Δ AICc	AICc Weight
1	richness ~ year + cca + year × cca + (year pair)	896.70	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. Abbreviations as in Table 1

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 a	881.15	1.77	0.15
4	richness ~ year + cca + year×cca + (year pair) + temperature + salinity	881.40	2.01	0.13
5	richness ~ year + cca + year×cca + (year pair) + temperature + oxygen + salinity + chlorophyll a	882.45	3.07	0.08
6	richness ~ year + cca + year×cca + (year pair) + temperature + salinity + chlorophyll a	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 a	887.03	7.64	0.01

dissolved oxygen content, salinity, and chl *a*) added as fixed effects to the baseline model with the lowest AICc (Table 2). We again compared model parsimony based on AICc. This analysis was completed using R version 4.0.3, with the packages 'vegan,' 'tidyverse,' 'lme4,' and 'AICcmodavg' (Bates et al. 2015, Mazerolle 2019, Oksanen et al. 2019, Wickham et al. 2019, R Core Team 2020).

2.3. Assemblage structure

To visualize changes in the larval rockfish assemblage over time, we created a non-metric multidimensional scaling (NMDS) plot using ordination based on the Bray-Curtis dissimilarity index over 2 dimensions. We averaged the larval 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 larval assemblage structure after protection. This analysis was completed using R version 4.0.3, with the packages 'vegan,' 'tidyverse,' and 'reshape2' (Wickham 2007, Oksanen et al. 2019, Wickham et al. 2019, R Core Team 2020).

To assess the effects of the environmental covariates on larval 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 larval species abundances and environmental covariates by year inside and outside of the 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

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 Cowcod Conservation Area (cca) and listed environmental covariates. Values are rounded to 2 decimals. Abbreviations as in Table 1

Model	Formula	AICc	Δ AICc
1	y ~ cca + temperature + oxygen + salinity + chlorophyll a	1384.82	0
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

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. This analysis was completed using R version 4.0.3, with the packages 'gllvm,' 'vegan,' 'tidyverse,' 'AICcmodavg,' and 'reshape2' (Wickham 2007, Mazerolle 2019, Oksanen et al. 2019, Wickham et al. 2019, Niku et al. 2020, R Core Team 2020).

3. RESULTS

3.1. Diversity

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 the

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 effect, and oxygen, year, and CCA inclusion showed positive effects on larval species richness (Fig. 3). 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; Fig. 4). Counterfactual plots from the preferred model show that predicted species richness is highest inside the CCAs at the lowest and highest observed temperature and oxygen levels, respectively (Fig. 5). Furthermore, predicted species richness is lowest outside CCAs at the highest and lowest observed temperature and oxygen levels, respectively (Fig. 5).

3.2. Assemblage structure

The NMDS plot shows a distinct separation between the year groupings (Fig. 6). Vector loadings of historically targeted rockfishes (*Sebastes goodei*, *S. levis*, *S. mystinus*, *S. ovalis*, *S. paucispinis*, *S. rufus*, and *S. serranoides*) are all directed towards the years following CCA implementation.

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 (Fig. 7). 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 chl *a*, and the rest of the

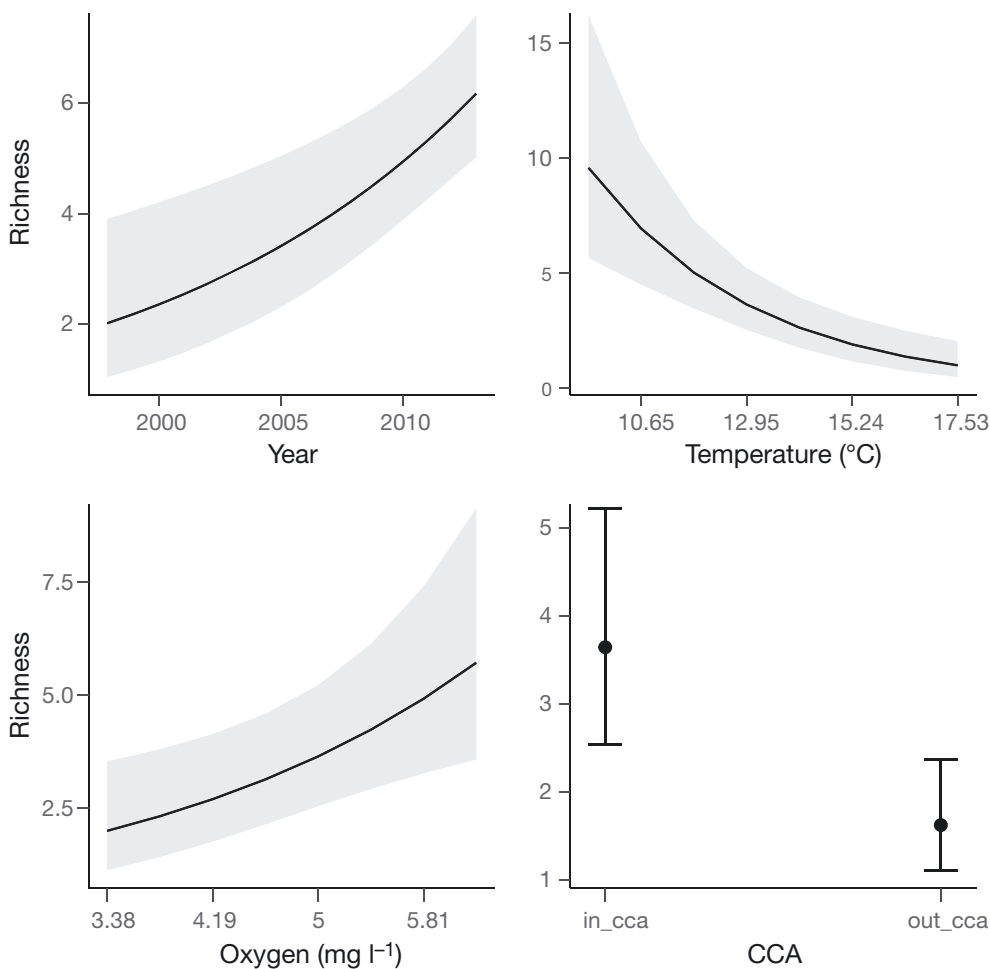


Fig. 3. Breakdowns of predicted richness values for the fixed effects of the preferred generalized linear mixed-effects model. For continuous variables (year, temperature, and oxygen), predictions (black line) are shown with 95% confidence intervals (grey shading). For discrete variables (CCA: Cowcod Conservation Area), predictions (black point) and 95% confidence interval (error bars) are shown

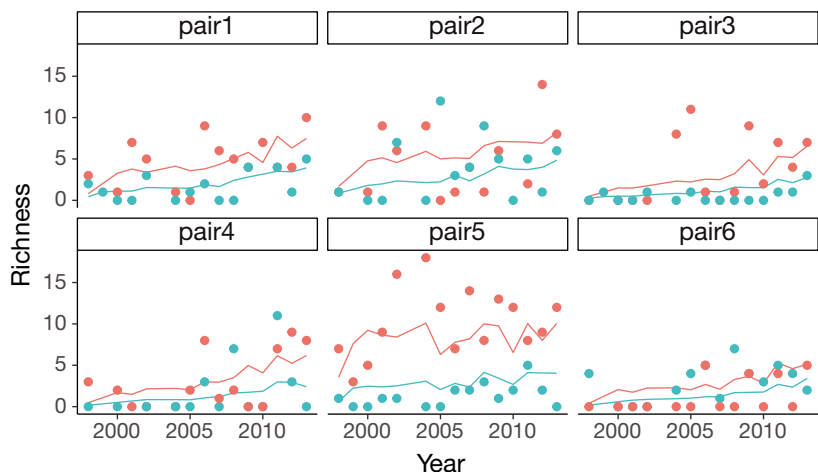


Fig. 4. Predicted larval rockfish species richness (lines) alongside observed larval rockfish species richness (points) for each site pair of the preferred generalized linear mixed-effects model. Lines and points show predicted and observed richness inside (red) and outside (blue) of the Cowcod Conservation Areas

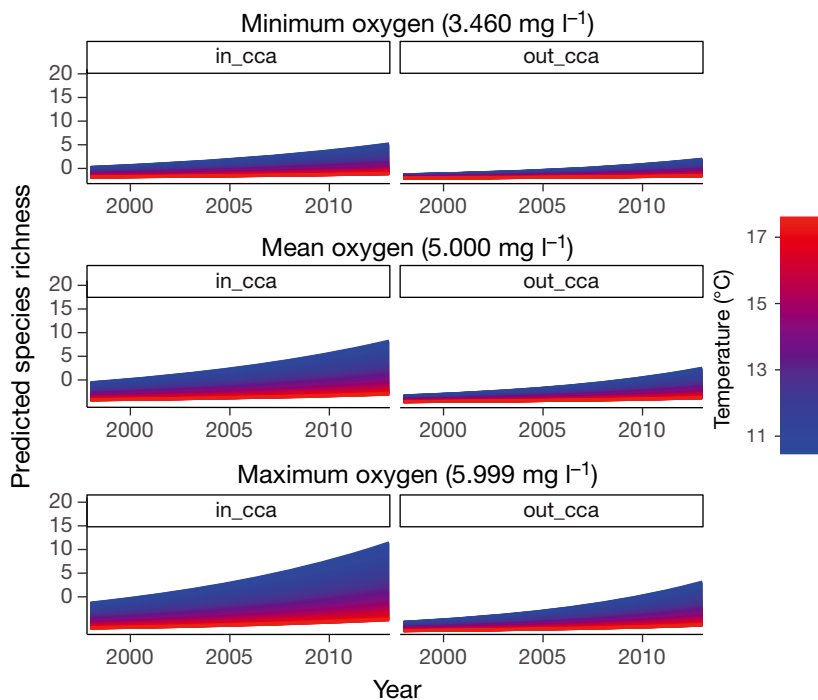


Fig. 5. Counterfactual plots of predicted richness for the preferred generalized linear mixed-effects model. Predicted richness is shown for varying temperatures and oxygen levels inside (in_cca) and outside (out_cca) of the Cowcod Conservation Areas. Temperature and oxygen levels range from the minimum to maximum values found in the data set

species overlapped with zero. Eight out of the 13 species abundances were positively related to CCA association; the other 5 species overlapped with zero (Fig. 7).

4. DISCUSSION

The diversity of larval rockfishes steadily increased between 1998 and 2013 in southern California. In addition, assemblage structure of larval rockfishes shifted from being dominated exclusively by short-lived, diminutive (extremely small) species to a mix of both diminutive species and long-lived apex predators. It is likely that the drivers of these dynamics are multifaceted and include protection from fishing, strong recruitment classes, and environmental conditions that were favorable for spawning.

4.1. Diversity

Larval richness was consistently higher and increased at a greater rate inside compared to outside CCAs. While the underlying mechanisms driving such increases in larval richness remain unclear, the IDH and the BOFFFF hypothesis may help contextualize the augmented larval richness observed within the CCAs through time. The cessation of fishing inside the CCAs removed a severe disturbance from rockfishes, particularly from the larger, slow-growing species that were the prime targets of fisheries (Thompson et al. 2017). According to the IDH, larger, slow-growing species are most likely to dwindle at high rates of disturbance, and removal of such disturbances may yield increased richness as those species recover (Connell 1978). If this is the case for rockfishes in the CCAs, the return and continued protection of these rockfishes may have led to an increase in the number of BOFFFFs within the CCAs. In comparison to younger females, older rockfishes produce more and higher-quality larvae (Love et al. 2002, Berkeley et al. 2004b, Sogard et al. 2008, Hixon et al. 2013, Stafford et al. 2014). These larvae with higher maternal investment then have an enhanced probability of growing faster and surviving

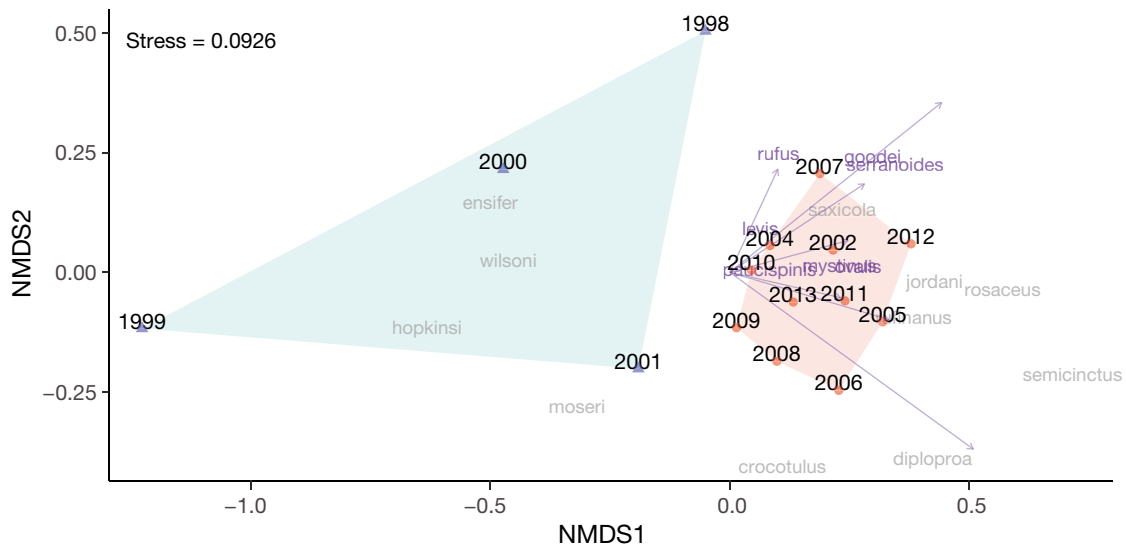


Fig. 6. Non-metric multidimensional scaling (NMDS) plot of larval rockfish (*Sebastes* spp.) abundances. Years are grouped before (blue) and after (red) Cowcod Conservation Area implementation. Species loadings are shown for historically targeted rockfishes (purple vectors). Untargeted and targeted species are labeled in grey and purple, respectively. We eliminated rare species (sum of yearly means <5) from the plot for visual clarity

to become recruits (Schroeder et al. 2019). Our finding that the difference in larval species richness between protected versus unprotected habitat was greater towards the end of the time series supports the idea that results are produced when protections are in place for longer time periods, and that locations where fish were more likely to survive to older ages produced more larvae and increased the odds of detecting formerly rare species (Love et al. 2002, Berkeley et al. 2004b, Alcalá et al. 2005, Sogard et al. 2008, Hixon et al. 2013, Stafford et al. 2014). Nonetheless, the mechanisms driving these changes in biodiversity remain unclear, and further studies are needed to fully elucidate these trends.

Studies conducted worldwide also demonstrate that mitigating fisheries disturbances with MPAs yields higher diversity. For example, MPAs exhibit higher and more stable fish diversity, ecological redundancy, and abundances of large-bodied fishes compared to partially protected and unprotected regions (Raymundo et al. 2009, Stelzenmüller et al. 2009, Bosch et al. 2022, Pettersen et al. 2022). Furthermore, long-term benefits of marine reserves on population structures, biomasses, and fisheries yields have been documented along the Great Barrier Reef (Russ et al. 1995, Russ & Alcalá 2004, Alcalá et al. 2005). Despite these findings, long-term studies directly linking protection to changes in fisheries biodiversity metrics are limited, and more research is needed to fully elucidate the effects of MPAs on biodiversity (García-Charton et al. 2008).

In addition to protection from fishing, favorable environmental variables positively correlated with larval rockfish diversity. The mixed-effects models suggest that larval richness is highest in years with colder and more oxygenated water. Temperature was the strongest driver of rockfish richness and was included in every model that had weight. Considering that 11 of the 15 years in our time series were cooler than average, consistently favorable environmental conditions in the SCB was likely a key factor in increasing larval rockfish species richness (Thompson et al. 2017). In the California Current Ecosystem (CCE) cooler, oxygenated waters are nutrient-rich and highly productive and can augment parental condition, larval survival, and recruitment (Moser et al. 2001, Schroeder et al. 2019). This 'minty' water (cooler, oxygenated, fresher water), which originates in the north and is transported south via the equatorward California Current, also induced higher abundance and diversity of young-of-the-year rockfishes (Sydeman et al. 2011, Ralston et al. 2013, Schroeder et al. 2019).

4.2. Assemblage structure

Between 1998 and 2001, the larval rockfish assemblage was characterized by relatively short-lived, diminutive species (e.g. *Sebastes ensifer*, *S. hopkinsi*, and *S. moseri*). By 2002, however, several larger-bodied, targeted (e.g. *S. paucispinis* and *S. rufus*) as

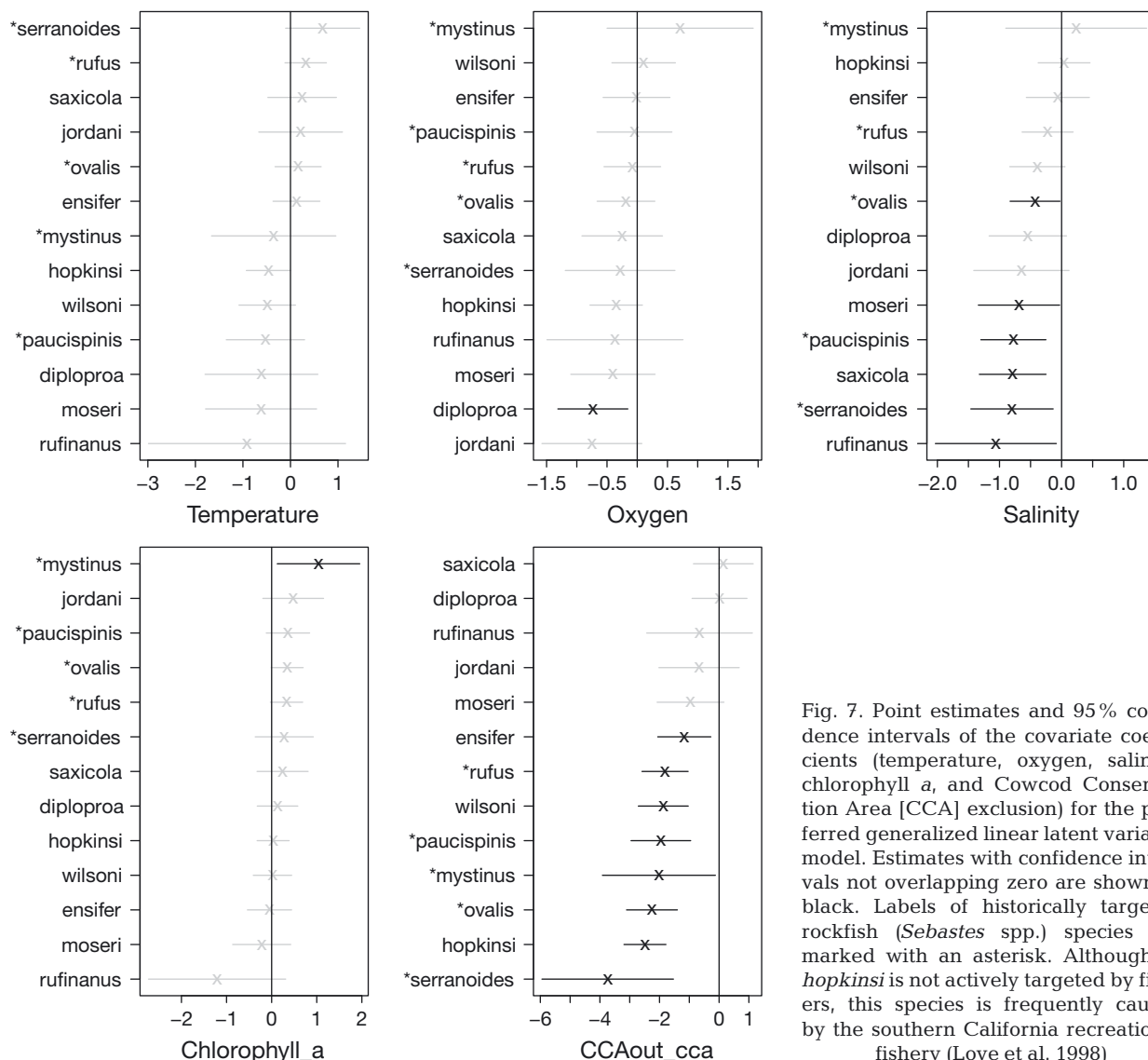


Fig. 7. Point estimates and 95% confidence intervals of the covariate coefficients (temperature, oxygen, salinity, chlorophyll *a*, and Cowcod Conservation Area [CCA] exclusion) for the preferred generalized linear latent variable model. Estimates with confidence intervals not overlapping zero are shown in black. Labels of historically targeted rockfish (*Sebastes* spp.) species are marked with an asterisk. Although *S. hopkinsi* is not actively targeted by fishers, this species is frequently caught by the southern California recreational fishery (Love et al. 1998)

well as diminutive untargeted rockfishes (*S. rosaceus*, *S. rufinanus*, and *S. diploproa*) came to define the larval assemblage. Given that the CCAs were implemented in 2001, the initial increase in the abundance of both targeted and untargeted species must have been driven by factors other than protection from fishing.

Rockfish spawning output is affected by the amount and age of adults and the environmental conditions experienced by potential parents (spawning output is reduced if adults are malnourished or otherwise stressed). The 2002 shift in larval assemblage structure was likely affected by both factors. Despite the profound differences in life histories of adult rockfishes, recruit abundance tends to be synchronous across nearly all species (Ralston et al.

2013). Rockfish recruitment was consistently low in the 1990s but rose to the highest level since 1988 in 1999 in southern California (Field et al. 2010). It is thus likely that the overall abundance of most rockfishes increased at the turn of the century, and that some species began spawning 3 yr later. In addition to the maturation of a strong recruitment class, there was a strong La Niña during and leading up to the 2002 winter spawning period. Productive La Niña years tend to provide optimal feeding conditions for adult rockfishes, and the abrupt change in larval assemblage composition in 2002 may have been influenced by high per capita fecundity (Ralston et al. 2013). Subsequent to 2002, strong rockfish recruitment classes in 2003, 2005, and 2009, as well as multiple cool, productive years further augmented

larval abundances in southern California (Field et al. 2010, Thompson et al. 2019).

While high recruitment and favorable environmental conditions affected larval rockfish abundances and assemblage structure, our results strongly suggest that the CCAs facilitated increases in rockfishes targeted by fishing. Indeed, larval abundances of all 6 targeted but only 2 of 7 non-targeted species were positively associated with the CCAs (Fig. 7). Previous analysis of the same data set also showed that rates of increase of larval abundances of 3 of 4 targeted but none of the 7 non-targeted species were significantly greater within than outside of the CCAs when controlling for habitat (Thompson et al. 2017). If fishing had continued at pre-CCA levels, the targeted species that contributed to the shift in larval assemblage structure beginning in 2002 would likely have been fished down and the assemblage may have been comprised mostly of diminutive species.

North of the SCB, several rockfish conservation areas (RCAs) were also established in the early 2000s to offset rockfish overfishing (Field et al. 2006). Similar to the CCAs, these RCAs have higher species richness, abundance, and mean lengths of rockfishes and other demersal fishes (Keller et al. 2014). It is likely that cessation of fishing pressure, high recruitment in previous years, and environmental conditions favorable to spawning contributed to the changes in larval rockfish diversity and assemblage structure over the past 2 decades.

4.3. The future

There are no records of rockfish diversity or assemblage composition prior to the onset of large-scale fishing in southern California, so we are unsure of what further changes to expect in the future. However, it is possible to speculate on coming trends in the condition of rockfish assemblages based on expectations illuminated through the lens of ecological theory. If significant, population-level effects of intergenera competition and predation and fishing protections in the CCA continue, then diversity dynamics may adhere to predictions of the IDH. At the beginning of the study, the rockfish assemblage was clearly depauperate due to more than a decade of recruitment failure and decades of intense fishing pressure. From 1998 to 2013, however, there was a steady increase in larval rockfish diversity and abundance of species targeted by fishing. Reduction of both environmental (low production) and anthropogenic (fishing) disturbance most likely caused this

pattern in a manner predicted by the IDH. As apex predator rockfishes return to pre-fishing levels, it is possible that they will outcompete the diminutive species for shared resources or directly consume the smaller species. The most common high trophic level rockfish in southern California, bocaccio *S. paucispinis*, is the fastest-growing rockfish between larval and young adult life stages, and this rapid growth is fueled by voracious piscivory (Field et al. 2010). Recently settled *S. paucispinis* primarily feed on other young of the year rockfishes such as *S. mystinus* and *S. goodei*, and adults continue to copiously feed on other rockfishes such as *S. jordani* (Field et al. 2010). Adult *S. paucispinis* reside primarily in mid-shelf (mean of 105 m depth), hard substrate habitat and share this region with at least 10 additional rockfish species (Love et al. 2009). It is conceivable that as populations of bocaccio and other piscivorous rockfishes such as *S. levis* and *S. rufus* increase in southern California, these apex predators will cull populations of the smaller rockfish, leading to a decrease of larvae from diminutive species and an overall reduction in rockfish diversity. It will be necessary to continue genetically identifying CalCOFI rockfish larvae to further elucidate patterns in diversity and assemblage structure.

Although the degree to which intra-genera competition and predation affect the larval rockfish assemblage is not clear, it is well known that cool, productive waters fuel primary production and augment both larval production and recruitment (Thompson et al. 2016, 2017, Schroeder et al. 2019). Subsequent to 2013, the west coast of North America experienced multiple, unprecedentedly large and long marine heatwaves (MHWs). The 2014–2016 Northeast Pacific MHW produced the warmest 3 yr period on record and was followed by 2 MHWs that were nearly as large in 2018 and 2019 (Jacox et al. 2018, Amaya et al. 2020, Fumo et al. 2020). Oceanographic modeling predicts that similar and even more extreme conditions than the recent North Pacific MHWs will become more common as oceans warm over the next 100 yr (Jacox et al. 2020, Gruber et al. 2021). Given the importance of cooler temperatures for maternal investment, larval abundances, and young-of-the-year recruitment, it is possible that environmental 'disturbances' to rockfish communities could increase in coming decades, leading to lowered larval diversity and abundances (Berkeley et al. 2004b, Sogard et al. 2008, Stafford et al. 2014). Indeed, rockfish recruitment and spawning output were both very low during the 1997–1998 El Niño that was the most recent warming event comparable

to the 2014–2016 MHW (Ralston et al. 2013, McClatchie et al. 2016)

In contrast to our expectation that rockfish recruitment and larval abundance would decrease during the warm conditions of 2014–2020, however, larval abundances were average to above average from 2014 to 2019 and recruitment from 2013 to 2016 was the highest ever recorded for several species (Schroeder et al. 2019, Thompson et al. 2019). The reason for this ecological surprise may be that although the CCE was very warm on average during the recent MHW, pockets of anomalously cool water originating from both the California Current and upwelling were prevalent throughout the CCE (Zaba et al. 2020, Thompson et al. 2022). In fact, the adult rockfishes were exposed to more cool, oxygenated, nutrient-rich subarctic water prior to spawning in 2013–2016 than almost all years from 1980 to 2012 (Schroeder et al. 2019). More broadly, MPAs evidently facilitate ecological resilience in a variety of ecosystems to climate-induced disturbances (Sandin et al. 2008, Micheli et al. 2012, Mellin et al. 2016, Roberts et al. 2017). One potential mechanism for this effect is the protection of large, highly fecund individuals within the bounds of the MPA, which may facilitate faster recovery following climatic stressors (Micheli et al. 2012). If a warming CCE is consistently associated with significant volumes of subsurface, cool water, then this novel oceanographic condition, alongside lasting protections offered by the CCAs, may mitigate deleterious effects of climate change on rockfishes.

4.4. Conclusion

We demonstrate that MPAs can positively influence larval fish diversity. We found increasing species richness of a taxonomically diverse genus of fishes following ecosystem protection for vulnerable species. While we do not know the natural state of the SCB rockfish assemblage, it appears the CCAs are aiding the recovery efforts of multiple species that are targets of fishing. More data are needed to fully evaluate the impacts of the CCAs on both rockfish diversity and assemblage structure. Although our study spanned 16 yr, many of the higher trophic level rockfishes in southern California can live 2 to 4 times the duration of our study. Continued sampling of the SCB and genetic identification of larval rockfishes would further elucidate the effects of protection measures and environment on larval diversity as the protected individuals age. Given that abun-

dances of many species were undoubtedly low at the initiation of our research, many of the adults in the system will continue to mature and increase spawning outputs over the subsequent decades. In addition, the ocean is changing more rapidly than ever, and there may be a secular impact of a warming environment. Continued monitoring will help us determine if the rockfish assemblage moves towards a steady state and, if so, the makeup of that state.

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