

The Effect of Marine Protected Areas on the Fine-Scale Depth Segregation of two Rockfish (*Sebastes*) Species

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Introduction

Over the last century, commercial harvest of groundfish off California's coast has accelerated due to advancements in fishing technology and increased demand (Miller *et al.*, 2014). The persistence of fishing pressure along the California coast has decreased species biomass and abundance of nearshore fisheries (Hamilton *et al.*, 2010). The Marine Life Protection Act was passed in 1999 and founded a network of Marine Protected Areas (MPAs) in an effort to offset the adverse effects of human activity in nearshore marine ecosystems. The first portion of the California MPA network was established in September of 2007 with the creation of 29 marine reserves across the state. These reserves were designed to preserve the natural biodiversity of marine ecosystems, function as a network, and to sustain important fishery populations, as well as to provide undisturbed areas for emerging scientific research and recreational enjoyment (Saarman *et al.*, 2013). Long-term monitoring conducted within MPAs and adjacent reference (REF) areas promotes better scientific understanding of the community dynamics of socioeconomically valuable species like rockfishes.

Rockfish are a broad taxonomic group in the genus *Sebastes*, including 62 species common to the California coastal region (Love & Yoklavich, 2002). These fishes tend to be long lived and slow to mature, often taking 5-11 years to reach reproductive maturity (Echevarria, 1987). They reproduce via internal fertilization, vivipary, and a pelagic larval stage (Love & Yoklavich, 2002). Specific environmental conditions and food availability are required for successful recruitment to occur, which can result in variable reproductive success (Love & Yoklavich, 2002). This trait, combined with their slow growth and late maturity makes them susceptible to overfishing. As such, they often respond well to MPA protection (e.g., Hamilton et al 2010). Safeguarding these populations is not only essential to protecting local biodiversity, but is of vital importance to the sustainable management of rockfish, which support a large commercial and recreational fishery on the US West Coast.

Gopher rockfish (*Sebastes carnatus*) and Black and Yellow rockfish (*Sebastes chrysomelas*) are sympatric species that inhabit rocky reefs along the entirety of the California coast. Over the last decade, commercial harvest of these species has continually increased, and

they have remained two of the top rockfish harvested both commercially and recreationally (Final California commercial landings). The two species are quite similar morphologically and genetically; differences in adult coloration are the primary field identification method (Narum *et al.*, 2004). Both are demersal fish that typically occupy a limited home range due to their solitary nature (Larson, 1972). There is substantial overlap in each species' diet, both mainly feeding on an array of crustaceans and small fishes (Hallacher & Roberts, 1985). They are known to separate spatially over small scales, with *S. chrysomelas* occupying shallower depths than *S. carnatus* (Hallacher & Roberts, 1985). Since these species occupy the same intermediate trophic level, spatial depth segregation may allow these species to coexist through resource partitioning (Hallacher & Roberts, 1985; Roughgarden, 1976).

Previous work investigated the factors that contribute to this interspecific competition and spatial separation by exploring social dominance and through removal experiments (Larson, 1980). Social dominance was an important interaction between *S. chrysomelas* and *S. carnatus*; *S. chrysomelas* were more aggressive when defending their home territory and generally succeeded in displacing *S. carnatus* (Larson, 1977). During removal experiments, both species expanded their depth range in the absence of their competitor which was typified by *S. carnatus* moving rapidly into shallower areas. By contrast, the range expansion of *S. chrysomelas* into deeper water was slower and less extensive (Larson, 1977). Although this study provides insight on the mechanisms that influence these species' close ecological relationships, it is unknown how MPA protection might influence or alter these patterns.

The California Collaborative Fisheries Research Program (CCFRP) is a long-term monitoring program that was established in conjunction with MPAs to monitor their effects on nearshore fish populations by utilizing an integrative approach to data collection through collaboration between scientists and local anglers. This strategy is an effective method to assess the resilience of MPAs and collect valuable data for stock assessments (Wendt & Starr, 2009, Yochum *et al.* 2011). The data used in this study were collected by CCFRP during a standardized fish trapping study which provided a unique opportunity to obtain data on species composition and the discrete depth at which individuals were caught. This is particularly important for species like *S. carnatus* and *S. chrysomelas* which appear to vary in their competitive abilities along a depth gradient.

Data have shown that relative abundance and biomass of many species in these protected areas have increased following the establishment of MPAs in California (Hamilton *et al.*, 2010; (White *et al.*, 2021; Lester *et al.*, 2009). With this in mind, we investigated whether the relative abundance of *S. carnatus* and *S. chrysomelas* increased over time within MPAs in contrast to REF areas. This information is important because the presence of one *Sebastes* species directly influences the others' depth distribution (Larson, 1977). However, the two species may interact differently in the absence of fishing pressure. As the population density rises in protected areas, there may be an associated increase in competition for food (Loury *et al.*, 2015). Subsequently, we expect that *S. chrysomelas* may become more aggressive in defending their preferred shallow habitat. These shallow water areas are highly desirable due to greater prey density caused by increased sunlight and nutrient availability. This stimulates robust primary productivity and supports organisms that *S. carnatus* and *S. chrysomelas* prey upon (Huyer, 1983).

This study compares depth distributions for both species between MPAs and reference areas to evaluate how these species respond to changes in overall species abundance and heightened competition. Specifically, this study investigates whether changes in fine-scale depth range were detected over time in two similar rockfish species with and without fishing pressure

using a standardized fish trap study. These data will help us understand the complex competitive dynamics between similar nearshore species and provide information for better nearshore management in the context of MPAs.

Methods

Study Area

The data used in this study were collected from the White Rock MPA in San Luis Obispo County during the Summer and Fall of 2008 and 2015. These data were part of a standardized trapping project conducted by CCFRP (Rasmussen 2010). The White Rock MPA is 7.53 square kilometers and restricts all commercial and recreational take from its waters. The adjacent REF areas are similar in environmental conditions and habitat. MPA and REF areas both contain multiple sampling cells, which were created to be 500m x 500m. Random stratified sampling was used when selecting cells. On average, four cells were selected to be sampled in either the MPA or REF areas and accessed by fishing vessels. Once at the location, general environmental conditions (e.g., swell, wind, temperature) were recorded. Every set contained 10 commercial fishing traps placed in a line with the specific depth of each trap recorded. Individual traps soaked in the water for approximately one hour before being retrieved. Fishes that were caught were identified to the species level and enumerated.

Analysis of Relative Abundance

We used R for all data processing, including packages devtools, plotrix, glmmTMB, MASS, and tidyverse. We investigated the changes in relative abundance for each species between areas over time by using the metric catch per unit effort (CPUE). CPUE was calculated as the number of fishes caught per set hour. To minimize zero-inflation, CPUE values were calculated at the set level rather than the trap level. However, at the set level there were still many occasions where species of interest were not caught. Since the data were right skewed, a more robust parametric test could not be used. A zero-inflated negative binomial model was used on each species to test the fixed effects of year and area and the random effect of cell ID on CPUE. We utilized a Broyden-Fletcher-Goldfarb-Shanno optimizer for *S. chrysomelas* because they were caught less often than *S. carnatus*.

A logistic regression was used to analyze the variation of presence across depth for each species. The presence or absence of a species in each trap served as the binary response variable. This model predicted the log odds of catching each species over a continuous depth from 10 ft to 80 ft, between areas, across years, and for their interaction.

Species Depth Distributions

The standardized measurement of Catch Per Unit Effort (CPUE) was used to estimate relative abundance of each species at numerous depths. CPUE was calculated at the trap level and quantified as the number of fish caught per trap hour. Traps were set at discrete depths from 10 ft to 80 ft. Depths were binned into 10 ft increments across the entire range sampled. Binning depths provided a way to visualize how CPUE changes with depth. The mean trap CPUE was then calculated for each depth bin along with the standard error. We created two separate plots

to compare both years and areas, one for *S. chrysomelas* and one for *S. carnatus*, that allow us to visualize which species was more abundant within each depth bin and where these species overlapped in occurrence.

To visualize which species had a higher CPUE at each depth bin, a ratio of *S. carnatus* CPUE over *S. chrysomelas* CPUE ratio was computed for each depth bin. A natural log transformation was done on the CPUE ratio values to reduce the extreme differences in the untransformed CPUE values. Values greater than zero indicated that *S. carnatus* were more abundant at that depth and values less than zero indicated *S. chrysomelas* were more abundant. This helped to detect if there was a change in which species were more dominant at various depths.

Results

Analysis of Relative Abundance

S. chrysomelas had a significantly lower Catch Per Unit Effort (CPUE) in the MPA during 2015 when compared with 2008 at the 0.1 alpha level ($p = 0.069$). However, *S. chrysomelas* did not have a significantly different CPUE in REF sites between 2008 and 2015 (Fig 1). *S. carnatus* had similar CPUE values between areas for both years sampled (Fig 2). Though no significance was detected, we noticed a general pattern of decline in CPUE in the MPA and REF sites over time for *S. carnatus*.

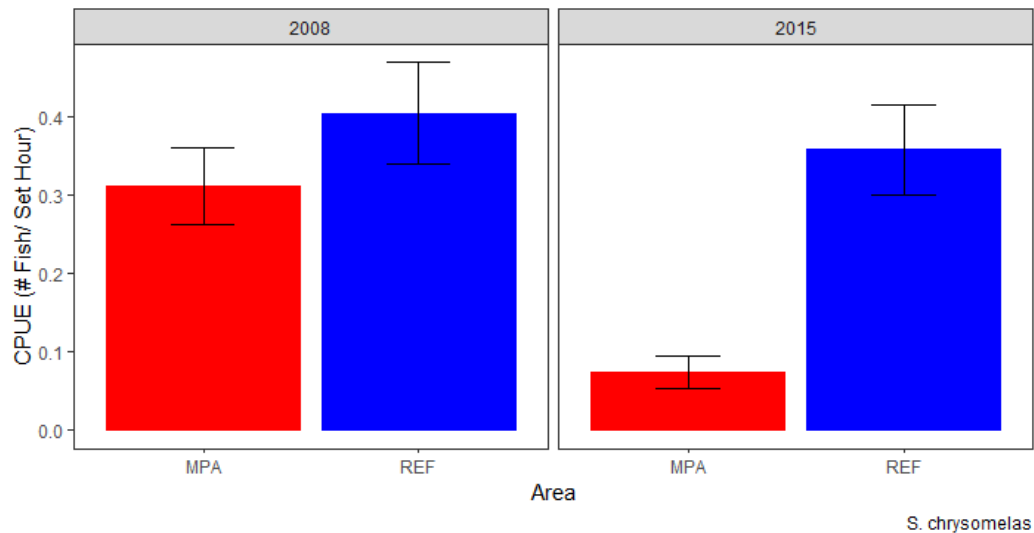


Fig 1. Comparison of *S. Chrysomelas* CPUE between MPAs and REF areas over time from 2008 to 2015. CPUE represents how many fish caught per set hour and is shown on the y-axis. The area is denoted on the x-axis and each panel shows a different year. Bars show the mean CPUE and error bars are one standard error from the mean.

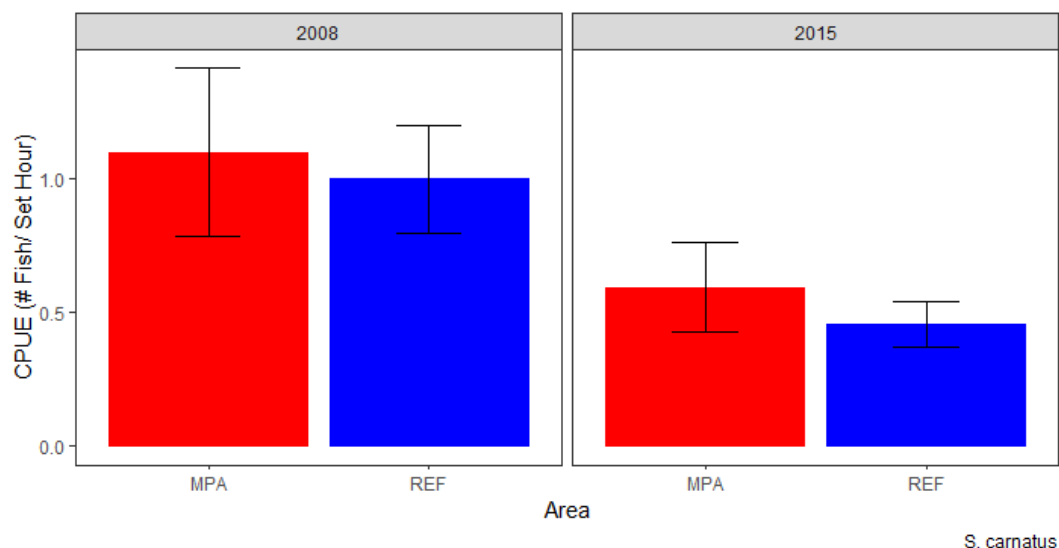


Fig 2. Comparison of *S. Carnatus* CPUE between MPAs and reference areas over time from 2008 to 2015. CPUE represents how many fish caught per set hour and is shown on the x-axis. The area is denoted on the y-axis and each panel shows a different year. Bars show the mean CPUE and error bars are one standard error from the mean.

Species Presence Analysis

A logistic regression was used to show the likelihood of species presence over the study depth using year and area as predictors. For *S. chrysomelas*, depth was a significant predictor of presence ($p < 0.001$). As depth increased, the probability of catching *S. chrysomelas* declined, suggesting that *S. chrysomelas* predominantly inhabit shallower waters. Area was a significant predictor of *S. chrysomelas* ($p < 0.001$) with a higher probability of *S. chrysomelas* presence in REF areas over the depths sampled. In 2015, there was a significantly lower likelihood of catching *S. chrysomelas* across all depths ($p < 0.001$). It is important to note that the data for *S. chrysomelas* do not fit the logistic regression well because this species was frequently not caught across all depths. Depth and year were both significant predictors of *S. carnatus* presence at the 0.1 alpha level (depth $p < 0.001$; year $p < 0.001$). As depth increased, the probability of catching *S. carnatus* increased; the probability of catching *S. carnatus* was higher in 2008 than 2015 at each depth sampled.

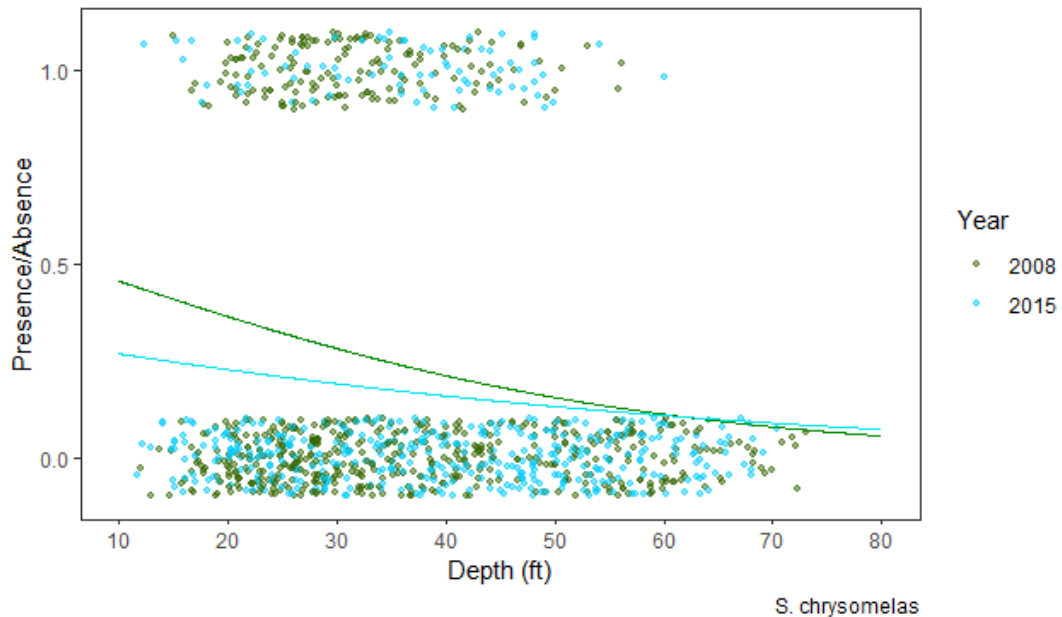


Fig 3. A logistic regression assessing the probability of capturing *S. chrysomelas* in a trap at continuous depths from 10 ft - 80 ft. The lines represent the logistic regression model and are colored to differentiate between the years sampled. Dots represent individual traps and are jittered around 1 indicating traps that caught *S. chrysomelas* and dots at 0 indicate traps that did not catch *S. chrysomelas*. 2008 had a significantly higher probability ($p = 1.23 \times 10^{-5}$) of capturing *S. chrysomelas* than 2015. Depth was a significant predictor of the probability ($p = 1.51 \times 10^{-11}$) of catching *S. chrysomelas*.

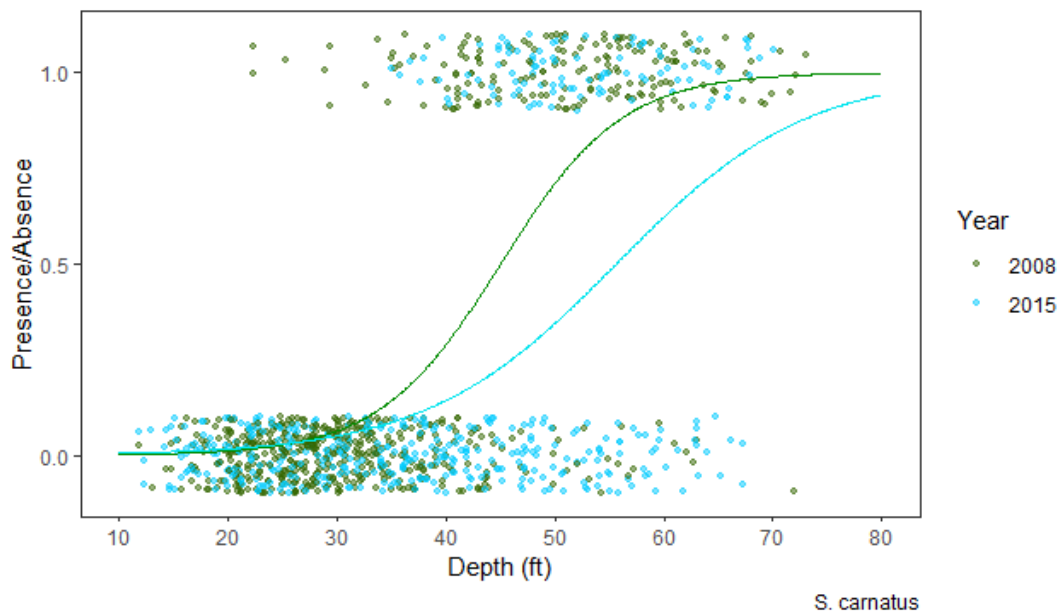


Fig 4. A logistic regression assessing the probability of capturing *S. carnatus* in a trap at continuous depths from 10 ft - 80 ft. The lines represent the logistic regression model and are colored to show years sampled. Dots represent individual traps and are jittered around 1 indicating traps that caught *S. carnatus* and dots at 0 indicate traps that did not catch *S. carnatus*. Year was a significant predictor of *S. carnatus* presence ($p = 9.95 \times 10^{-5}$) There was a significantly higher likelihood of catching *S. carnatus* with increasing depth ($p = 2.00 \times 10^{-16}$).

Species Depth Distributions

We examined the depth distributions of each species within their established range to explore how abundance at various depths may have changed over time. The depth range and distribution patterns between 2008 and 2015 were similar for *S. chrysomelas* in the REF areas, with depth ranges from 15 ft bin to 55 ft bin. Depth ranges were condensed to 15 ft - 45 ft in the MPA. Abundance in both areas was concentrated around the 25 ft - 35 ft depth bins (Fig 5.). The only notable difference is that CPUE across various depths is lower in the MPAs for both years, especially in 2015 which was noted earlier (Fig 1.). Similarly, the depth range and distribution patterns for *S. carnatus* remain consistent between years with individuals occupying depths from 35 ft to 65ft and a peak in abundance around 55 ft - 65 ft (Fig 6.). There is a noticeable decline in CPUE for both areas in 2015 as previously shown (Fig 2).

The log transformed ratio of *S. carnatus* CPUE to *S. chrysomelas* CPUE indicates which species has higher relative abundance at each discrete depth bin. In the MPA and REF in 2008 and the REF area in 2015, *S. chrysomelas* had higher relative abundance in the 15 to 35 ft depth bins and *S. carnatus* had higher relative abundance from 35 ft to 65 ft (Fig 7.) The only divergence from this trend is in the 2015 MPA, where dominant relative abundance switches from *S. chrysomelas* to *S. carnatus*.

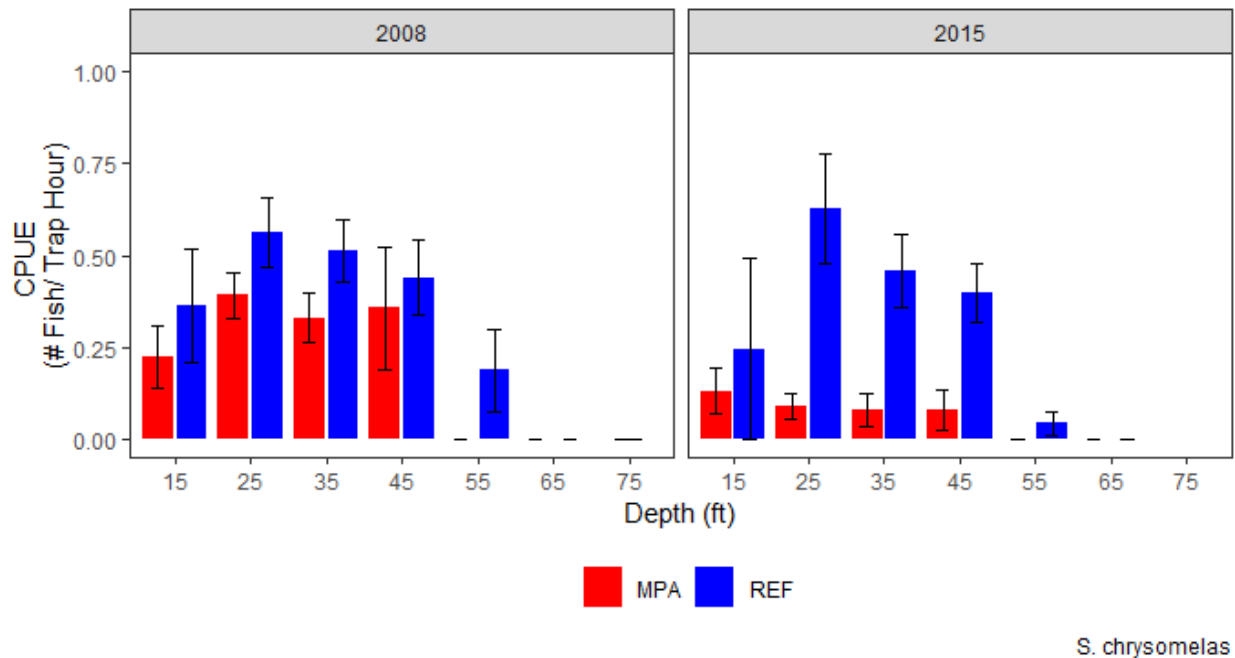
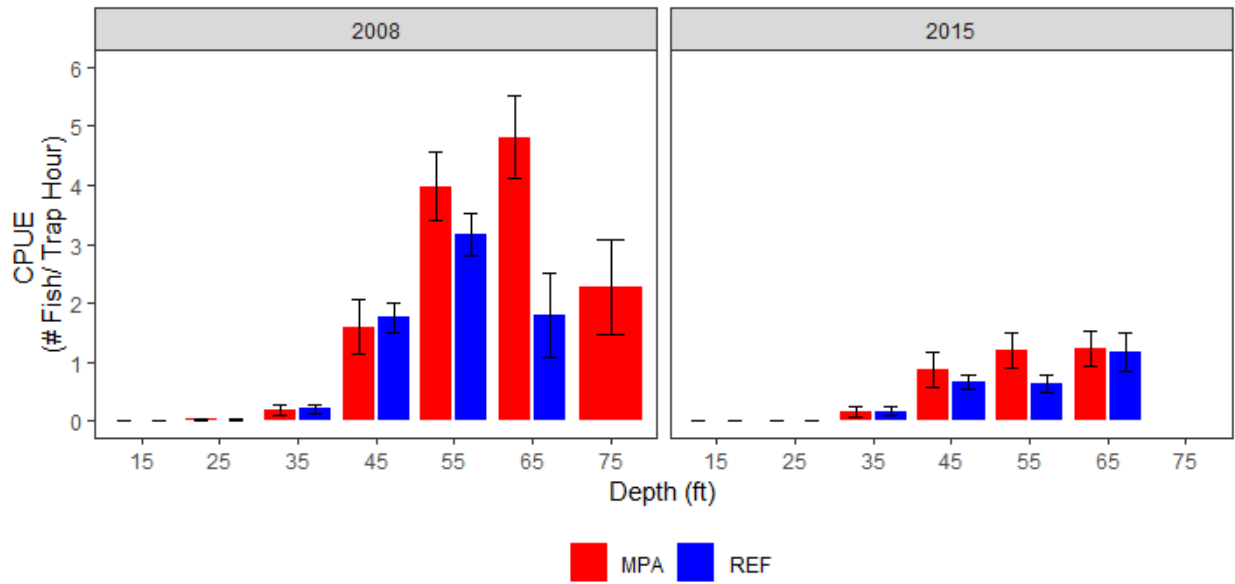


Fig 5. Depth distributions of *S. chrysomelas* within MPAs and REF areas over time. Discrete depths were binned into 10 ft increments. CPUE was calculated as the number of fish caught per trap hour. Depth ranged from 15 ft - 55 ft in REF areas and had a more condensed range in MPAs from 15 ft - 45 ft. REF areas had consistently higher CPUE for both years. Peak abundance was centered around 25 ft - 35 ft.



S. carnatus

Fig 6. Depth distributions of *S. carnatus* within MPAs and REF areas over time. Discrete depths were binned into 10 ft increments. CPUE was calculated as the number of fish caught per trap hour. In both areas and years *S. carnatus* occupied the same depth range of 35 ft - 65 ft except in the 2008 MPA where *S. carnatus* was found in the 75 ft depth bin. Abundance was concentrated around 55 ft - 65 ft across areas and years.

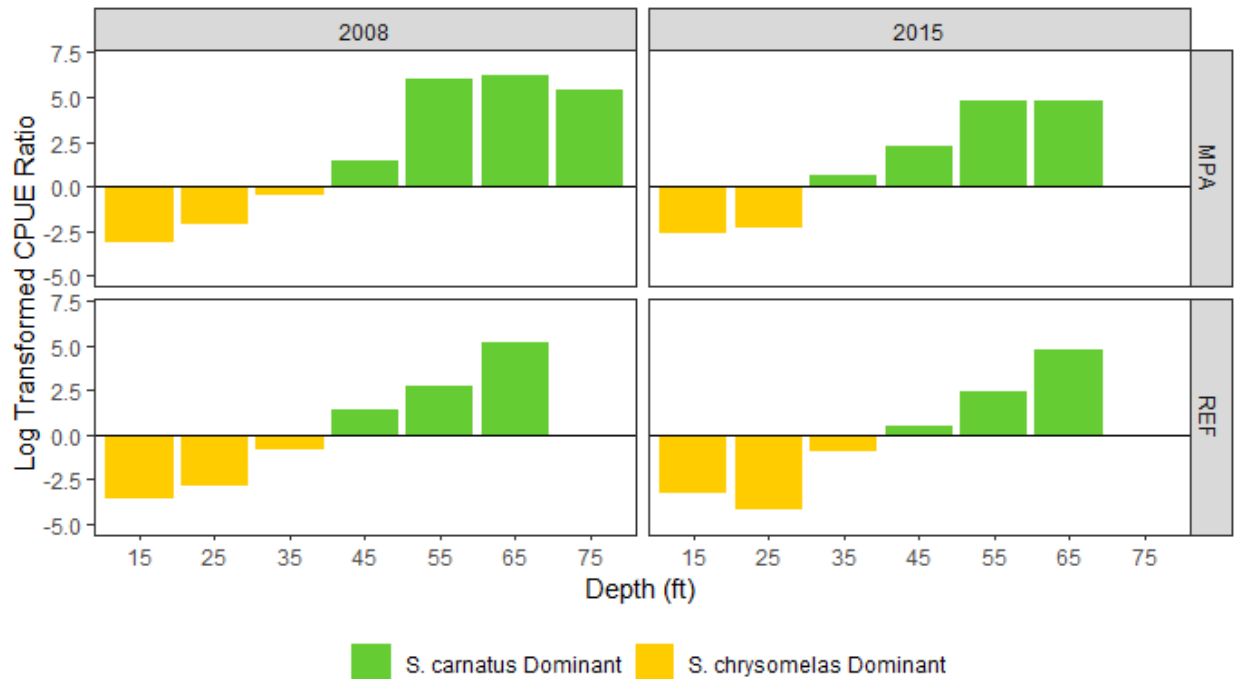


Fig 7. CPUE ratio for *S. chrysomelas* and *S. carnatus* over increasing depth in the MPA and REF areas between years. The y-axis is the log transformed ratio of *S. Carnatus* CPUE to *S. Chrysomelas* CPUE. When values are greater than 0, *S. carnatus* has a higher CPUE and when values are less than 0, *S. chrysomelas* has a higher CPUE. *S. Chrysomelas* have a higher CPUE than *S. carnatus* in the depth bins 15 ft - 35 ft except in the 2015 MPA when *S. Carnatus* has a higher CPUE in bin 35 ft. *S. Carnatus* have a higher CPUE in depth bins 45 ft - 65 ft consistently.

Discussion

The overall takeaways from this analysis are that *S. chrysomelas* and *S. carnatus* appear to occupy distinctly different depth ranges. Each species' depth distributions hold a consistent pattern regardless of area or year. The relative abundance of each species, regardless of area, did seem to decline in 2015, but was only statistically significant in the MPA for *S. chrysomelas*. There is evidence that suggests MPAs typically increase the relative abundance of many targeted fish species (Hamilton *et al.*, 2010; Lester *et al.*, 2009), suggesting that MPA protections may allow exploited populations to recover; however, this was not true for either *Sebastes* species in this study.

This general decline in relative abundance was observed amidst one of the most intense marine heat waves (MHW) to date that lasted from 2013-2015 (Cheung & Frölicher, 2020). Marine heat waves are anomalous warm water events that are becoming more frequent and extreme due to anthropogenic climate change (Hobday *et al.*, 2016). MHWs can have drastic effects on upwelling systems, primary production, and fisheries (Brodeur *et al.*, 2019; Cavole *et al.*, 2016; Cheung & Frölicher, 2020). During these warm water events, thermal stratification increases and reduces the mixing of cool, nutrient rich waters into the euphotic zone (Zaba & Rudnick, 2016). Under stratified conditions, less nutrients are available for primary producers and phytoplankton communities are dominated by smaller species (Largier *et al.*, 2006). This reduction in phytoplankton biomass results in a corresponding decline in copepod and euphausiid biomass (Brodeur *et al.*, 2019; Leising *et al.*, 2015). These macrozooplankton form the foundation of the marine food web and declines during the MHW may have caused less energy to be available for higher trophic levels. Previous research has shown that there has been a corresponding decline in fish biomass for some species during MHWs (Cheung & Frölicher, 2020). A reduction in food availability due to large scale oceanographic events may be a possible bottom-up explanation for the decrease in relative abundance of *S. carnatus* and *S. chrysomelas* over time.

Along with oceanographic effects, there appears to likely be additional factors influencing the drastic decline in CPUE for *S. chrysomelas* within the MPA during 2015. Two possible explanations for this rapid change in CPUE are top-down control by fish predators within MPAs and differences in relative abundance of the two species. Increased abundance of top fish predators in the absence of fishing pressure may have led to a decreased abundance of intermediate trophic level predators such as *S. carnatus* and *S. chrysomelas* within MPAs (Britten *et al.*, 2014; Estes *et al.*, 2011). A study has shown that targeted species in the California Channel Islands MPAs have had increased relative abundance and doubled the total biomass of top fish predators within reserves as compared to outside (Hamilton *et al.*, 2010). Many of these targeted species are predators of *S. carnatus* and *S. chrysomelas*. It is likely that these two species experience increased predation and stronger top-down control within these protected ecosystems (E & M, 1996; Shears & Babcock, 2002). One of the main predators of *Sebastes spp.* are Lingcod, *Ophiodon elongatus*; *O. elongatus* populations are increasing along the US West coast, especially within MPAs (Jagiello and Wallace, 2005; Beaudreau & Essington, 2007). In one study, *O. elongatus* predation on *Sebastes spp.* was several times greater in MPAs compared to outside (Beaudreau & Essington, 2007). The second potential explanation for the marked decline of *S. chrysomelas* in 2015 is the differential abundance between these species. According

to CDFW, commercial landings in the Morro Bay area for *S. carnatus* were two times greater than *S. chrysomelas* in 2008 and 2.5 times greater in 2015 (Final California commercial landings). *S. carnatus* CPUE remained higher than *S. chrysomelas* for all years and areas; therefore, even if both species are preyed upon at the same rate, the decline of CPUE will be more noticeable for *S. chrysomelas*.

Understanding changes in relative abundance is necessary because the presence of one *Sebastes* species will affect the depth distribution of the other *Sebastes* species (Larson, 1980). We expected an increase in species abundance and competition in MPAs to force *S. carnatus* to contract their depth range. However, in the 2015 MPA, *S. carnatus* did appear to move into shallower water, although further research would be necessary to confirm this trend. Two possible explanations are that increased competition forced *S. chrysomelas* to move into new feeding grounds or that *S. chrysomelas* were less abundant allowing *S. carnatus* to take advantage of this open space and expand their range to shallower habitat. The latter is more likely because *S. chrysomelas* are more socially dominant (Larson, 1980). It may be that the drastic decline in *S. chrysomelas* CPUE in the MPA during 2015 allowed for *S. carnatus* to move into their preferred shallower habitat (Larson, 1977).

Overall, *S. chrysomelas* occupied a distinct depth range in shallower waters whereas *S. carnatus* occupied deeper waters which confirms findings from previous work. Throughout time, the depth distributions for both of these species remained relatively consistent, with the exception of *S. carnatus* moving shallower in the 2015 MPA. This may be preliminary evidence of a shift in the habitat range of *S. carnatus*. During 2015, the studied MPA was only eight years old; many MPA effects take time to observe and updated trapping data is necessary to investigate how abundance has changed over the subsequent years.

The California MPA network has become an integral part of conservation efforts for nearshore marine ecosystems. Understanding the dynamic relationships of similar *Sebastes* species over time is necessary to adapt to more effective management strategies for these economically important species. Collecting fishery-independent trapping data and analyzing the influence of oceanographic events and MPAs on the competitive dynamics of *S. carnatus* and *S. chrysomelas* will help to better grasp these complex ecological relationships

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