

EVALUATING RELATIVE ABUNDANCE, FISH LENGTH, AND MARINE
PROTECTED AREA EFFECTIVENESS FOR FOUR KEY ROCKY REEF SPECIES
ALONG THE NORTHERN CALIFORNIA COAST

By

Leon Davis

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Committee Membership

Dr. Andre Buchheister, Committee Chair

Dr. Timothy Mulligan, Committee Chair

Dr. Joseph Tyburczy, Committee Member

Dr. Jose R. Marin Jarrin, Committee Member

Dr. Erin Kelly, Graduate Coordinator

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ABSTRACT

EVALUATING RELATIVE ABUNDANCE, FISH LENGTH, AND MARINE PROTECTED AREA EFFECTIVENESS FOR FOUR KEY ROCKY REEF SPECIES ALONG THE NORTHERN CALIFORNIA COAST

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Marine protected areas (MPAs) were created with the purpose of helping conserve and restore diminished populations of marine organisms. Measuring the effectiveness of MPAs requires long-term monitoring, investigating the abundance and size distributions of the species that utilize the conservation areas, and comparing the results to neighboring reference sites that are not currently protected. In this study, observations from long-term MPA monitoring in northern California (2010-2019) were modeled with substrate, oceanographic, spatial, temporal, and body size variables to describe the variability in abundance and size of three fish groups: Black rockfish (*Sebastes melanops*), the Blue rockfish group (comprised of Blue rockfish (*Sebastes mystinus*) and Deacon rockfish (*Sebastes diaconus*)), and Lingcod (*Ophiodon elongatus*). Models were also used to explain the differences in the abundance and size associated with protection status (MPA vs. reference). The data consisted of two MPAs and their paired reference sites (accessed from the ports of Eureka and Fort Bragg, CA), and another set of two auxiliary reference sites north of Trinidad, CA that were not paired with an MPA. Lagged oceanographic covariates had strong relationships with relative abundance of Black rockfish and illustrated the importance of upwelling as a long-lasting driver of adult relative abundance. Lagged oceanographic effects could be products of the

long-term effects that upwelling has on recruitment. Substrate covariates and distance to port played an important role in describing the variability in relative abundance and length of the species, while substantiating previous studies. Weak, but detectable, effects of protection status on abundances of lingcod and lengths of all species were also found. The presence of detectable signals indicates that the MPAs within this study are beginning to positively influence abundances and lengths of the fish that reside within them, further supporting their utility and functionality as tools of conservation that can be used by fisheries managers. This study adds general information and critical insight into the population dynamics, environmental drivers, and management effectiveness of the species studied, along the California North Coast.

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INTRODUCTION

In northern California, Rockfish (*Sebastes spp.*) and Greenling (*Hexagramidae*) are the primary species that make up the nearshore fishery (Rosales-Casian and Gonzalez-Camacho, 2004). Rockfish catch composition in the nearshore fishery on the California North Coast is dominated by Black rockfish (*Sebastes melanops*) and Blue rockfish (*Sebastes mystinus*), while Lingcod (*Ophiodon elongatus*) are the most highly targeted greenling species (Schroeder and Love, 2002; Rosales-Casian and Gonzalez-Camacho, 2004). The Rockfish (*Sebastes spp.*), Cabezon (*Scorpaenichthys marmoratus*), and Greenling (*Hexagrammus spp.*) complex (RCG complex) is an important resource to both commercial and recreational fisheries. Historical fishing pressure on the RCG complex has remained steady, since the 1990's, but catch rates have decreased indicating a reduction in abundances and spawning population sizes in the California Current System (Love et al, 1998; PFMC, 2005; Cope et al, 2016; Cope et al, 2019). Nearshore rocky reef fish are typically longer-lived species that mature late in life, making them susceptible to overfishing (Bobko and Berkley, 2004). Increased fishing pressure and increases in the occurrence of climate anomalies, such as marine heatwaves and El Nino events, may further increase the susceptibility of Pacific Rockfishes to declines in abundance (Cheung and Frölicher, 2020). The susceptibility of Rockfish and Lingcod to deleterious environmental conditions and fishing pressure requires them to be studied more deeply. This study has therefore chosen 3 Rockfish species and Lingcod for further evaluation.

Species of Interest

Black rockfish range from Alaska to southern California inhabiting spaces and crevices between rocks along rocky reef formations along the coast to depths >300 m but they are more commonly found within shallower waters <50 m (Miller and Shanks, 2004). As a long-lived (30+ years) and late maturing (6 years) species, Black rockfish are susceptible to overfishing (Bobko and Berkley, 2004). Black rockfish are livebearers, releasing pelagic larvae into the water column where they reside in the epipelagic zone. Currents subsequently carry pelagic juveniles inshore to estuaries where they settle over eelgrass, kelp beds, and, mainly, the rocky intertidal. Juveniles inhabit nearshore estuaries and intertidal areas until about 60 mm total length (TL) then move offshore to nearshore rocky reefs and outcroppings, inhabiting these areas into adulthood (Pastén, 2003).

Blue rockfish are typically found in large schools inhabiting the areas above and surrounding rocky reefs from the surface to 90 m in depth (Laidig et al., 2003). This pelagic lifestyle coincides with more moderate migratory patterns; unlike many rockfish species, they do not display strong site fidelity but instead are more mobile and inhabit areas over many different reefs. Blue rockfish range from Baja, Mexico, to Alaska, USA, inhabiting depths to >200 m. Blue rockfish have long lifespans exceeding 40 years (Laidig et. al, 2003), with maturation occurring at 5 or 6 years (Echeverria, 1987). Blue rockfish are also live-bearing, pelagic spawners whose planktonic larvae are carried inshore into the rocky intertidal and kelp beds. Juvenile settlement occurs in May for fish in central California and in June for fish in Northern California (Laidig, 2010). Similar to Black rockfish, Blue rockfish juveniles leave the nursery grounds to inhabit rocky reefs

and outcroppings as sub-adults and adults. Deacon rockfish (*Sebastes diaconus*) is a species that is very similar morphometrically to Blue rockfish, and it was only recently being identified as a distinct species from Blue rockfish (Frable et al., 2015). Deacon rockfish have ranges that are more northly, from Northern California to British Columbia, and they display different behaviors. For example, although Deacon rockfish share a similar depth range as Blue rockfish, they are often found in the deeper extensions of the range and are uncommon in waters <30 m (Bizzarro et al., 2020).

Lingcod are benthic predators that are sought after recreationally for their strength and large size. Relative to Rockfish, Lingcod have shorter lifespans (20 years), grow faster, and reach sexual maturity earlier at around 2-4 years (Silberberg et al., 2001; King and MacFarlane, 2003). In contrast to Rockfish mating and spawning, Lingcod (primarily females) complete yearly nearshore spawning migrations, where females spawn in cracks, crevices, and ledges along rocky reefs with strong currents, placing demersal egg masses directly onto the rock. Following the spawning event, females leave immediately, while males tend to the eggs, aerating, cleaning, and incubating them, until hatch (Giorigi and Congleton, 1984). Tagging studies in northern California suggest that adult lingcod do not migrate over great distances, typically moving less than 1 km (Mulligan et al., 2017). For example, in a study by King and Withler (2005), males were shown to utilize the exact same nest, for spawning, over multiple years. Declines in abundance of Lingcod and Black rockfish (as well as many others not incorporated into this study) have led fisheries managers to impose regulations that help populations rebound from a

diminished state; one such management action was the creation of marine protected areas.

MPAs

Marine protected areas (MPAs) have become important research and management tools, aimed at returning at-risk or overfished populations to levels that support sustainable harvest (Gell and Roberts, 2003). By serving as zones with little to no take (recreationally or commercially), MPAs have become useful methods of reducing the impacts of fishing pressure on some species (e.g., Black rockfish, Blue rockfish, and Lingcod), specifically along the California coast. Many MPAs have benefited species by allowing them to rebound from historical depletion, with some notable examples including lobster populations from the Mediterranean to Australia, and groundfish stocks off George's Bank in the Gulf of Maine (Gell and Roberts, 2003; Parnell et al., 2005). MPAs also serve to aid species that may be negatively affected by changing ocean conditions, as related to climate change, by providing a buffer in the form of reduced fishing pressure (He and Silliman, 2019). Effective MPAs help stimulate populations of fish and invertebrates in the protected areas, generating a spill-over of individuals which is then available for harvest to fisheries outside of the MPA (Gell and Roberts, 2003; Parnell et al., 2005; Goni et al., 2008; Harmelin-Vivien et al., 2008; Lenihan et al., 2021). MPAs have also been shown to increase potential harvest and economic value without significantly harming the economic state of communities in which they are a part of (Gell and Roberts, 2003).

A network of new MPAs was established along the California coastline in 1999 following the recognition of the need to conserve the long-term health of marine life, under the Marine Life Protection Act (MLPA). MPA placement occurred gradually, with some MPAs in southern California being established in 2001, while others in northern California in 2012. They were designated based on a range of criteria including historical fishing pressure, distance from port, and availability of suitable habitat (Gleason et al., 2010). The Ocean Protection Council has created a three-tier system to prioritize MPA monitoring based on five specific metrics: MPA size, habitat size, level of protection, areas of special biological significance, and historical protection. The three-tier system ranks the MPAs based on these five metrics. In general, many of the MPAs in tier 1 have experienced more deleterious impacts. Tier 1 MPAs are a top priority for long-term monitoring efforts, and the data collected by researchers within tier 1 MPAs (which were the focus of the present study) allow for a broad evaluation of the performance of the MPA network. Long-term monitoring becomes even more important as a changing climate imposes more deleterious effects on fish communities. The efforts of long-term monitoring allow researchers the opportunity to evaluate how populations are adapting or changing as a response to a changing climate (i.e., how well an organism responds to increased heat) without the negative effects of fishing pressure.

Examining Rockfish and Lingcod abundances, spatial variation, and habitat preference within and outside of MPAs provides information on the effectiveness of MPAs along the Northern California Coast. It also provides management officials with data on the ecological status, potential for future harvest, and how climate change is

affecting the species inhabiting the protected areas. Recreational and commercial interest in these species illustrates a need to investigate factors that influence individual species' abundance and size distributions, and to facilitate the sustainable management of these valued species. Research into what affects these species, especially protection within MPAs, is particularly important in understudied, data-limited areas in which they are harvested, including the Northern California Coastline (Dick and McCall, 2010).

The California Collaborative Fisheries Research Program (CCFRP) has maintained a long-term monitoring project designed to allow the evaluation of California's rocky-reef MPAs. Based on catch data from the CCFRP from 2007-present (<https://www.mlml.calstate.edu/fisheries/ccfrp-interactive-data-app/>), total catch-per-unit effort (CPUE) within MPAs, from their longest studied MPAs, was greater than in paired reference sites for Rockfish and Greenling species. A previous baseline evaluation of MPAs in northern California (Staton, 2017) used distance to the nearest port, depth, and habitat complexity to explain the variation among MPAs and paired reference sites in fish abundance, size distribution, species richness and diversity. This previous baseline study revealed no significant difference in CPUE, species richness, or species diversity between MPAs and their paired reference sites, nor between the different MPAs (Staton, 2017). However, Staton (2017), did conclude that distance from the nearest port was a significant factor in explaining the variability in CPUE and species diversity between MPAs and reference sites. These findings were consistent with that of Barrett et al. (2012), where higher abundances of North Coast fishes were observed at sites farther from the nearest port before the establishment of the MPAs. In addition to monitoring

abundances and other metrics of population health, the long-term monitoring of MPAs allows researchers to gain a greater understanding of drivers of variability in overall population dynamics. For example, another evaluation of MPAs (Kelmartin, 2018) aimed to understand how habitat suitability was driving fish distribution. Kelmartin (2018) found that habitat preferences of fishes utilizing the MPAs were species-specific and driven by different habitat metrics. For example, habitat measures that best describe habitat suitability for Black rockfish were depth, distance to reef edge, and aspect, whereas Canary rockfish (*Sebastes ruberimus*) habitat was best predicted using depth, distance to reef edge, and vector ruggedness. Long-term monitoring of MPAs contributes to understanding of how environmental factors influence abundance and size of Black rockfish, Blue and Deacon rockfish, and Lingcod. Long-term monitoring of MPAs provides an opportunity to collect information that is valuable for fisheries managers which aides them in generating informed regulations on harvest or producing forecasts of the health of each fishery. Long-term monitoring of MPAs also helps fisheries managers in understanding the impacts of fishing pressure, as MPAs serve as a control, demonstrating what population structures may look like in the absence of fishing pressure. The long-term monitoring conducted by the CCFRP also aids in distinguishing between the effects of fishing pressure and the effects of a changing climate, which is a key issue as defined by the MLPA. Understanding what is driving population dynamics, in association to long-term monitoring, is also necessary for understanding how population dynamics will change in the future.

Environmental Drivers of Rockfish

Habitat

Rockfish are associated with hard rocky bottoms but likely have different affinities for structures of the rocky bottom. The depth range of the three species of interest extends from shallow to deep (0-200m). Previous studies have shown depth to be a significant variable in predicting CPUE, species diversity, and size distribution (Staton, 2017; Kelmartin, 2018). Habitat characteristics influence the productivity of a reef, and thus affect demersal fish populations (e.g., Aburto-Oropeza and Balart, 2001). For example, heterogeneous growth, feeding, and rates of predation across reefs may influence an individual species' abundance and size distributions over a reef (Shima et al., 2008). Data on habitat structure, substrate type, and spatial arrangement can be predictive of several quantitative fish community metrics (Gratwicke and Speight, 2005; Anderson et al., 2009). Vector ruggedness has also been shown to be a significant predictor of Rockfish distribution (Young et al., 2010) and an important predictor in measuring habitat suitability of Canary rockfish (*Sebastes pinniger*) along the California North Coast (Kelmartin, 2018).

Habitat complexity has been shown to be a significant predictor of rockfish abundance (Aburto-Oropeza and Balart, 2001; Gratwicke and Speight, 2005; Anderson et al., 2009). One reason for this may be because increases in habitat complexity and size allow for increased foraging opportunities as well as increased availability of refuge for fishes (MacArthur and Levins, 1964). However, complexity was not a significant predictor of species abundance in Staton's (2017) previous baseline study of the

California North Coast region, potentially due to the short timeframe of the study (2 years). The present study utilized a longer, 7-year dataset to test for significant effects of habitat complexity.

Oceanography

Oceanographic effects on nearshore rocky reef fish communities along the northern California coast have not been thoroughly investigated, particularly with respect to longer term, lagged effects on fishes. Wind-driven upwelling in the region has been shown to play a critical role in supporting primary production, subsequent zooplankton production, and healthy fisheries (Bjorkstedt et al., 2002; Barth et al., 2007; Sivasundar and Palumbi, 2010). For example, decreased phytoplankton and zooplankton abundances resulting from reduced upwelling have been shown to negatively affect recruitment of larval fishes (Beaugrand et al., 2003). Similarly, rockfish recruitment has been shown to be higher on nearshore reefs near upwelling fronts (Bjorkstedt et al., 2002). Furthermore, upwelling has been shown to play a major role in the recruitment of larval fishes, with upwelling having a dome-shaped (unimodal) relationship with recruitment; at high and low levels of upwelling, recruitment is low, but recruitment is high between the two extremes (Cury and Roy, 1989; Roy et al., 1992). Despite the studies focused on the shorter-term impact of upwelling on system productivity and fish recruitment, few have examined the longer term, lagged effects of upwelling on the abundance of fishes after several years. The effects of oceanographic conditions during the important juvenile stage of rockfish could potentially be a significant predictor of abundance and size distributions of adults, years after their initial recruitment. The exact mechanism for such an effect

could be varied, and include upwelling's impact on recruitment success, food availability, survival, or movement, but examining such potential lagged oceanographic effects could be an important issue that has received little attention. Identifying linkages between lagged upwelling and the abundance, presence, and size of the species of interest could provide deeper understanding, improved forecasts, and allow for more informed changes to management regulations. Although environmental factors are important for describing changing population dynamics, it is important to also consider the relative fishing pressure.

Measures of Fishing Pressure

The chronic effects of past fishing practices may play an important role in shaping the current dynamics of abundance and size distributions for long-lived species. Fishing pressure, historically, in California waters has been high, with much of the pressure located in densely populated areas, such as the Southern California Bight and Central California/the San Francisco Bay Area (Shroeder and Love, 2002; Briggs, 2016). Fishing pressure and access to fishing grounds have been regulated largely by fuel costs and weather. As the distance to fishing grounds increases, fishing pressure is dampened due to higher costs to fishermen and increased risk of being caught in unfavorable weather. Consequently, distance to port, as a proxy for relative fishing pressure, has been shown to be a significant predictor of fish abundance and size (Starr et al., 2008; Barrett et al., 2012; Staton, 2017; Mulligan et al., 2017). Due to the longevity of nearshore rocky reef species, rebounding from intense fishing pressure requires many years (Starr et al., 2015). Intense fishing pressure in the late 1980s through the early 2000s at some locations in

California may still be detectable within populations today, showing decreased population sizes or smaller average size. Utilizing the hypotheses and knowledge behind environmental and fishing pressure's effects on the population dynamics of fishes, this study incorporated data from long-term monitoring efforts to create a set of objectives with the goal of aiding fisheries managers and researchers.

Study Objectives

Long-term monitoring of MPAs along the California North Coast by the CCFRP has allowed for continued observation of rocky reef populations, providing valuable information on MPA effectiveness and changes in fish populations. Previous MPA baseline evaluations in this region only used two years (2014 and 2015) of data (Staton, 2017, and Kelmartin, 2018), but now there are 5 more years of data available, which allows for a more comprehensive examination of the factors affecting the variability in abundance and size of Black rockfish, Blue and Deacon rockfish, and Lingcod, along the California North Coast. This longer data set can also be used to begin assessing the effectiveness of MPAs as compared to reference sites.

This study includes 7 years of long-term CCFRP-like monitoring data (from years between 2010-2019) to examine the changes and drivers in Black rockfish, Blue and Deacon rockfish, and Lingcod populations along the California north coast. I focused on these species because they are some of the most biomass-dominant species on rocky reefs in the region and they are recreationally and commercially important to the groundfish fishery in California. MPA effectiveness was observed by comparing the effects of protected and non-protected areas on the abundance and size of the three

species. The objectives of this study were to (1) evaluate the changes in the abundances and lengths through time, as influenced by variables related to habitat, lagged oceanographic conditions, fishing pressure, space, and time; and (2) assess the effectiveness of MPAs with regard to fish abundance and length. The primary hypothesis of this study is that lagged oceanographic factors, habitat variables, distance to the nearest port, and spatial and temporal factors would play an important role in describing the variability in abundance and size of the species. A second hypothesis of this study is that MPAs positively influence abundance and size of the fishes within the conservation areas, relative to their associated reference sites. Previous studies have determined that it may take up to 20 years to see the true effects of MPAs for longer lived rockfishes (Starr et al., 2015), but with approaching 10 years of data I hypothesized that we might begin to see the positive effects from the establishment of the MPAs.

The conclusions generated from this study provide useful information to fisheries managers by evaluating the drivers of fish abundance and MPA effectiveness, contributing to the understanding of stock dynamics and addressing the need and financial investment for long-term monitoring. Specifically, my work improves the understanding of how different benthic habitat metrics relate to fish abundance and length, as well as how oceanographic variables (e.g., average and cumulative upwelling) can have lagged relationships with catch rates after several years. Current literature generally focuses on large-scale climatic indices (Pacific Decadal Oscillation, North Pacific Gyre Oscillation) as lagged variables to describe changes to population structure, but this study attempted to describe changes in population structure with regional scale,

lagged oceanographic indices. This study will aid fisheries managers and researchers by providing valuable insight into how abundance and size of these species fluctuate through time. The analysis of MPAs will also provide insight into the effectiveness of MPAs in reaching their intended goals within reasonable timelines.

METHODS

Sampling Sites

A total of six sites were sampled for this study along the California North Coast (Figure 1), including two MPAs (South Cape Mendocino State Marine Reserve [SMR] and Ten Mile SMR), their paired reference sites (North Cape Mendocino and Westport, respectively), and 2 additional reference sites (Trinidad). The reference sites selected for each MPA were chosen because of their spatial proximity, habitat similarity, and comparable environmental conditions. Each sampling site was sampled from 2010-2019, except in 2012, 2013, and 2016.

Within each of the six sampling sites (2 MPAs and 4 reference sites), sampling stations consisting of adequate habitat quality were defined using 500-meter by 500-meter cells (Figure 2). Stations were defined from bathymetry maps, with depths ranging from about 15 to 45 m where substrate was $\geq 20\%$ hard (rocky) bottom. Stations were also divided into two depth strata: deep ($>30\text{m}$) and shallow ($<30\text{m}$). Up to 13 sampling stations were designated within each site. Four stations were randomly selected from each site (two from each of the shallow and deep stations) and sampled during a sampling trip.

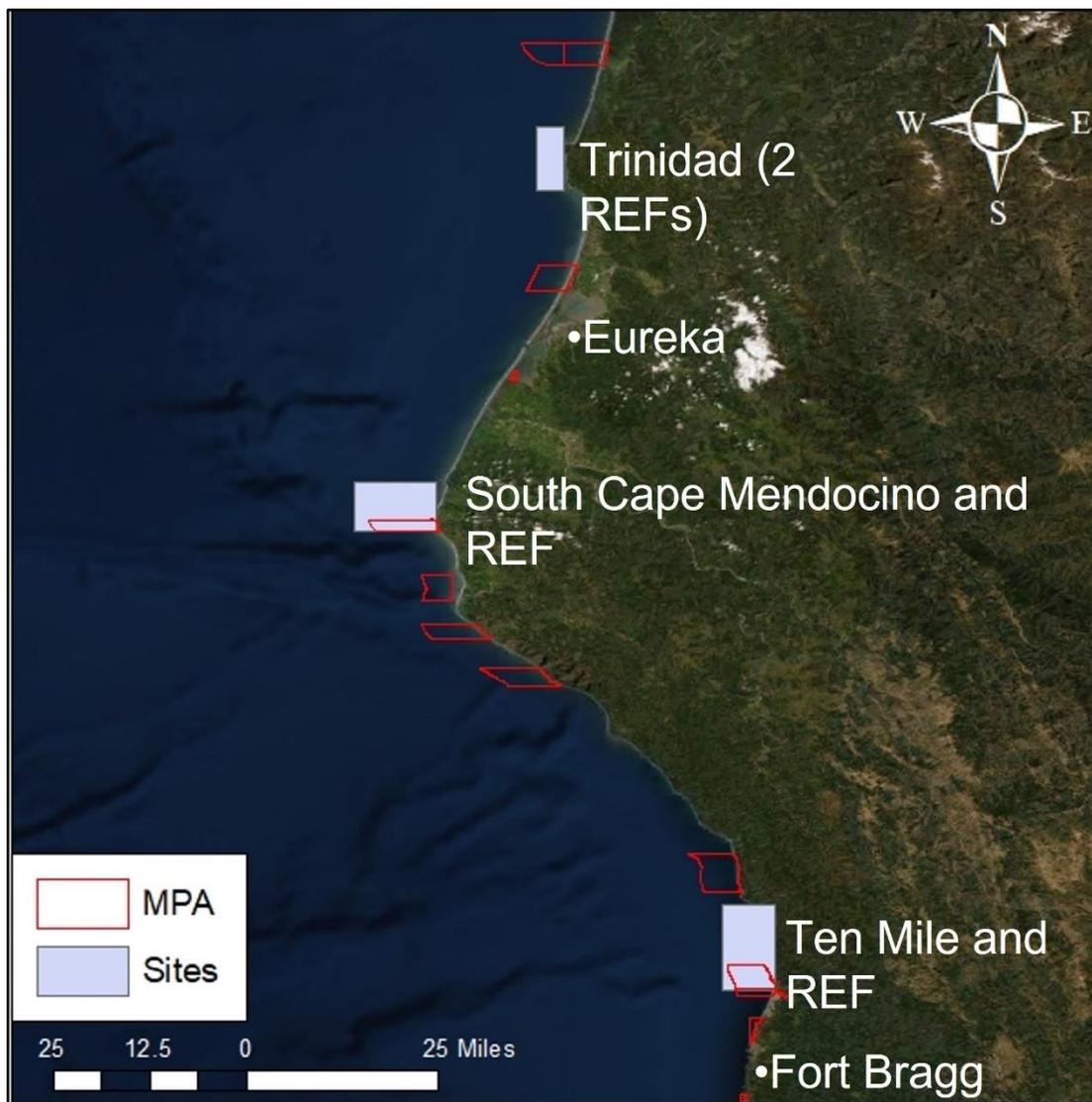


Figure 1. Location of sampling sites out of the ports of Trinidad (Trinidad reference sites [REF]), Eureka (North Cape Mendocino REF and South Cape Mendocino State Marine Reserve [SMR]), and Fort Bragg (Westport REF and Ten Mile State Marine Conservation Area [SMCA]) along the northern California coastline (2010-2020). Red lines delineate marine protected areas (MPAs) along the coast, with blue shading identifying the three areas that were sampled, each with 2 sampling sites.

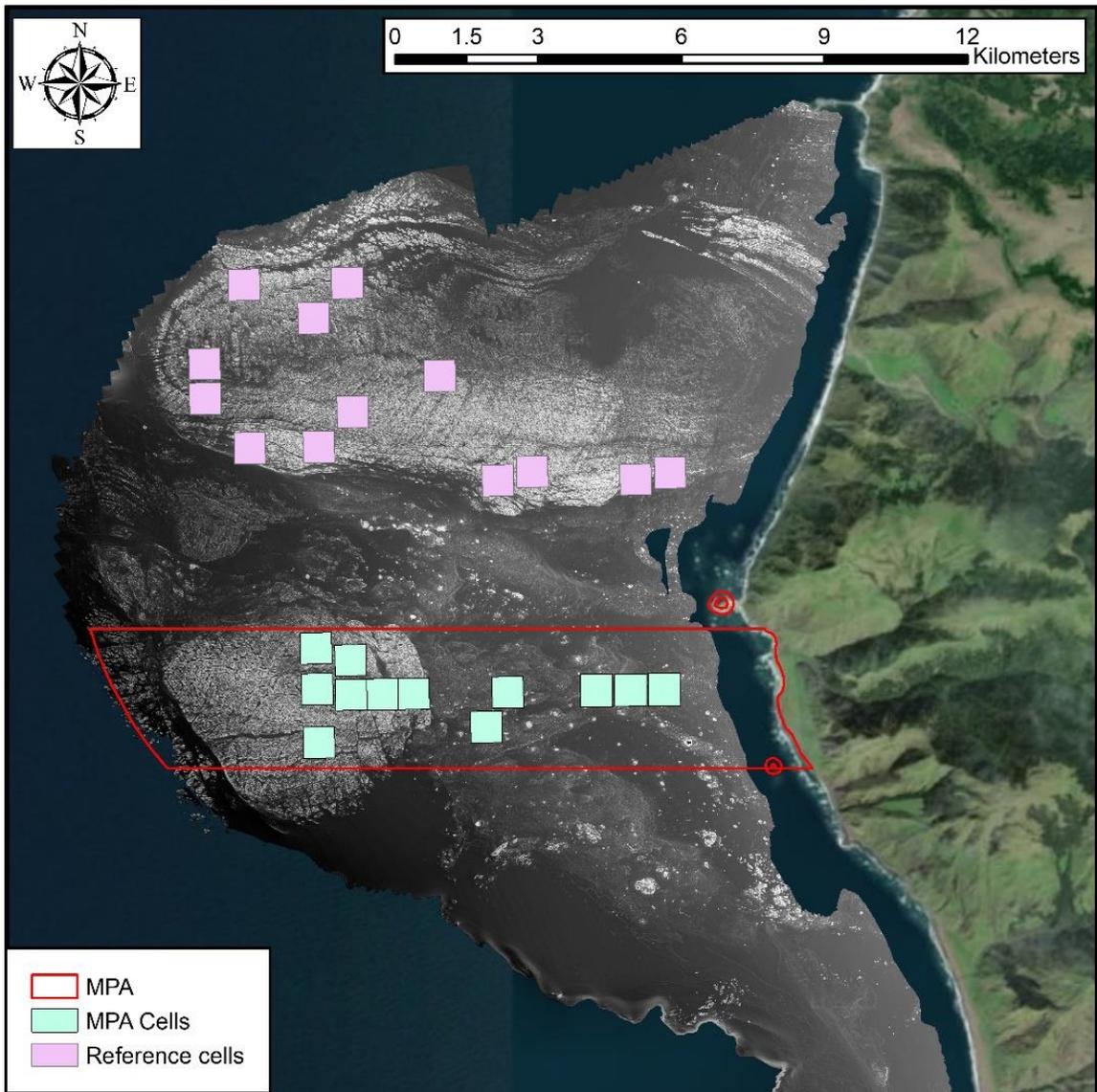


Figure 2. Example of sampling stations (500m by 500m cells) within the South Cape Mendocino State Marine Reserve (MPA; blue squares; southern site) and within the North Cape Mendocino reference site (pink squares; northern site).

Sampling Methods

A standardized protocol was used to sample the two MPAs and four reference sites. Sampling occurred between the months of May and October, as these were months when weather conditions were most favorable for sampling. Each site was sampled 2 to 5 times per year, dependent on available funding. For each sampling trip, a locally chartered boat from the nearest port was used to visit a site. Within the visited site, four of the pre-defined sampling stations (two shallow and two deep stations) were randomly selected for sampling. Upon arrival to one of the four stations, sampling would occur with four anglers fishing as the boat drifted through the station for 15 minutes with the engine either idling or off, depending on the captain's preference. Three 15-minute drifts would be done within the station to cover as much rocky habitat as possible before moving to the next sampling station. In instances where high wind speed, or strong currents, would push the vessel out of the sampling station before a complete 15-minute drift could occur, the charter captains would re-align the vessel to follow the same drift path, until the 15-minute drift could be completed. All four sampling stations, in a site, were typically sampled within 3 hours in a given sampling day (Table 1).

Table 1. Number of sampling trips and stations sampled each year. Each one-day sampling trip consisted of sampling four randomly selected stations within an MPA or reference site.

Year	Number of trips	Number of Stations Sampled
2010	20	80
2011	20	80
2014	8	32
2015	8	32
2017	12	48
2018	18	72
2019	18	72
Total	104	416

Hook-and-line sampling methods, used in the monitoring process, followed the procedures of Barret et al. (2012) and Mulligan et. al. (2017). Hook-and-line was used because extensive underwater surveying (e.g., SCUBA, underwater drone, or acoustic receivers) of these organisms was impractical due to high costs, depth limitations of these alternative methods, and the oceanographic variability of the California North Coast. Hook-and-line sampling for fishes was completed with four anglers, each using one of four gear types: un-baited shrimp-fly, shrimp-fly baited with cut market squid (*Doryteuthis opalescens*), plastic swim bait (6-12 oz) with shrimp-fly teaser, or a metal diamond jig (4-9 oz) with a shrimp-fly teaser (Figure 3). Fishing gears were fished to target ground fish species, and the depths at which gears were fished ranged depending on what species were being caught and where fish were located on onboard fish finders. For example, when fish were located directly on the bottom (as determined by the fish finder), fishers were instructed to have fishing gears 1-2 feet off the bottom. When fish

were in the middle of the water column, fishers were instructed to bring gears up to the depth in which the fish occupied. These different gear types were selected to exploit potential differences in selectivity and catch rates, and to mimic the gears that are frequently used by the local recreational fishing community. Anglers consisted of volunteers and paid technicians from the local communities. Technicians and volunteers were trained during each sampling trip to maximize catch. In addition to the four anglers, two scientific crew members were responsible for: identifying, measuring, and tagging (for a separate study) and releasing fish; monitoring drift location and boat position; assisting with any sampling issues (tangled lines, replacing gear, communicating with charter captain); and recording data. Each captured fish received a GPS location upon capture, was identified to species, measured for total length (mm), tagged with a FLOY tag to track movement and released. Access to sampling locations and gear for the project was locally sourced, to help generate commerce in the local community and promote further cooperation among the recreational and commercial fishing fleets, researchers, and fisheries managers. All sampling methods conducted were first approved by the Institutional Animal Care and Use Committee (IACUC; IACUC#2020.F.59) before the onset of sampling.

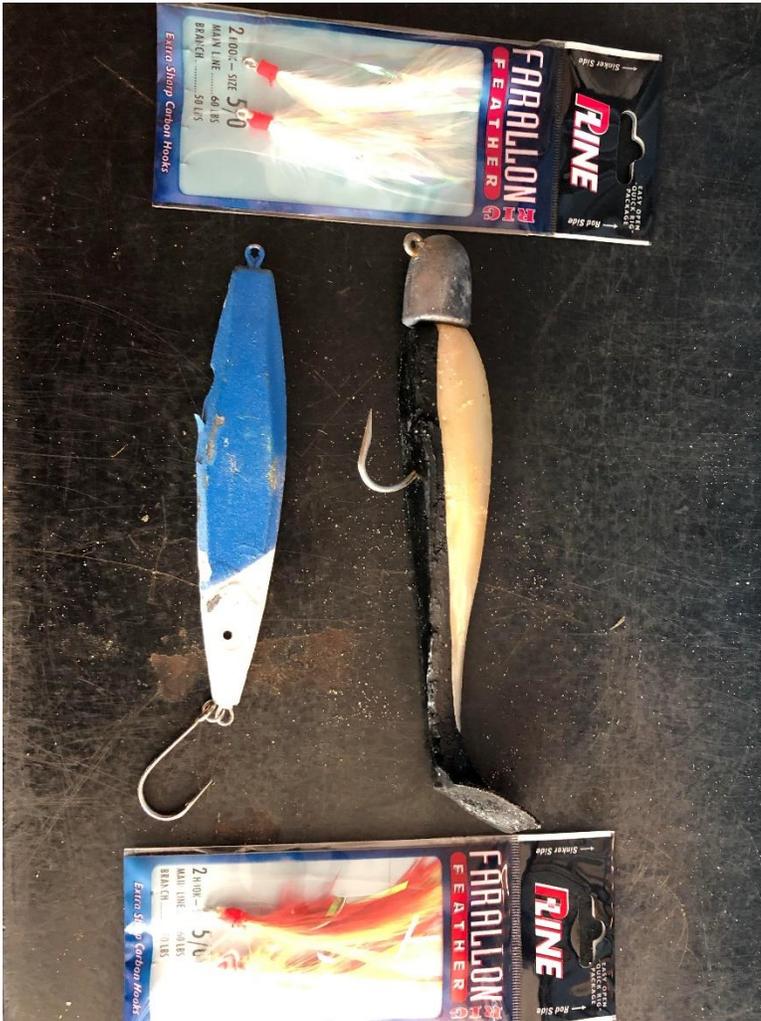


Figure 3. The 4 gear types used throughout each sampling event: Shrimp flies (top and bottom), metal diamond jig (left), and soft plastic 6 in. swimbait (right).

Blue and Deacon rockfish

The dataset used in this study incorporates data collected by Barrett et al. (2012), Staton (2017), and Kelmartin (2018) between 2010-2015, and more recent data collected from 2017-2019. During the majority of this time Blue rockfish and Deacon rockfish were considered to be one species. This resulted in observations of the two species being grouped together under the single species identifier of Blue rockfish. Deacon rockfish were first described in 2015 with the reclassification of Blue rockfish (Frable et al., 2015), and were not identified as separate species in this study until 2017. To maintain continuity, this study has continued to group the two species as one, “Blue rockfish”, within the statistical analyses.

Explanatory Variables

To complete the objectives of this study, data were collected on a suite of explanatory variables related to the environment (specifically substrate and oceanography), fishing pressure, spatial location, year, fish size bin, and protection status (Table 2). Environmental variables included substrate features related to the benthic habitat at sampling stations as well as oceanographic conditions lagged based on the approximate age of captured fish (see details below). Distance to port was determined relative to the sampling station fish were captured in. Spatial and temporal variables were constructed at the port and year level, respectively. Finally, the protection status variable was constructed at the site level (Figure 1; e.g., North Cape REF) and only pertained to MPAs and their paired reference sites; analysis of protection status effects do not include data from Trinidad sites as these sites do not have a paired MPA.

Table 2. Covariates used within analyses. Covariates marked with * were not included in models describing length.

Variable	Reason for Inclusion
Vector Ruggedness Measure (VRM)	Measure of habitat complexity; strong predictor in previous studies (Kelmartin, 2018)
Depth	Reflects habitat preferences of fish; strong predictor in previous studies (Staton, 2017)
Hard Cover	Reflects habitat preferences of fish; strong predictor in previous studies (Staton, 2017)
Percent reef	Modified hard cover variable to compare preference for complex habitat or hard substrate
Distance to port	Proxy for fishing pressure; strong predictor in previous studies (Starr et al. 2008; Barrett et al. 2012; Staton, 2017)
Cumulative Chlorophyll*	Expected effects on juvenile development and production (via food availability and growth)
Cumulative Temperature*	Expected effects on juvenile development and production (via food availability and growth)
Cumulative Upwelling*	Expected effects on juvenile development and production (via food availability and growth)
Averaged Upwelling*	Expected effects on juvenile development and production (via food availability and growth)
Year	Accounts for interannual variability
Port	Accounts for regional spatial variability
Protection Status	Tests MPA-related effects relative to reference sites
Fish Size Bin*	Accounts for catch differences by size resulting from gear selectivity or population demographics

Substrate variables

To help predict fish abundance and size, fish habitat was quantified using four different habitat metrics: vector ruggedness measure (VRM), depth, percent hard cover, and percent reef. VRM is a 3-dimensional metric that incorporates aspect and slope into a single measure (Sappington et al., 2017). Substrate variables were calculated at the station level; substrate variables were generated as the variable's mean value in each sampling station. Substrate covariates required the use of spatial modeling programs and were calculated using ArcGIS software (ArcMap 10.6.1, or ArcGIS 10.7.1, by Esri) for each sampling station. Quantifying substrate factors consisted of using rasters developed from bathymetry maps from the California Seafloor Mapping Project. Station-specific means of VRM, hard cover, and depth were calculated from rasters of each variable using overlaid polygons of each station (Figure 4). To calculate the percent reef at a station, the boundaries of individual rocky reefs were first approximated at each site by setting a consistent VRM threshold that delineated the major, mostly contiguous sections of the reef. This boundary was determined through an iterative process of increasing the VRM threshold until only the reef habitat appeared to be identified. This process involved iteratively generating new rasters of hard cover that revealed substrate with VRM values above the predetermined threshold. Polygons of the sampling stations were then overlaid on the newly created raster that designated the individual reefs, and the percentage of the total area that was classified as reef for each station was extracted.

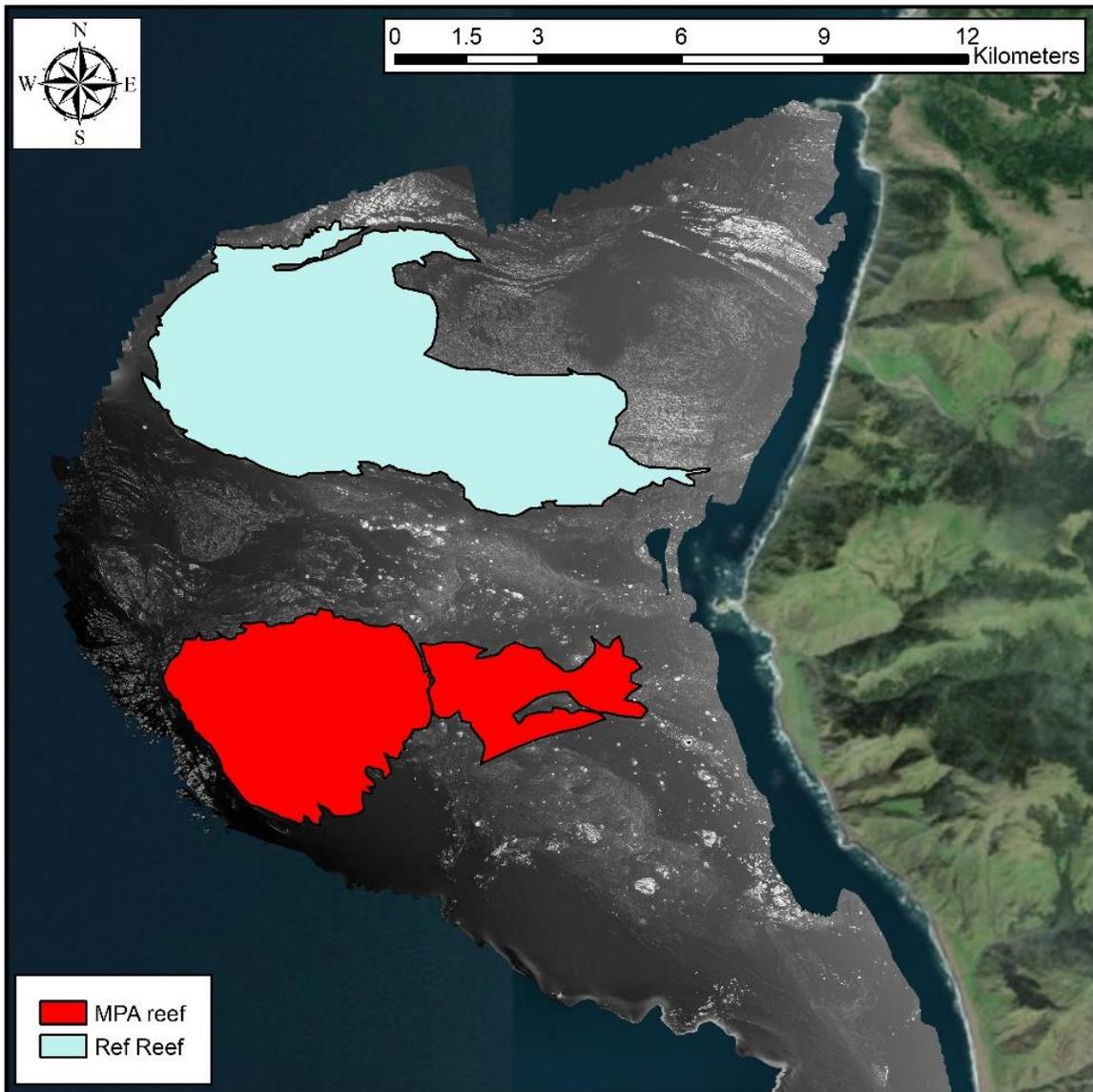


Figure 4. Digitization of the reefs that make up the sampling area of the South Cape Mendocino State Marine Reserve (MPA; red reef; southern site) and within the North Cape Mendocino reference site (blue reef; northern site). Digitization of these reefs represents areas used for constructing hard cover. VRM values were sequentially increased to differentiate reef from gravel/sandy bottoms.

Oceanographic variables

Four oceanographic covariates were constructed using daily observations from satellite or model-derived data obtained from ERDDAP (National Oceanographic and Atmospheric Administration, National Marine Fishery Service, Southwest Fisheries Science Center), which is an assemblage of satellite and buoy data. The four oceanographic variables included two metrics derived from the coastal upwelling transport index (CUTI) (specifically average upwelling and cumulative upwelling), sea surface temperature (SST), and chlorophyll concentrations. CUTI data was downloaded from NOAA (<http://mjacox.com/upwelling-indices/>), while chlorophyll and sea surface temperature were obtained from data on daily observations from multiple satellite sources (<https://coastwatch.pfeg.noaa.gov/erddap/index.html>). Other index measures were averaged, daily, across a section measuring one degree of latitude (110km) by approximately 3 km of longitude. Each one-degree section encompasses a different pair of sampling sites therefore creating three distinct upwelling areas (Fort Bragg, Eureka, and Trinidad). All oceanographic indices were obtained from 2000 (the start of most of the available data) through 2019 to evaluate lagged effects of upwelling on fish populations.

Cumulative measures of chlorophyll, sea surface temperature, and upwelling were calculated to be more representative of the aggregate effect of these variables on fish recruitment or their juvenile stages. These metrics were calculated following modified methods used for degree days (e.g., Cheznik et al., 2014; Honsey et al., 2019) by taking the sum of daily deviations from a threshold. Degree days is often used as a method of

quantifying the cumulative days that are beneficial towards an organism's growth. A cumulative metric for site s and year i ($X'_{s,i}$) can be calculated as: $X'_{s,i} = \sum_{d=1}^{365} (X_{s,i,d} - \bar{X}_i)$ for all $X_{s,i,d} > \bar{X}_i$, where X represents one of the three variables (chlorophyll concentration, sea surface temperature, or upwelling), d represents the days of the year, and \bar{X}_i is a threshold value (either a mean or median) for variable X in year i . The site-specific threshold values for temperature and upwelling were generated by taking the mean value, whereas the median value was used for chlorophyll concentrations because they were not normally distributed, and the median is less influenced by large outliers. Chlorophyll was first log transformed; no transformations were applied to the other variables. In the cumulative calculation if the difference between a daily observation and the threshold was negative (i.e., $X_{s,i,d} < \bar{X}_i$) for any variable, that difference was treated as a zero; negative values were treated as zeros and not included in the summation in order to calculate the area between an annual curve of $X_{s,i,d}$ and the \bar{X}_i threshold. In addition to these three cumulative oceanographic metrics, I also calculated an average annual upwelling index using the CUTI index; the averaged upwelling metric only incorporated data from the summer months, to reflect the upwelling season along the northern California coast.

All oceanographic variables were lagged to represent the conditions during the approximate early life history stages of each of the focal species. This was done assuming oceanographic variables would have effects on the recruitment strength of the fish with future impacts on adult populations (Cury and Roy, 1989; Bjorkstedt et al., 2002; Barth et

al, 2007). Each species of fish was divided into three size categories (small, S; medium, M; large, L) to act as a coarse proxy for age-classes and to help account for differences in gear selectivity. Von Bertalanffy models from the literature (Six and Horton, 1977; Laidig et al., 2003; Hamel et al., 2009; Appendix 1 Appendix 3) and histograms of observed fish length were used to set the bounds of each size grouping and the approximate median age for each size bin (Table 3). The lag periods for the oceanographic variables were determined from these approximate median fish ages. To account for uncertainty and variability in fish ages within the size bins, I chose to use a three-year window of lagged oceanographic data for the averaged upwelling metric, with the three-year window centered on the approximate birth year of the fish. For example, medium black rockfish were expected to be approximately 5 years old, and if they were sampled in 2016, then the corresponding lagged oceanographic period would be 2010, 2011, and 2012. The resulting oceanographic variables were lagged cumulative oceanographic metrics (chlorophyll, temperature, and upwelling) and lagged average upwelling, calculated as the average across the lagged three-year window.

Table 3. Length measurements in mm used to delineate three size bins for each species. Numbers in parentheses are the approximate ages (in years) of fish within that size bin.

Species	Small	Medium	Large
Black rockfish	<300 (2)	300-400 (5)	>400 (15)
Blue Rockfish	<200 (2)	200-250 (5)	>250 (13)
Lingcod	<500 (1)	500-700 (3)	>700 (7)

Other variables

Port, distance to port, year, protection status and fish size were five additional variables used to explain variability in fish abundance and size. Port was a regional identifying variable designating one of three ports (Eureka, Fort Bragg, or Trinidad) used to access a sampling location. Distance to port was calculated as the distance (km) from the center of a sampling station to the mouth of the nearest port (Eureka or Fort Bragg). Year represented the year of sampling, and protection status indicated whether a site was protected as an MPA (South Cape SMR and Ten Mile SMR) or whether it was a reference (REF) site. Fish size was categorized into three size bins (S, M, L; see Table 3).

Statistical Analyses

Prior to conducting statistical analyses, survey data were summarized using the methodology of Starr et al. (2015) and the CCFRP. To account for unequal fishing effort, CPUE was calculated as total catch per angler hour. On a sampling trip, an individual

fisher would contribute approximately 3 angler hours. CPUE was generated for each species by port and year sampled.

Examining Environmental Effects (Objective 1)

For each of the three focal species, statistical models were developed to examine the effects of explanatory variables on 1) the relative abundance of fish caught and 2) the size of fish captured. The specific type of statistical model was chosen appropriately for each of the two response variables, based on the characteristics and distribution of the data. Zero-altered models were used to model the relative abundance of fish, while generalized linear mixed models (GLMMs) were used to model fish size (see details below). A common model selection procedure was used for each species and response variable using Akaike's Information Criterion (AIC), in which a large set of possible models were constructed with all possible combinations of covariates. All models were ranked by AIC, and AIC differences (delta AIC) were calculated as the AIC value for a given model, minus the lowest AIC from the best model. I chose the model with the lowest AIC value (i.e., delta AIC = 0) as the best, final model; however, models with delta AIC values <2 are considered to have substantial support.

Modeling Relative Fish Abundance

Zero-altered models were used to examine the environmental effects on the relative abundance of the three species because there were many observations with zero counts for the three species across all samples (Appendix 4). Zero-altered models account for the excessive number of zeros in a data set by breaking the data up into two parts,

modeling them separately, and then combining the two parts together to generate predictions (Zuur et al., 2009). A total of over 15,000 models were fitted for each species. For the first component (positive element), a zero-truncated GLM was used to model the positive observations (i.e., catches) after all zeros had been excluded. This zero-truncated GLM used a Negative Binomial distribution in models of Black rockfish and the Blue rockfish group (instead of a Poisson distribution) to account for over-dispersion in the count data, and a Poisson distribution in models of Lingcod (as no over-dispersion was detected). For the second component (binomial element), a logistic model with a binomial distribution was used to model the probability of occurrence. The predictions from the two components are multiplied together to generate the final, overall prediction. The zero-altered models were fit using the “pscl” package in R (Zeileis et al., 2008). Explanatory variables included substrate variables, oceanographic variables, distance to port, site, year, and size bin. Protection status (MPA vs. REF), and an interaction term between site and protection status was also included in the analysis of MPA effects. The model selection procedure involved generating all possible combinations of covariates for the positive and binomial elements, separately; however, constraints were set on models to have no more than 8 explanatory variables to limit model complexity and the number of assessed models. The models with the lowest AIC, for the two parts (positive and binomial) were then brought together to create the full zero-altered model. The two parts were constructed separately as the current dredge function could not produce all possible combinations of zero-altered models due to the inordinately high number of models.

All final, fitted models were evaluated to ensure distributional assumptions were met using appropriate diagnostics. Model diagnostics were assessed graphically by plotting Pearson's residuals against fitted values and against each predictor variable. Patterns in the residuals did not indicate a lack of fit or lack of independence in the final models. Rootograms were also used to assess model fit (Kleiber and Zeileis, 2016). Response plots with partial residuals were used to display the predicted effects of the covariates, when all other included covariates were held at their median (continuous covariates) or mode (categorical covariates). All covariates were assessed for issues with collinearity using pairs plots and correlation coefficient values prior to model selection; no issues with collinearity were found. The earliest years required for the covariates that were lagged to sometimes extended farther back in time than available data. Fish with assumed birth years preceding the year 2000 were omitted (n=309 out of 2,940) because there was not adequate satellite or buoy data for their associated lagged variables.

Modeling Fish Length

Mixed-GLMs were used to examine the effects of the predictor variables on the size of the three species. Mixed effect models accounted for the nested structure of observations, specifically the lack of independence among individual fish caught within the same sampling stations in a year. Models of fish size used the normal distribution. Modeling fish length did not include the size covariate, nor did it incorporate any lagged oceanographic variables because lagged oceanographic variables were hypothesized to predominantly influence relative fish abundance. All included covariates were standardized (mean=0, standard deviation=1) to prevent errors when fitting the models.

Model selection began with first finding the optimal random effects structure (using a full model with all covariates) before determining the optimal fixed effect structure (Zuur et al., 2009). The inclusion of a year-specific station identifier as a random effect was deemed to be the best random structure based on AIC (compared to a station identifier that was not year-specific) when models were fit using restricted maximum likelihood. Model selection to determine the optimal fixed effect's structure (using maximum likelihood) involved using AIC to compare among models with all possible covariate combinations while maintaining the same random effect structure. Conditional R^2 values, or the proportion of the variability explained by both the fixed and random effects, were used as an overall metric of model fit for final models (Nakagawa and Schielzeth, 2013). Histograms of model residuals, standardized Q-Q plots, and residual vs. fitted values plots were used as diagnostics to evaluate model assumptions. Response plots with partial residuals were used to visualize the predicted effects of each of the covariates on length while holding all other covariates at their median (continuous covariates) or mode (categorical covariates). All analyses were done in R (R Core Team, 2021); the GLMMs were fit using the "lme4" package, conditional R^2 values were determined using the MuMIn package, and the response plots were made using the visreg package. Collinearity between variables was, again, assessed using pairs plots and correlation coefficients; no issues with collinearity were found.

Assessing MPA Effectiveness (Objective 2)

Assessing the effects of MPAs relied on methodologies and models similar to the previous analyses of relative fish abundance and fish size. However, these MPA analyses

used a reduced data set that excluded Trinidad because Trinidad did not have paired MPA-reference sites. These models also included protection status as a covariate (MPA vs. reference) and an interaction term between port and protection status as additional explanatory variables. These variables were excluded from the earlier analyses because the signals generated by the MPA-reference covariate might have been highly influenced by effects from Trinidad. Model selection and model visualizations were identical to the process described previously.

RESULTS

The numbers of fish caught, and the mean size of fish caught varied across years and port (Table 4 and Table 5). Fort Bragg was the only port that was sampled in all seven years; the Eureka port was sampled 5 of the 7 years, and the port of Trinidad was sampled 4 of the 7 years. Total Black rockfish catch was highest out of the port of Trinidad and lowest out of Fort Bragg, while Blue rockfish catch was highest out of Fort Bragg, and lowest out of Eureka. Total catch of Lingcod was highest out of Fort Bragg and the lowest out of Trinidad. The mean length of all three species was the greatest out of Eureka and smallest out of Fort Bragg (Table 5).

Table 4. Number of Black rockfish, Blue rockfish (the combination of Blue rockfish and Deacon rockfish), and Lingcod caught out of the ports of Eureka, Fort Bragg and Trinidad, CA between 2010 and 2019.

Species	Port	2010	2011	2014	2015	2017	2018	2019	Total
Black rockfish	Eureka			308	125	190	116	121	860
	Fort Bragg	115	264	192	42	52	58	53	776
	Trinidad	1023	734				708	384	2849
	All Ports	1138	998	500	167	242	882	558	4485
Blue rockfish	Eureka			68	33	58	95	156	410
	Fort Bragg	256	199	129	122	149	124	199	1178
	Trinidad	212	87				86	65	450
	All Ports	468	286	197	155	207	305	420	2038
Lingcod	Eureka			85	63	96	60	32	336
	Fort Bragg	65	130	116	98	101	58	40	608
	Trinidad	49	88				17	9	163
	All Ports	114	218	201	161	197	135	81	1107

Table 5. Mean length (mm) and standard deviation (in parentheses) by port of Black rockfish, Blue rockfish (the combination of Blue rockfish and Deacon rockfish), and Lingcod from 2010 to 2019.

Species	Port	2010	2011	2014	2015	2017	2018	2019	Total Average
Black rockfish	Eureka			400 (37.3)	396 (36.2)	405 (41.0)	416 (35.9)	404 (50.3)	404 (40.2)
	Fort Bragg	319 (54.4)	334 (54.1)	351 (44.1)	352 (68.1)	356 (55.1)	367 (48.3)	381 (73.8)	344 (56.3)
	Trinidad	374 (58.1)	380 (67.0)				356 (68.2)	355 (60.9)	369 (64.2)
	All Ports	369 (60.1)	368 (67.1)	381 (46.4)	384 (50.3)	394 (48.8)	365 (66.8)	368 (63.3)	371 (67.8)
Blue rockfish	Eureka			308 (49.5)	319 (40.2)	308 (68.2)	307 (54.2)	305 (54.1)	308 (54.4)
	Fort Bragg	263 (60.5)	292 (52.2)	255 (58.2)	256 (65.6)	258 (54.1)	280 (54.2)	296 (46.1)	273 (58.2)
	Trinidad	325 (55.0)	319 (47.2)				266 (49.1)	273 (38.5)	305 (56.4)
	All Ports	291 (65.8)	300 (62.1)	273 (60.7)	269 (66.3)	272 (62.4)	285 (55.1)	296 (49.3)	287 (90.0)
Lingcod	Eureka			595 (118.4)	607 (117.6)	590 (130.8)	650 (145.8)	680 (202.4)	624 (138.4)
	Fort Bragg	525 (108.6)	523 (110.7)	616 (89.2)	618 (105.4)	600 (98.8)	651 (90.3)	619 (112.1)	586 (111.9)
	Trinidad	582 (119.1)	611 (138.7)				674 (165.4)	638 (138.0)	610 (137.4)
	All Ports	549 (116.3)	558 (129.9)	607 (102.5)	614 (110.0)	595 (115.0)	654 (126.8)	643 (153.5)	598 (124.7)

To account for unequal effort among ports and years of sampling, CPUE was calculated and demonstrated varying trends through time based on protection status (i.e., MPA, reference site) and sampling port for each species (Figure 5). Black rockfish showed a relatively consistent CPUE through time out of the ports of Eureka and Fort Bragg. Blue rockfish, meanwhile, showed a trend of increasing CPUE out of Eureka, though there was no difference between the MPA and the reference sites throughout the years sampled. Lingcod CPUE out of Eureka decreased through time, with negligible differences in CPUE between the MPA and paired reference site. Out of Fort Bragg, Black rockfish and Blue rockfish CPUE was fairly consistent across years sampled, but concluded with a slight increase in abundance and differences between the MPA and paired reference site; in the last year of sampling (2019), MPAs had greater CPUE than their paired reference sites. Lingcod CPUE was much more variable out of Fort Bragg, with dramatic increases in 2014 and 2015, followed by a generally decreasing trend until 2019. However, CPUE in MPAs were higher for Lingcod in 2018 and 2019 relative to the reference site. CPUE of Black rockfish was higher out of Trinidad compared to the other ports, with higher values in later sampling years (2018-2019) than in earlier sampling years (2010-2011). CPUE of Blue rockfish and Lingcod, out of Trinidad, was approximately similar between early and later sampling years. Lingcod CPUE out of Trinidad, however, was slightly lower compared to the other ports.

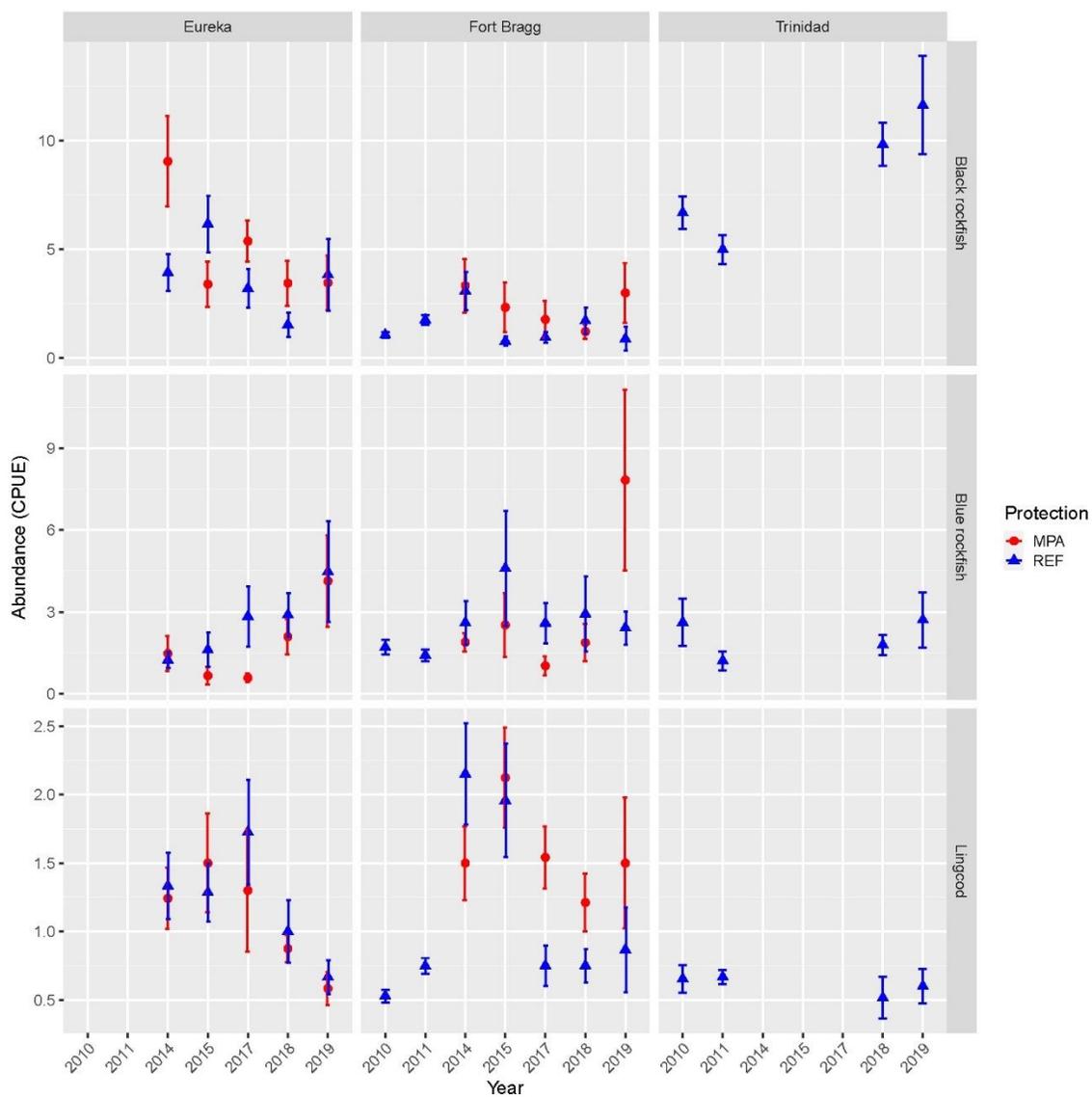


Figure 5. Catch per unit effort (CPUE) by port and year for Black rockfish, Blue rockfish, and Lingcod in MPAs (circles) and their reference sites (triangles).

Variability in abundance

The final hurdle models of relative fish abundance were created by combining the best-fit model for the zero-truncated positive count model with the best-fit binomial model that predicted the probability of presence (i.e., the logistic regression model). The delta AIC values for the top-ranked models (excluding the best-fit models) typically ranged between 0.1-1.2, suggesting a strong level of support for those models. However, the structure of the closely ranked models (for both the positive element and binomial components) maintained the same structure as the best, top-ranked model but contained additional covariates. Thus, the top-ranked models were more parsimonious and selected as the best models, because the addition of more covariates did little to describe more variability in the response.

The structure of the final model and the effects of the covariates varied between species (Figure 6). No two species had the same model structure. The nature of the effect of the continuous covariates remained the same between the positive [count] component and binomial component [probability of obtaining a positive count], except for one instance (i.e., the effect of cumulative upwelling on Lingcod). Except for port, all categorical variables were consistently included in final models, across all species. Depth and distance to port were the only continuous variables included in final models of all species. When included in final models, distance to port always had a positive effect on the response when included in the best-fit model, except for the binomial model for Black rockfish. In models of Black rockfish, however, continuous covariates always had the opposite effect of the Blue rockfish group and Lingcod, when included in final models.

Despite the nuanced differences in effects of the covariates on the positive components of the models, the main focus in this study will be on the combined effects resulting from the product of the two components of the zero-altered models. These combined effects are presented below, organized by the general covariate categories.

Species	Substrate								Pressure	Oceanography								Temporal		Spatial		Size Structure		
	VRM		Depth		Hard Cover		Percent reef		Distance to port	Cumulative Chlorophyll		Cumulative Temperature		Cumulative Upwelling		Averaged Upwelling		Year		Port		Size Bin		
	P	B	P	B	P	B	P	B	P	B	P	B	P	B	P	B	P	B	P	B	P	B	P	B
Black rockfish		+	+	+															*	*	*	*	*	*
Blue rockfish																			*	*	*	*	*	*
Lingcod																			*	*			*	*

Figure 6. Relative effects of predictor variables for best-fit, zero-altered models of relative fish abundance. Zero-altered models consist of two components (Positive component [P], and Binomial component [B]). Positive relationships between the response variable and the predictor variables are illustrated in green (+), while negative relationships are in red (-). The blue coloration (*) identifies categorical variables that were included in the best-fit models. Predictor variables are listed as columns and grouped into general categories in bold.

Substrate effects

Depth, vector ruggedness, and percent hard cover were the most prominent substrate variables included in the final zero-altered models (Figure 6). The effects of substrate variables were strongest for Black rockfish (based on the steepness of the trends and the relative spread of the partial residuals) and the directionality of the effects for Black rockfish differed from those of the other species (Figure 7).

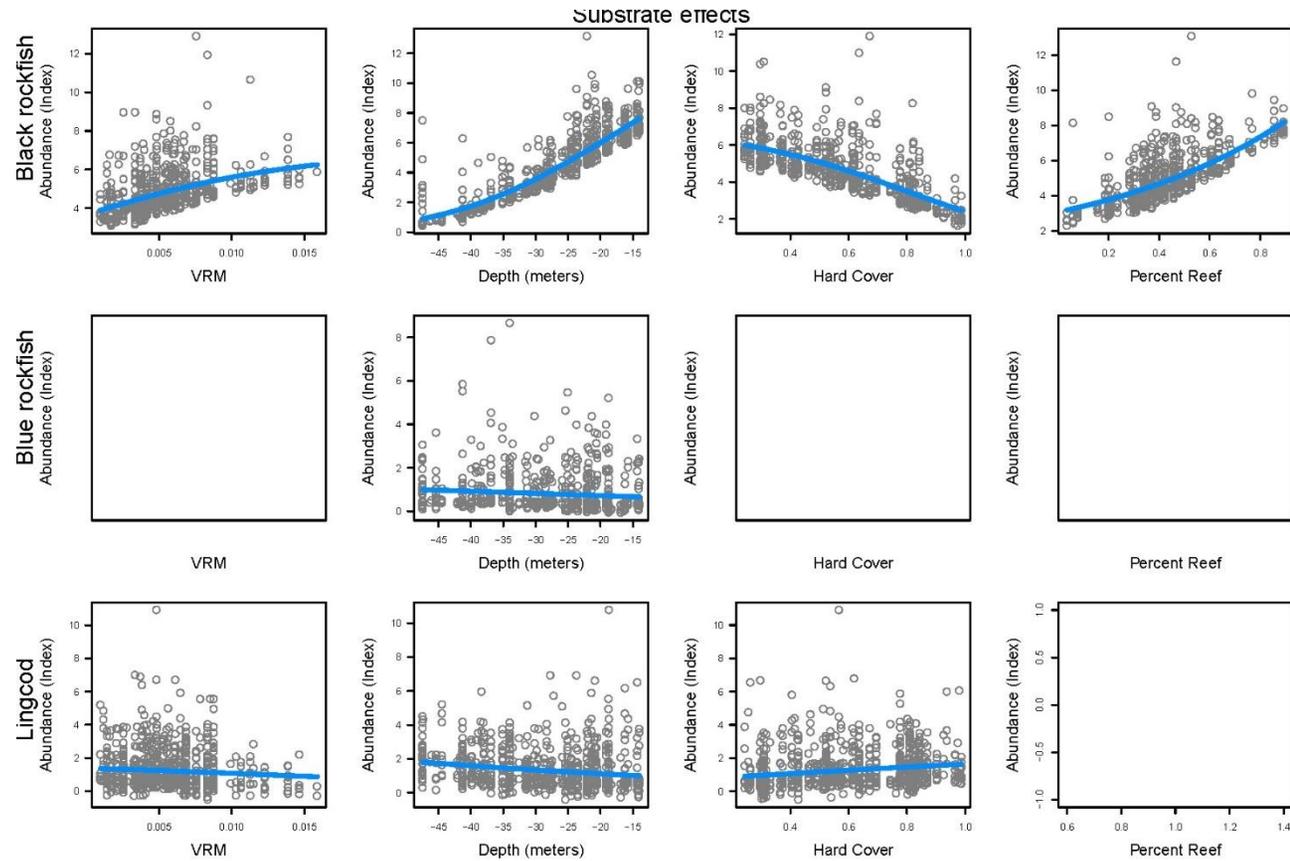


Figure 7. Effects of four substrate covariates on predicted catches of Black rockfish, the Blue rockfish group, and Lingcod based on final zero-altered models. Blue lines are the estimates of relative abundance (when holding all other covariates at their medians), generated from the product of estimates from zero-truncated models (positive) and logistic regressions (binomial). Points are partial residuals. Blank panels represent covariates that were not included in the final, best-fit models. VRM is vector ruggedness measure. Hard cover and percent reef are presented as proportions.

Vector ruggedness was included in final models only in the binomial element (Figure 6). In the final model of Black rockfish, VRM had a positive effect on the probability of obtaining a positive count resulting in a proportional change of 60% (from 3.9 to 6.3 fish) in the combined estimate of relative abundance (Figure 7). VRM had a negative relationship, however, with Lingcod, resulting in a proportional decrease of 37% (from 1.4 to 0.9 fish) across observed VRM values. For both species, most observations fell between VRM values of 0.001-0.010.

Both relative abundance and probability of presence of Black rockfish were positively influenced by depth; that is, count increased as depth became shallower. Depth, however, had a negative effect in the final models of the Blue rockfish group and Lingcod (i.e., count decreased as water depth became shallower). Depth had the biggest effect on the relative abundance of Black rockfish and was associated with a proportional increase of 738% (from 0.9 to 7.6 fish) as depths decreased, or became shallower, from about 47 m to 15 m. Depth had weaker, negative influences on relative abundance for Blue rockfish and Lingcod. Depth was associated with a proportional decrease of 44% in relative Lingcod abundance (a decrease from 1.8 to 1.0 fish) as depth became shallower.

Percent hard cover had a positive effect on counts and the probability of obtaining a positive count on Lingcod but had a negative effect on the probability of obtaining a positive count on Black rockfish (Figure 6). Lingcod had a slight, 79%, increase in the count of fish (from 0.9 to 1.6 fish) as percent hard cover increased (Figure 7). Black rockfish showed a strong decrease in the probability of obtaining a positive count with

increasing values of hard cover, resulting in a proportional decrease of 56% (from 6.0 to 2.5 fish) in relative abundance.

Percent reef was included in only one final model (Figure 6). In models of Black rockfish, it positively influenced relative abundance (Figure 7). Relative abundance increased from 3.2 to 8.2 fish (157%) across the range of observed values for percent reef. Most Black rockfish were caught over habitat with 30-70% reef substrate.

Oceanographic effects

Cumulative upwelling and average upwelling were the most influential of the lagged oceanographic covariates included in the final zero-altered models (Figure 6). Cumulative upwelling and average upwelling were included in two of the three final models, whereas cumulative chlorophyll and degree days were only included in one model each. Lagged oceanographic effects were strongest in Black rockfish while weakest in Lingcod (Figure 8).

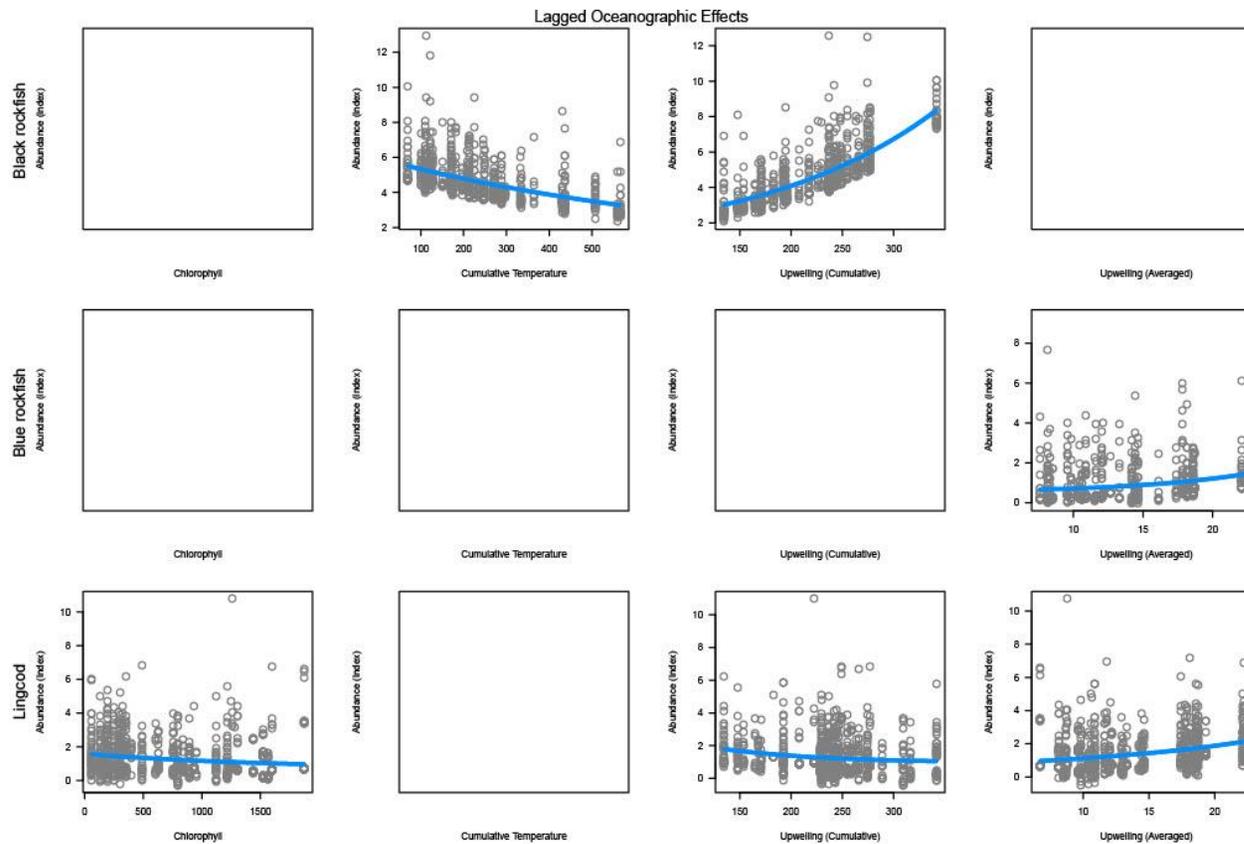


Figure 8. Effects of four lagged oceanographic covariates on predicted Black rockfish, the Blue rockfish group, and Lingcod catches based on final zero-altered models. Blue lines are the estimates of relative abundance (when holding all other covariates at their medians), generated from the product of estimates from zero-truncated models (positive) and logistic regressions (binomial). Points are partial residuals. Blank panels represent covariates that were not included in the final, best-

fit models. Chlorophyll is measured as a concentration while cumulative and averaged upwelling were measured as indices of intensity.

Cumulative chlorophyll was included only in the final model of Lingcod (Figure 6). Cumulative chlorophyll had a negative effect on counts in the positive element of the final zero-altered model of Lingcod. The negative effects of cumulative chlorophyll in the positive element generated weak, negative effects in the final estimates of relative abundance, decreasing by 38% (from 1.6 to 1.0 fish) across cumulative chlorophyll concentrations (Figure 8). Cumulative chlorophyll and cumulative temperature each were included in only one final model. However, cumulative chlorophyll was a significant predictor in the positive component in the final model of lingcod ($Z=-3.08$, $p<0.05$), whereas cumulative temperature was not a significant predictor in the positive component of final model of Black rockfish ($Z=-1.66$, $p=0.09$).

Cumulative temperature exhibited an overall negative relationship in the final zero-altered model of Black rockfish (Figure 6). The negative effects, from the cumulative temperature covariate, in the positive element of the zero-altered model resulted in a negative effect in estimates of relative Black rockfish abundance. Relative abundance estimates declined by 40%, from 5.5 to 3.3, across the observed degree day values (Figure 8). Although the cumulative temperature covariate was only included in one final model, the effect of the covariate on relative abundance was strong.

Cumulative upwelling and averaged upwelling were the most influential predictors of the lagged oceanographic variables, with each being included in 2 of the 3 final models (Figure 6). Cumulative upwelling had a positive effect on counts of Black rockfish, whereas it had a negative effect on counts of Lingcod. Black rockfish counts

had a proportional increase of 177% (from 3.0 to 8.4 fish) in relative abundance, across the range of cumulative upwelling values (Figure 8). Lingcod experienced a proportional decrease of 41% (from 1.8 to 1.1 fish), across the range of cumulative upwelling values (Figure 8). Interestingly, this negative effect on relative Lingcod abundance was the net result of a positive effect of cumulative upwelling on the probability of fish presence combined with a negative effect on the positive count of the species (Figure 6).

Averaged upwelling had a positive, but relatively weak, association with both Blue rockfish and Lingcod relative abundances (Figure 6). In the positive element of zero-altered models, the Blue rockfish group and Lingcod displayed positive effects from averaged upwelling. Averaged upwelling also had a positive influence on probability of obtaining positive counts (binomial element) in Lingcod. Combined zero-altered elements resulted in proportional increases of 128% (from 0.7 to 1.5 fish) and 130% (from 1.0 to 2.2 fish) in the Blue rockfish group and Lingcod relative abundance, respectively (Figure 8).

Spatial, Temporal, and Size Effects

Distance to port (a proxy for fishing pressure), port, year, and size were all influential predictors in the final models (Figure 6). Distance to port displayed stronger effects in final models of Black rockfish and the Blue rockfish group, than that of Lingcod (Figure 9). Predicted Black rockfish relative abundance declined by 79% as the distance to port increased from 0 to 44 km. This decline in Black rockfish was driven by the probability of catching the species, which declined from 90% at values closest to port to 19% at the

greatest distance from port. Blue rockfish had the greatest proportional change in relative abundance, from 0.3 to 4.4 fish (1403% increase) across the observed distances from port. The uncertainty associated with this proportional change is relatively high, however.

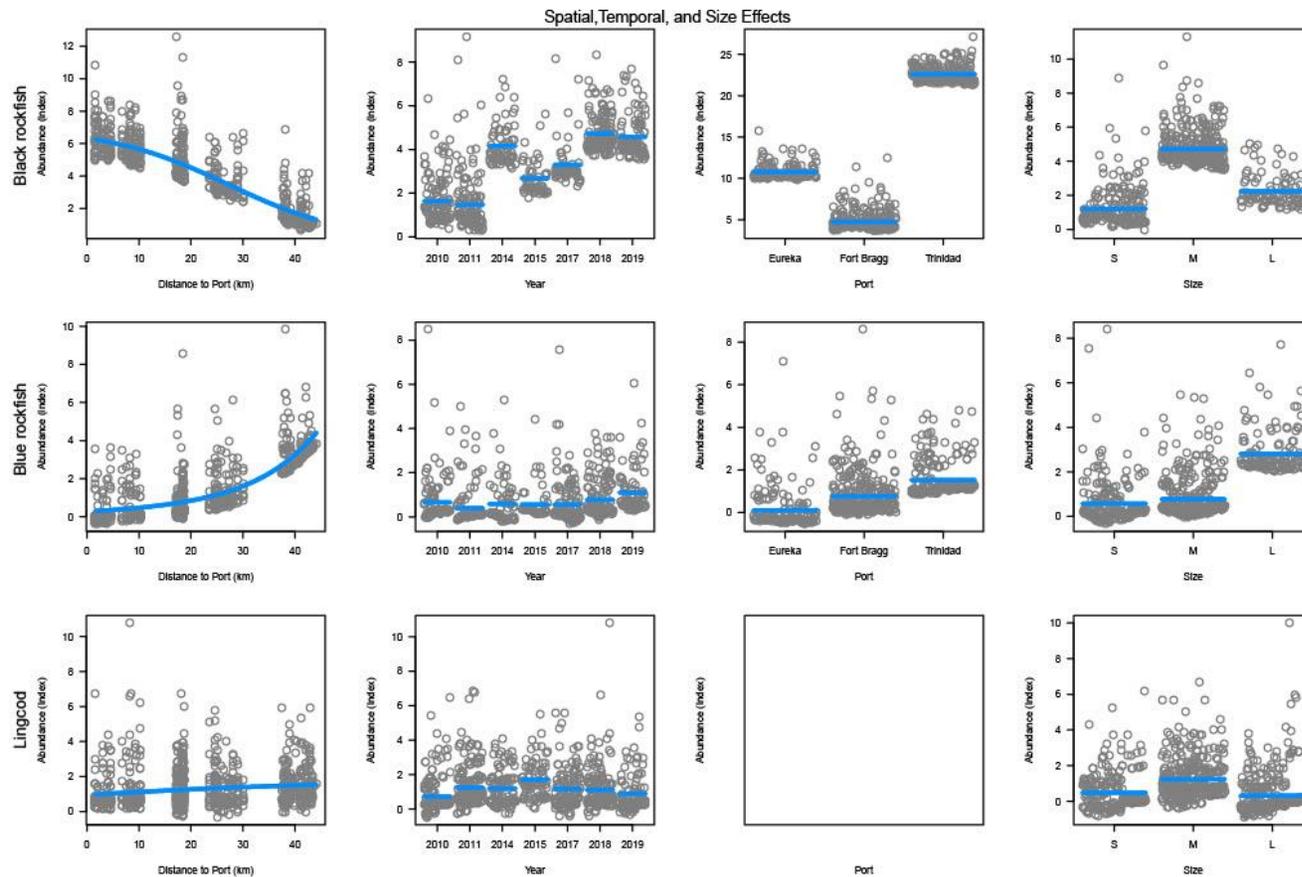


Figure 9. Effects of spatial, temporal, and size covariates on predicted Black rockfish, the Blue rockfish group, and Lingcod catches based on final zero-altered models. Blue lines are the estimates of relative abundance (when holding all other covariates at their medians), generated from the product of estimates from zero-truncated models (positive) and logistic

regressions (binomial). Points are partial residuals. Blank panels represent covariates that were not included in the final, best-fit models. It should be noted that no sampling occurred in the years 2012, 2013, and 2016.

Catch across years varied between species (Figure 9). Relative abundance of Black rockfish showed a generally increasing trend in catch. Although the overall trend is positive, Black rockfish counts declined in 2015, compared to that of 2014 and 2017 (no sampling occurred in the years 2012, 2013, or 2016), but show a continual increase, in subsequent years. The Blue rockfish group had generally similar relative abundances across all years, although 2011 had slightly lower relative abundance and 2019 had slightly increased relative abundance (Figure 9). Variability in the partial residuals were high for Blue rockfish counts, however, suggesting greater uncertainty in the estimated relative abundances. In contrast to the Blue rockfish group and Black rockfish, Lingcod displayed a slightly dome-shaped (unimodal) relationship between relative abundance and year with a peak in 2015; however, the uncertainty associated with estimated relative abundances is high based on the partial residuals (Figure 9).

Port was only included in the final models of Black rockfish and Blue rockfish (Figure 6). For both species, relative abundance was greatest out of the port of Trinidad (Figure 9). Uncertainty was greater in models of Blue rockfish, however, suggesting that relative abundances out of the ports of Trinidad may not be that different from any other port. The effects of port in final models of Black rockfish and Blue rockfish are relatively similar in nature to estimates generated from CPUE estimates of species by port and year (Figure 5 and Figure 9).

Fish size bin had strong effects on the estimates of relative abundance for all species (Figure 9). For Black rockfish, medium sized fish had the highest relative abundance.

Blue rockfish in the large size group had the highest mean relative abundance. Lingcod relative abundance was approximately similar across each size group with slightly greater mean counts of medium sized fish.

Variability in Length

Model selection with AIC was used to determine the best model structure for explaining the observed variability in fish lengths. Comparisons revealed mixed GLMs to be substantially better than mixed GAMs, with AIC values lower than that of mixed GAMs by 11-19 points. Among the 381 models examined with all possible covariate combinations for each species, the best models based on AIC had structures that included all covariates (Figure 10). AIC differences between the optimal and next best models ranged from 2.5-2.9 for each species. The effects of the covariates on fish length were largely consistent across species, except for Blue Rockfish (Figure 10). However, the final models did not explain much of the variability in the length of the three species, with conditional R^2 values of: 0.21, 0.15, and 0.12 for Black rockfish, Blue rockfish and Lingcod, respectively. Response plots of the effects of individual predictors (see below) demonstrate that most predictors had relatively minor effects on fish length.

Species	VRM	Depth	Hard Cover	Percent Reef	Distance to port	Year	Port
Black rockfish	-	-	-	+	+	*	*
Blue rockfish	-	+	-	+	-	*	*
Lingcod	-	-	-	+	+	*	*

Figure 10. Relative effects of predictor variables for best fit GLMMs of fish length. Positive relationships between the response variable and the seven predictor variables (columns) are illustrated in green (+), while negative relationships are in red (-). The blue coloration (*) identifies categorical variables that were included in the best-fit model.

Substrate effects

The effects of the four substrate covariates on length were generally weak for all three species, with the proportional effects typically being <5% across the observed ranges of the covariates (Figure 11). VRM had minor negative effects on length across all species; fish length was predicted to decrease by only 3% for Black rockfish and 2% for Blue rockfish across the observed VRM values, but Lingcod decreased by 7% (Figure 11). Depth had a negative effect on lengths of Black rockfish and Lingcod (i.e., lengths were lower at shallower depths) but depth had a positive effect on Blue rockfish lengths (Figure 10 and Figure 11). Although the effects of depth on the length of Lingcod and Blue rockfish were negligible, Black rockfish length was predicted to decrease 18% (from 312 mm to 256 mm) across the range of observed depths. Hard cover had weak negative effects on length for Black rockfish and Lingcod ($\leq 3\%$), but Blue rockfish lengths were predicted to decrease by 28% (from 188 mm to 145 mm) across the observed scaled hard cover values (Figure 11). Unlike that of the previous covariates, the relationship between length and percent reef was positive across all species. Again, the relationships were negligible for Black rockfish and Lingcod (with increases of only 5% and 2%, respectively), whereas length had a more substantial increase of 21% (149 to 181 mm) in Blue rockfish over the range of percent reef values.

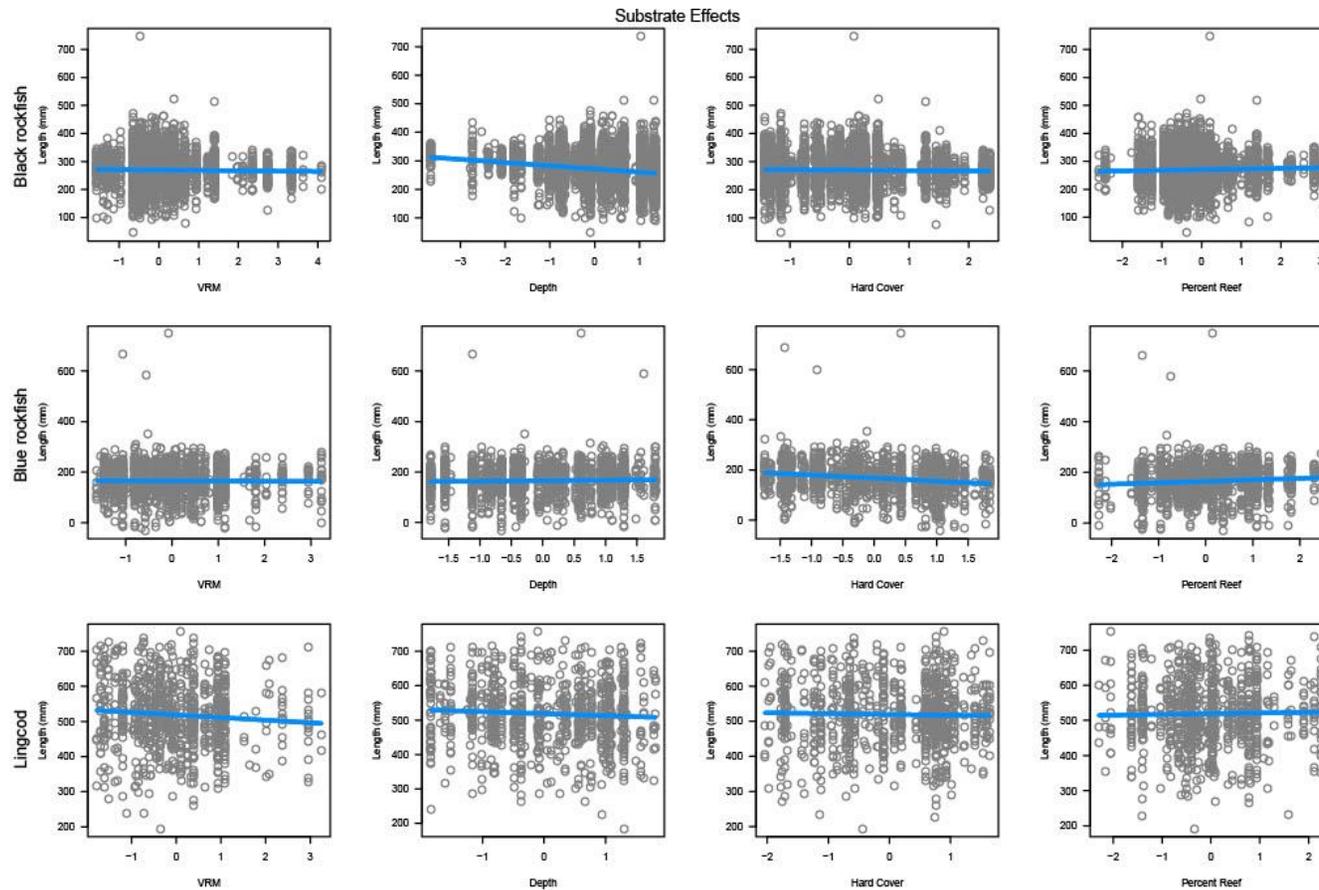


Figure 11. Effects of the four substrate covariates on predicted Black rockfish, the Blue rockfish group, and Lingcod lengths based on final GLMMs. Blue lines are the estimates of length (when holding all other covariates at their medians, and all other categorical covariates at their modes), generated from the product of estimates from GLMMs. Points are partial residuals. All covariates were scaled to have a mean of 0 and a standard deviation of 1.

Spatial and Temporal effects

Distance to port, year, and port had varying effects on length across species (Figure 10 and Figure 12). First, the magnitude of the relationship between distance to port and length was consistently larger than most of the substrate effects. Second, year was only positively associated with length (i.e., length increasing with each year) with one species. Finally, the relationship between port and length was variable across each species, with no individual port associated with larger fish across all species.

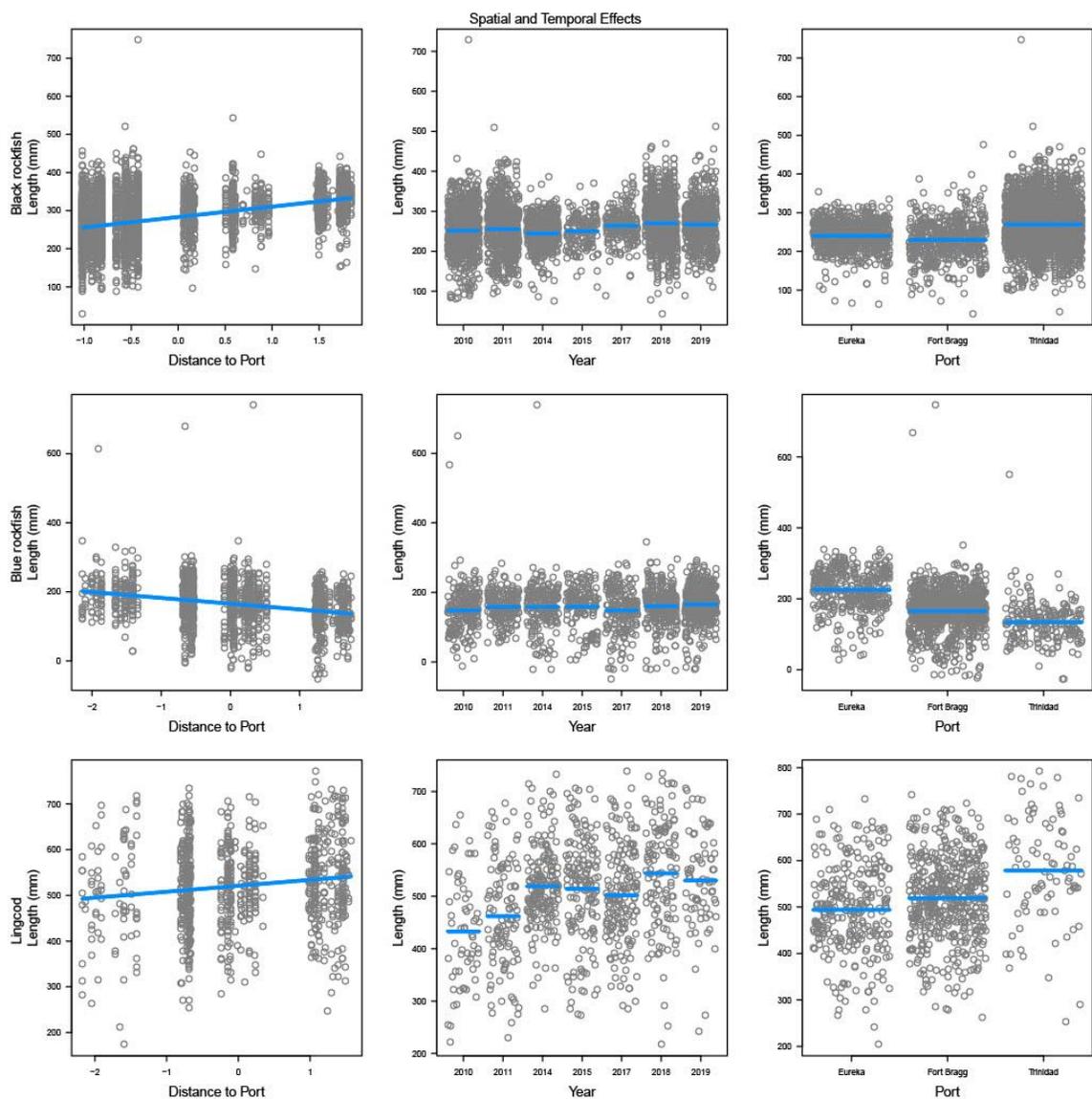


Figure 12. Effects of spatial and temporal covariates on lengths of Black rockfish, the Blue rockfish group, and Lingcod, based on the best fit GLMMs for each species. Blue lines are the estimates of length (when holding all other continuous covariates at their medians, and all other categorical covariates at their modes), generated from the product of estimates from GLMMs. Points are partial residuals. All covariates were scaled to have a mean of 0 and a standard deviation of 1.

The relationship between distance to port and length was positive for Black rockfish and Lingcod, while negative for Blue rockfish (Figure 10 and Figure 12). Distance to port, along with the random effect, explained most of the variability in models of Black rockfish and Blue rockfish; conditional R^2 values of models including only distance to port, and the random effect, of Black rockfish, Blue rockfish, and Lingcod were 0.19, 0.14, and 0.03 respectively. Black rockfish and Blue rockfish had the greatest proportional change in length, with respect to distance to port. Length increased from 255 mm to 333 mm (31%) in Black rockfish, while Blue rockfish decreased from 201 mm to 136 mm (32%) across the observed distances. Despite being included in all the best-fit models, year did not have strong effects on length for any of the three species and exhibited high variability in its partial residuals. Estimates of length of Black rockfish and Lingcod were greatest out of the port of Trinidad (270 mm and 579 mm), while Black rockfish length was smallest out of Fort Bragg (230 mm), and Lingcod length was smallest out of Eureka (494 mm). Blue rockfish length was greatest out of the port of Eureka (225 mm), while smallest out of Trinidad (134 mm).

MPA effects

Effects of protection status (i.e., MPA vs. reference site) on relative fish abundance and fish length were evaluated using the best fit models that resulted from a model selection procedure for each of the three species. A total of about 25,000 zero truncated models (n=154-262), 7,500 logistic regression models (n=725-928), and 765 mixed GLMs (n=842-1594) were generated for each of the three species, using all possible combinations of the possible covariates. The model with the lowest AIC was chosen as the final, best-fit model for each set of comparisons, although delta AIC values for the second-best models also indicated some reasonable support as well, ranging from 0.4 – 3.3 depending on the species and model.

In the best-fit models of relative fish abundance, an effect of protection status was only included in the model for Lingcod (Figure 13). Lingcod had a higher probability of occurrence in the MPA sites (0.61) relative to the reference sites (0.49), and this helped drive estimates of Lingcod relative abundance that were 24% greater in the MPAs. Despite this, the magnitude of the difference was small (1.5 fish in MPAs relative to 1.2 fish in the reference sites) and the uncertainty in the estimates was large given the variability in the data (Figure 13). Protection status did not receive substantial support, as indicated by AIC, for inclusion in the best-fit models of Black or Blue rockfish.

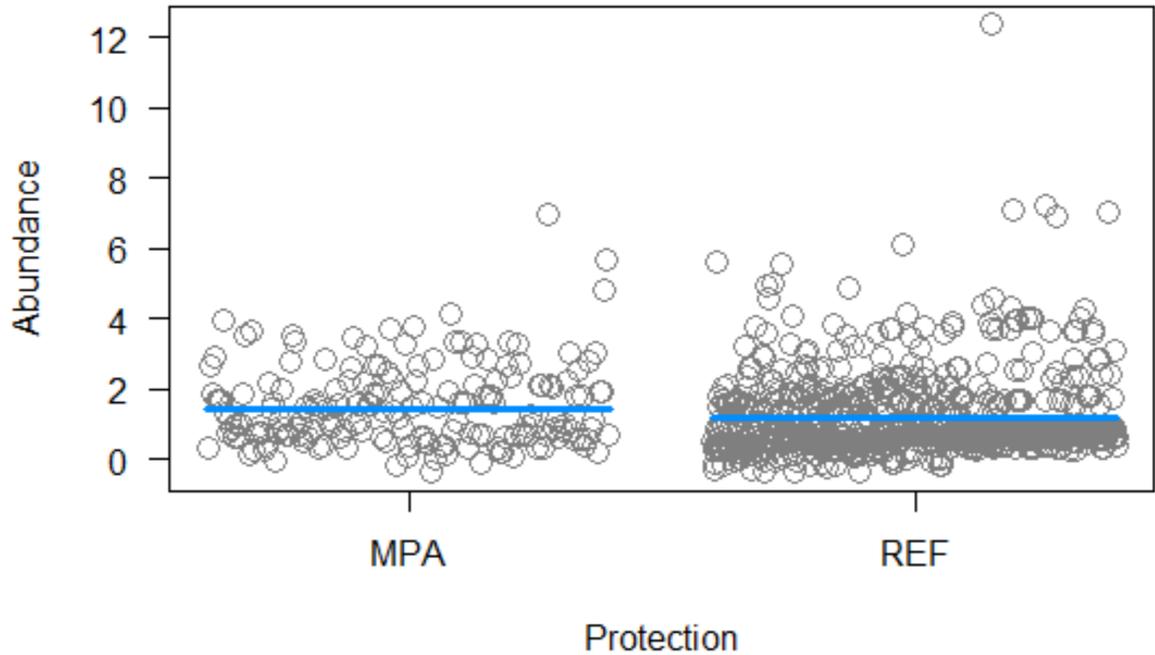


Figure 13. The effect of protection status on relative abundance in the final hurdle model of Lingcod when all other covariates are held at their median (continuous variables) or mode (categorical variables). Blue lines are the estimates of length (when holding all other continuous covariates at their medians, and all other categorical covariates at their modes), generated from the product of estimates from zero-truncated models (positive) and logistic regressions (binomial). Points are partial residuals.

The best-fit models of fish length, for all species, included an interaction between protection status and port, though the interaction was only significant in Blue rockfish ($t=-3.54$, $p<0.05$; Figure 14). The effects differed by species. The effect of protection status on lengths of Blue rockfish varied by port; Blue rockfish lengths were 35 mm (21%) shorter in the MPA out of Eureka (South Cape Mendocino SMR) relative to its reference site, whereas fish in the MPA out of Fort Bragg (Ten Mile SMR) were 22 mm (14%) longer than fish in their paired reference site. Protection status, although it showed a positive trend, had negligible effects on lengths of Black rockfish and Lingcod out of the port of Eureka (7% and <1% larger in the MPA, respectively) and Fort Bragg (7% and 3% larger in the MPA, respectively).

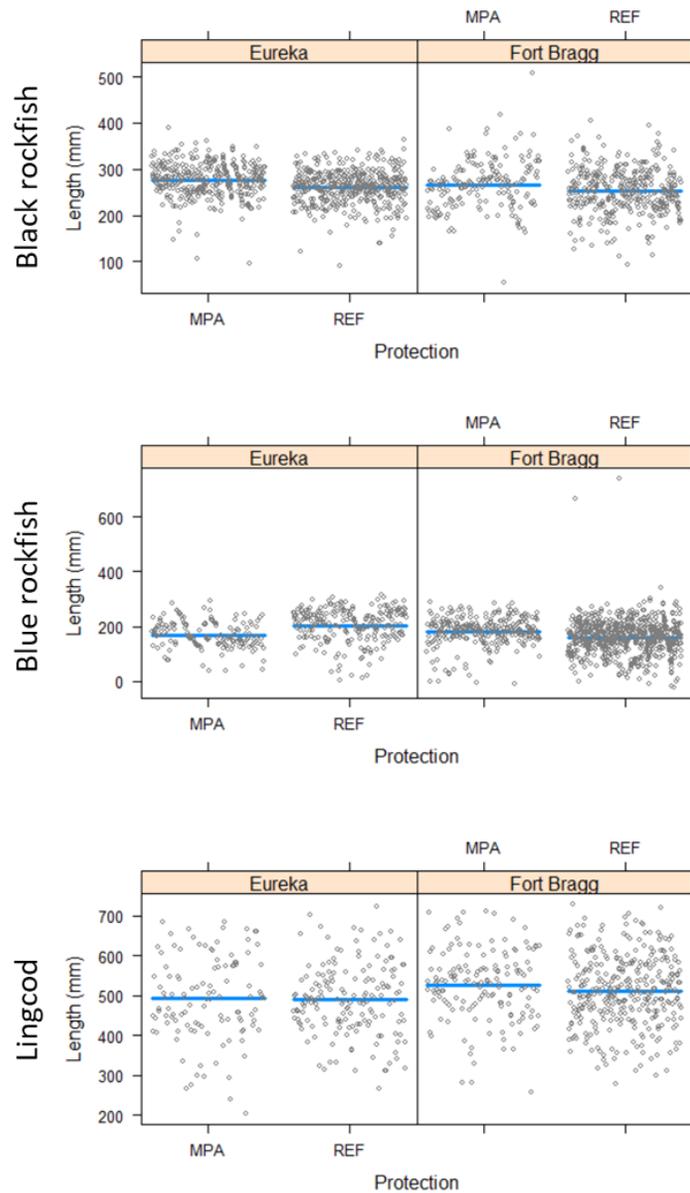


Figure 14. The effect of protection status, by port, on length, in the final hurdle model of Black rockfish, the Blue rockfish group, and Lingcod when all other covariates are held at their median (continuous variables) or mode (categorical variables). Blue lines are the estimates of length (when holding all other continuous covariates at their medians, and all other categorical covariates at their modes), generated from the product of estimates from GLMMs. Points are partial residuals.

DISCUSSION

Long-term monitoring of MPAs along the north coast of California aids fisheries managers and researchers in creating effective management strategies related to harvest regulation, protection, and restoration of Black rockfish, the Blue rockfish group, and Lingcod. MPAs also act as a powerful tool for examining the effects of local fishing pressure versus other factors. The results generated from this study indicated that substrate, oceanography, spatial and temporal factors, and fish size affected species abundance and size, although the specific relationships varied across species. The results also provide insight into likely time frames for seeing positive effects from MPA establishment, in the form of notable increases on abundance and size.

Analysis of abundance

Effects of Environmental Predictors

Substrate covariates were prominent factors in the final models of all species. Models predicting abundance of Black rockfish were especially influenced by substrate covariates, with all substrate covariates being included in the final models. The strength of the relationship between the substrate covariates and abundance was also stronger for Black rockfish than for the Blue rockfish group or Lingcod. The strength of the effects may be related to the increased number of positive counts obtained by Black rockfish, as compared to the other groups. This may also explain why the relationships seen in the Blue rockfish group are stronger than those seen in Lingcod.

Substrate covariates played an important role in describing variability in abundance and had the strongest effects on relative abundance of Black rockfish (Figure 6 and Figure 7). The effects of depth on abundance of Black rockfish coincide with the results found by Staton (2017); Black rockfish abundances are greater at shallower depths and decrease in deeper locations. The proportional change in relative abundance (738% increase) also suggests that depth may be one of the most important drivers of rockfish abundance, among the substrate variables tested within this study. In contrast, the percent of hard cover had the second greatest effect on Black rockfish, negatively influencing relative abundance (56% decrease). Intuitively, the negative relationship with hard cover suggests Black rockfish abundance is greater with decreased rocky substrate, which conflicts with the notions in current literature that Black rockfish are associated with rocky substrate (e.g., Carr 2001). However, vector ruggedness measure (VRM) and percent reef were also good predictors of relative abundance in Black rockfish (with VRM yielding a proportional increase of 60% and percent reef a proportional change of 157%). Black rockfish abundances may be driven more so by the presence of complex habitat (i.e., habitat with increased vector ruggedness) than habitat that consists of only hard bottoms. For example, more complex habitat could provide Black rockfish with more refuge from predators, which may be important for juvenile or small rockfish (Johnson, 2006). Locations with more refuge (from increased vector ruggedness) could translate into larger abundances at that site, whereas less complex reefs might have decreased abundances due to increased predation of juvenile or small rockfish that aren't able to find adequate refuge. Predation may not be the sole limiter of population

abundances, however. The relationship between abundance and reef complexity may also be related to behavioral or density dependent factors related to prey availability. Increases in reef complexity would not only allow for greater refuge from predators but would allow for more areas to potentially ambush prey. The VRM and percent reef covariates may also be picking up signals from metrics that we did not account for, such as an edge effect, in the form of the distance from the edge of the reef, or the interface between substrates. Edge effects have been documented in other reef-associated species, with increased densities of fishes occurring at the interface between a reef and another type of habitat (Dorenbosch et al., 2005; Langlois et al., 2005).

Though substrate covariates were prominent in the final models for fish abundance (Figure 6), they displayed stronger relationships to relative abundance of Black rockfish than in both the Blue rockfish group or Lingcod (Figure 7). Habitat preferences and site selection of Blue rockfish and Lingcod have been widely studied, and suggest that Blue rockfish and Lingcod both should have strong relationships with hard, rocky reefs, at varying depths (Jorgenson et al., 2006; Petrie and Ryer, 2006; Tolimieri et al., 2009). The weak or absent relationships within this study may be related to two methodological constraints of this study. First, it should be reminded that the Blue rockfish group in this study consisted of observations of both Blue rockfish and Deacon rockfish. Deacon rockfish were first described in 2015 (Frable et al., 2015) and not identified as separate species in this study until 2017. Since 2017, the proportion of Deacon rockfish in the Blue rockfish group captured for this project has been increasing,

making up 22%, 42%, and then 60% of the Blue rockfish group in 2017, 2018, and 2019, respectively. This increasing trend may be reflective of the scientific crews' ability to correctly identify the species, with the later year being truly reflective of previous proportions. Deacon rockfish appear similar to Blue rockfish but display different behaviors and habitat preferences, such as depth preferences, feeding habits, site fidelity, and migratory (diel) movements (Frable et al., 2015; Rasmuson, 2021). Within this study, the effects of the substrate covariates may be masked by the differences among these two species. Second, the site selection process and the sampling stations generated for this study follow those of Staton (2017). Consequently, they may only predominately encompass favorable habitat preferences of the Blue rockfish group and Lingcod. In association with selection of favorable habitat, the selected sampling stations may not present enough variability for models to detect differences in habitat complexity. Future studies should consider modeling Deacon and Blue rockfish separately when examining how environmental factors drive relative abundance, and potentially expanding the range of substrate conditions.

Lagged oceanographic covariates were generated as proxies for quantifying the potential effects of oceanographic conditions on the juvenile stages of the studied species. Combined, these lagged covariates act as a measure of the effect of ocean productivity on the species in their larval and juvenile stages. Although the covariates were exploratory in nature, they still proved to be useful coarse tools that aided in describing the variability in abundance of Black rockfish, the Blue rockfish group, and Lingcod. The relationship of

fish abundance to these lagged oceanographic covariates are consistent with hypotheses proposed by fisheries oceanographers that regional oceanographic factors are key drivers of rockfish recruitment and growth (e.g., Bjorkstedt, 2002; Laidig, 2010; Wheeler et al., 2017). Although not all lagged oceanographic variables had a strong relationship with abundance, they may be capturing signals that are related to potential growth and survivorship of fishes in their juvenile stages.

The effects of lagged oceanographic covariates had relationships that signaled the effects of system productivity upon the species in this study. Increased relative abundance of Black rockfish and decreased temperatures coinciding with increased abundances at more intense upwelling (i.e., increased cumulative upwelling) is the essence of upwelling's positive influence on juveniles and recruitment. Increased temperatures can increase rockfish growth rates and the rate at which sexual maturity is reached (e.g., Yelloweye rockfish (*Sebastes ruberrimus*); Harvey, 2009). However, the growth of the Yelloweye rockfish is also dependent on adequate nutritional supply; the higher temperatures increase the fish's metabolic rate and food supply demands. In the California Current System, increased temperature tends to be associated with decreased upwelling, these conditions have been strongly correlated with the presence of nutrient-poor copepods and decreased krill abundance (Cavole et al., 2016). Conversely, lower temperatures are associated with stronger upwelling and lipid-rich copepods, and increased krill abundance (Becker et al., 2007; Fontana et al., 2016). As prominent food sources for both larval and juvenile rockfish (Ralston et al., 2013), the abundance and

quality of these prey groups would likely affect rockfish nutrition, metabolic rates, and population dynamics. In this study, the response of relative abundance of Black rockfish to favorable upwelling conditions is consistent with the importance of the productivity of the upwelling system as a driver of fish abundance. The positive relationship between relative abundance of Black rockfish and cumulative upwelling is consistent with current literature as Black rockfish tend to have increased levels of recruitment with increased levels of upwelling (Markel and Shurin, 2020).

The positive relationships between upwelling and Black rockfish relative abundance (as well as increased relative abundances at decreased temperatures as a result of increased upwelling) may be capturing other signals that have been shown to be important predictors of rockfish recruitment, such as the onset of the upwelling season, the timing of the spring transition, or an anomalous oceanographic event (Barth et al., 2007; Bograd et al., 2009; Holt and Mantua, 2009). Cumulative upwelling was quantified as the sum of the difference between daily upwelling intensity and the yearly mean intensity; meaning that increased cumulative upwelling calculations is the result of consistently stronger upwelling throughout the year, pulses of abnormally increased upwelling intensity, an early onset to the productive upwelling season, or some combination of these. The strength of regional upwelling has been shown to be relatively consistent from year to year, without abnormally strong pulses, with deviations at the decadal or multi-decadal scale (Jacox et al., 2014). This supports that upwelling may just be beginning earlier in the year, resulting in increased cumulative upwelling indices.

Upwelling beginning earlier in the year would provide more opportunity for larval and juvenile fish to be in contact with habitat and conditions that are favorable for growth (Bjorkstedt et al., 2002; Wheeler et al., 2017), which coincides with Cushing's (1990) match-mismatch hypothesis and may be an explanation for the increased abundances seen in all species. Alternatively, the positive effects may be driven by the anomalous warm water event, known as "the blob". The blob was a warm water event between 2015 and 2016 that increased temperatures in the California Current System which decreased upwelling and resulted in projections of decreased recruitment and adult fish abundances (Cheung and Frolicher, 2020). In this study, the positive signals of upwelling, on all species, may be capturing the poor recruitment that was associated with the blob: decreased abundances of Black rockfish at increased temperatures, and decreased abundance of all species due to decreased upwelling (cumulative and averaged).

The lack of more noticeable relationships with oceanographic conditions and the Blue rockfish group may be a product of Blue rockfish and Deacon rockfish being considered together, as previously mentioned. The grouping of the two species may be preventing any signals from the oceanographic covariates from being detected. Blue rockfish and Black rockfish share similar affinities towards upwelling productivity (Larson et al., 1994; Laidig, 2010; Markel and Shurin, 2020), and would therefore be expected to have similar relationships between relative abundance and the oceanographic covariates. The differences in behaviors, ranges, and preferences, between Blue rockfish

and Deacon rockfish may again be obscuring any signal, and it is advised that future work differentiate these two species.

Spatial, Temporal, and Size Effects

In this study, the results from the spatial, temporal, and size covariates provide support for use of these covariates in past and future models, while also suggesting potential improvements for future models. In Staton's (2017) GAMs of CPUE, distance to port was an important predictor, that had a positive relationship with CPUE for Black rockfish and a dome-shaped (unimodal) relationship with CPUE for Lingcod and Blue rockfish (CPUE was lower at short and long distances from port, and highest at moderate distances from port). Although the relationships differ in this study (as distance to port negatively affected Black rockfish relative abundance, and positively affected the Blue rockfish group and Lingcod) the strength of the relationship between distance to port and relative abundance of Black rockfish and Blue rockfish supports the continued importance of distance to port as an important covariate. The differences in the relationships may be due to the differences in the data used. Although this study incorporates more years of data, the previous work included more ports (i.e., more variability in distance to port). Those additional ports also had extremely different levels of fishing pressure: one site was considered far from port with overall high levels of fishing pressure and low CPUE, while another was a moderately far from port with relatively low fishing pressure. In this study, abundances of Black rockfish were greatest out of Trinidad (Figure 9), and the stations closest to port had the best habitat and most of

the observations. Although I initially expected that Trinidad could be skewing the effects of distance to port, the negative relationship between distance to port and relative abundance of Black rockfish remained upon the removal of Trinidad data, indicating that some other factor may be influencing the negative relationship. Bringing the data from additional ports would provide more robust insight into the effect of distance from port, and potentially provide clarity as to why different relationships are being seen.

Black rockfish and the Blue rockfish group displayed strong differences in relative abundance between ports. Both Black rockfish and the Blue rockfish group were most abundant out of the northern most port, Trinidad. These results indicate that Trinidad may hold the most suitable habitat for these species. The result may also indicate that some unaccounted-for environmental factor related to Trinidad, may be driving the increased abundances seen out of this port. Further investigation into the environmental dynamics associated with Trinidad should be considered within future studies. Examination of the spatial distribution of Black rockfish relative abundance reveals a latitudinal trend of increasing abundance with distance north. The California Department of Fish and Wildlife describes the range of Black rockfish as from Southern California to the Aleutian Islands, Alaska, but uncommon south of Santa Cruz, California. The decrease in relative abundance moving south, towards Fort Bragg, would coincide with the range described, and it might be expected that population density would decrease towards the southerly limit of the species range. This same latitudinal trend may be present in the Blue rockfish group as well. The Oregon and Washington Departments

of Fish and Wildlife describe Deacon rockfish abundances to be highly concentrated off the coast of Oregon and northern California, while the California Department of Fish and Wildlife describes Deacon rockfish abundances to be greatest out of central and southern California. These opposing latitudinal preferences are seen within the spatial results from the analysis of abundance; Trinidad (northern site) and Fort Bragg (southern site) hold the highest abundances of the sampled ports, and the preferences of Blue rockfish and Deacon rockfish may be the driver behind why these two ports hold more fish than our central site (Eureka).

In models of relative abundance of Black rockfish year was also an important covariate, although the exact mechanisms that drive abundance of fish may not be exactly clear. One explanation of the effects of the year covariate on the relative abundance of Black rockfish may be tied to differences in cohort strength (beyond any differences captured by the lagged oceanographic variables) that could contribute to the increasing trend seen in the year effect. The increasing trend in abundance may also be reflective of effective management practices. From 2015-2019, the California Department of Fish and Wildlife imposed daily, sub-bag limits, or a reduction in daily recreational take. The reduction in fishing pressure may be the reason catch rates increased in later years, such as 2018 and 2019, in contrast to 2010 and 2011 (Figure 9). Lastly, the year covariate may be tied to oceanographic events. Increased sea surface temperatures in 2014, followed by an El Nino in 2015-2016 (resulting in “the blob”), were present within the California Current System (Levine and McPhaden, 2016; Cheung and Frolicher, 2020). Increased

water temperatures, within an optimal range, increase the metabolic rates of fish, which subsequently drives fish to feed more often (Houde, 1974; Buentello et al., 2000; Neuheimer, 2013). An increase in feeding activity, and a decrease in available food (as a product of decreased upwelling from the blob), could have made fish hungrier and more vulnerable to capture in 2014 and 2015, especially since warmer coastal waters in this region generally coincide with reduced upwelling, and lower ocean productivity and food availability. The year covariate is likely capturing a combination of signals produced by environmental, physiological, or anthropogenic variables, beyond those that were considered in the models. Regardless, these yearly trends in relative abundance can be considered a standardized index of annual abundance for these species and are useful in monitoring of the populations. Future models should continue to include this covariate in order to capture annual changes and any unmodeled signals.

The size covariate shows higher catches of fish in the medium and large bins, relative to the small bins, across all species. This is related to the size selectivity of hook and line fishing gear. For example, some observed Blue rockfish lengths in the small size bin (Table 5) were smaller than the larger fishing lures (Figure 3) that are not well-suited for or designed for catching such small fish. Inclusion of size as covariate in the models of abundance helped standardize for differences in catch rates due to the size selectivity of the gear.

Analysis of Length

Predicting fish length can be challenging due to the many factors involved with fish growth and the wide variability in fish lengths. Distance to port was consistently the strongest predictor of fish length (Figure 12); however, the effect it had on lengths for the Blue rockfish group (reduced length with distance to port) was unexpected. Other predictors also played important roles in describing the variability in length, though different species appear to have affinities towards different environmental factors, suggesting the lengths of fish are not universally affected by the same habitat. The year and port covariates also had different effects across species, which may allude to other mechanisms that are influencing growth across the species.

Distance to port has been shown to be a good proxy for relative fishing pressure (Starr et al. 2008; Barrett et al. 2012; Staton, 2017), and mean length was expected to increase as distance to port increased was seen for Black rockfish and Lingcod. Relative fish size has been shown to be negatively impacted in areas with high fishing pressure and can be expected to decrease through time with increased pressure (Cambell and Pardede, 2006; Wilson et al., 2010; Valles et al., 2015; Goetze et al., 2017). The positive relationship between length and distance from port for Black rockfish and Lingcod is assumed to reflect the proportionally lower fishing pressure experienced by areas farther from port. Here along the California northern coast some sampling sites are more than 40 km from the nearest port. The distance, coupled with inconsistent and variable weather, and a low human population density (compared to that of other major ports in California),

result in comparatively low fishing pressure. The reasons behind the negative relationship seen between distance to port and length of the Blue rockfish group, though, remains unknown. Though the models didn't explain a large amount of the variability in length of each species, distance to port continued to prove itself a useful predictor and proxy for fishing pressure (Figure 10).

Depth, hard cover, and VRM were the strongest habitat predictors of length for Black rockfish, the Blue rockfish group, and Lingcod, respectively. As previously mentioned, all species are associated with similar habitat, yet the difference in the relative effects of the substrate predictors suggest that subtle differences in habitat may influence fish growth. The relationship between depth and size of Black rockfish seen in this study (i.e., Black rockfish are smaller as depth increases) is the opposite of what has been seen in other species of Rockfishes (Richards, 1986), but may still relate to a stratification of fish size with increasing depths. This same size stratification may also be present at varying degrees of hard cover, for the Blue rockfish group, and VRM for Lingcod. More research is needed to further solidify conclusions about the relationships between the different substrate factors and their independent effects on fish size; such analyses would benefit greatly from having individual age information to correct for the effect of age on fish size.

The analysis revealed that lengths of Black rockfish and the Blue rockfish group were relatively similar through time, but that the length of Lingcod increased through time. Though the relative abundance of Lingcod did not appear to change through time,

the increase in average size suggests that the fish are growing. The increase in Lingcod length could be the result of one or more strong cohorts or year-classes being continuously sampled through time. Adult Lingcod, especially males, have slow growth rates (Smith and MacFarlane, 1990), and the results showed a relatively gradual annual change in length from the earliest sampling year to latest sampling year (about 100 mm or ~23% over 9 years).

The effect of port on lengths, as with the year covariate, could be driven by various un-modeled factors. Black rockfish length, like abundance, increased in a northerly direction in this study. The latitudinal trend in increasing length, again, may be a product of the natural range of Black rockfish, with abundances and sizes being greater towards the center of their range. The Blue rockfish group was largest at the central sampling site (Eureka) and smaller at the northern and southern sampling sites (Trinidad and Fort Bragg, respectively). The separation of the species may reveal latitudinal trends that are representative of their ranges as well. Blue rockfish are more common south of Monterey Bay, California, while Deacon rockfish are more common north of Monterey Bay, California (Bizzarro et al., 2020). Modeling the lengths of the species separately might reveal that Blue rockfish increase in length to the south, and that Deacon rockfish grow larger with distance northward. The Lingcod range extends from Alaska to Baja California; because of the large range of Lingcod, latitudinal trends in size were not expected. Interestingly, lengths of Lingcod were largest out of the port of Trinidad, whose sampling sites were much closer to port than that of Eureka or Fort Bragg. The

analysis of abundance also highlighted Trinidad as the port with the highest relative abundance of Black rockfish and the Blue rockfish group. Fishing pressure on Lingcod may be lower out of Trinidad; the deleterious effects of fishing pressure, on size, are not affecting Lingcod as strongly out of Trinidad (Cambell and Pardede, 2006; Wilson et al., 2010; Valles et al., 2015; Goetze et al., 2017). To test this hypothesis would require further investigating the relationship between the interaction of port and distance to port, and length.

MPA Effectiveness

In this study, it was hypothesized that the positive effects of the MPAs might begin to be detected through the modeling of relative abundance and fish size. However, strong positive signals generated by MPAs were not evident and this could be related to the timing of the establishment of MPAs. First, as previously mentioned, Starr et al., (2015) showed that an extensive amount of time (sometimes 20+ years) is needed to begin to see strong positive effects from the establishment of MPAs, and this study is observing the effects roughly 5 years after the implementation of MPAs on the north coast, as MPA establishment in northern California only occurred in 2014. In some Rockfish Conservation Areas (RCAs) off the coast of British Columbia, marine protected areas also did not show any positive effects after 9 years of conservation (Haggarty et al., 2016). Second, the MPAs and their paired reference sites in this study are located relatively far from port (>20km) and in areas with volatile environmental conditions for many months of the year. These characteristics result in reduced overall fishing pressure,

especially when compared to the MPAs in central and southern CA observed by Star et al. (2015). In concert, decreased historical fishing pressure and a short observation period would dampen the positive signals that should be expected from the establishment of MPAs (Rodwell et al., 2003). Despite the conditions masking any positive effects from these specific MPAs, the results of this study did show that there were some small, but detectable, positive effects associated with the MPAs. Most notably, Lingcod demonstrated slightly higher relative abundances inside the MPAs than the reference sites, as well as larger mean size at the South Cape Mendocino SMR. Also, Black rockfish had larger mean sizes at both MPAs, relative to their paired reference site. The results of this study coincide with the general findings of the CCFRP (Final Report, 2021): Black rockfish size was larger in MPAs whereas relative abundance (CPUE) was not different from that of paired reference sites, and Lingcod relative abundance (CPUE) and biomass was found to be higher in MPAs than in paired reference sites. Although the differences are not dramatic and uncertainty is evident within model estimates, the signals produced within the study warrant continued monitoring of the protected areas, given the expectation that positive benefits of MPAs could take 20+ years to become strongly evident (Starr et al., 2015).

Modeling Methods and Uncertainty

Zero-altered models and GLMMs proved to be useful in describing the variability in relative abundance, size, and MPA effects. The strong relationships illustrated between the covariates and relative abundance are evidence of the utility of zero-altered models to

model fishery-independent data (Maunder and Punt, 2004). Future fishery-independent studies utilizing count data should explore the use of these zero-altered models as well as zero-inflated models, which were not used in this study. Although some models did not explain a large amount of the observed variability (e.g., models for fish length), the modeling methods were still able to detect effects for several variables, while still meeting the assumptions necessary for modeling these data (e.g., nesting of observations within the GLMMs and accounting for large proportions of zeros). The models also allowed for an assessment of the effects of the MPA implementation. Future work would benefit from increasing the sample sizes (which were limited in this study due to funding constraints), considering additional variables and including observations from more MPAs and habitats.

Although the modeling methods implemented in this study have found clear trends in the data and the results for some covariates have reiterated findings of previous research, it is important to note some of the uncertainty associated with the final models. First, the modeling packages “pscl” and “visreg” that were utilized in R Studio, did not produce confidence bounds for the predicted covariate effects nor was it able to include a random effect for repeat sampling at the same stations; future work could use the “glmmTMB” package (which was only recently brought to my attention) to generate those confidence intervals and include random effects. Second, the fishing gear utilized in this study was chosen to mimic those used by the fishing community, which are often used to target larger fishes. Due to the size selectivity of the gear, the results and

conclusions about Black rockfish, the Blue rockfish group, and Lingcod may be more reflective of fish in the medium and large bins; future studies should consider whether the inclusion of smaller fish in this type of analysis would alter the patterns found here.

A third source of uncertainty comes from the construction of lag periods for association with environmental variables. As age data (e.g., from otoliths) was not available at the time of analysis, ages for the three size bins were estimated using Von Bertalanffy models with an appreciable level of uncertainty. This uncertainty increases with fish size because larger fish of each species encompass a greater range of potential ages. This methodology was an exploratory approach to look at the effects of the lagged environmental variables. Despite the imprecise measure of fish age, the signals produced by this procedure suggest that this warrants further investigation. In the absence of age data or an age-length key, increasing the number of size bins could help decrease the relative uncertainty, especially with regards to fish in the large bin.

CONCLUSION

Understanding how environmental and oceanographic conditions are related to fish abundance and size can have important implications for fisheries management. Given the relationship of relative fish abundance to lagged oceanographic variables, my results suggest that the drivers of rockfish recruitment can have long lasting effects on fish populations. Examining and understanding these longer lasting, detectable effects will also be beneficial as we face a changing climate. For example, modeling how fish abundances respond to increases in sea-surface temperature could allow fisheries scientists to generate better estimates of abundance as the occurrence of marine heatwaves in the Northeastern Pacific become more common (Cheung and Frölicher, 2020). The presence of strong lagged relationships, seen in this study, suggest more frequent marine heatwaves may have detrimental consequences on relative abundances of Black rockfish, but these implications demand more research. Continued long-term monitoring also becomes much more important as fish are becoming more impacted by climate, while still being subjected to fishing pressure.

The continued long-term monitoring of MPAs by the California Collaborative Fisheries Research Program has allowed for the modeling of relative abundance, fish size, and the effects of MPAs along the California north coast. The results and conclusions from this study add to the broader knowledge of marine protected areas, and conservation expectations in general. Proper design, placement, and implementation are important when creating MPAs; it is also important to understand how different variables

affect MPA inhabitants to generate appropriate expectations on the timelines of effectiveness (Agardy et al., 2011). Here, weak (but detectable) signals of positive MPA effects were identified in the two monitored MPAs for some species, and this is consistent with the notion that more time is needed before strong effects are noticed in MPAs (Starr et al., 2015), particularly those that have experienced less intense historical fishing pressure.

Managing the MPAs and the enforcement of the MPAs has been, and continues to be, a controversial and difficult task. Long distances to MPAs coupled with the relatively smaller human population of the North Coast (i.e., fewer trained enforcement officers) creates a problem for fisheries managers to implement continued enforcement at the MPAs examined in this study. The increased distance of the MPAs means that responding to calls of fishers inside the protected areas takes much more time. This may ultimately allow for fishing pressure to exist within MPAs. Enforcement, however, is critical for maintaining the goals of the MPAs; the goals of the MPA (i.e., to restore diminished populations) requires that there is as little fishing pressure as possible, for which enforcement is necessary. Here along the California North Coast, long-term monitoring in association with more enforcement of MPAs would allow for more accurate estimates of MPA effectiveness.

The effectiveness of MPAs does not rely solely on the ecological dynamics pertaining to the species that inhabit them, it is also a social issue. The CCFRP has shown that effective communication is key in improving the public opinion about MPAs (Mason

et al., 2020), which is critical for the long-term success of these conservation areas.

Continued long-term monitoring by the CCFRP can substantiate the usefulness of MPAs and help to bridge gaps in trust among researchers, managers, and fishers. These efforts will also provide opportunities for researchers to gather critical information pertaining to fish population dynamics, which will help maintain fundamentally strong and effective management practices.

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APPENDIX

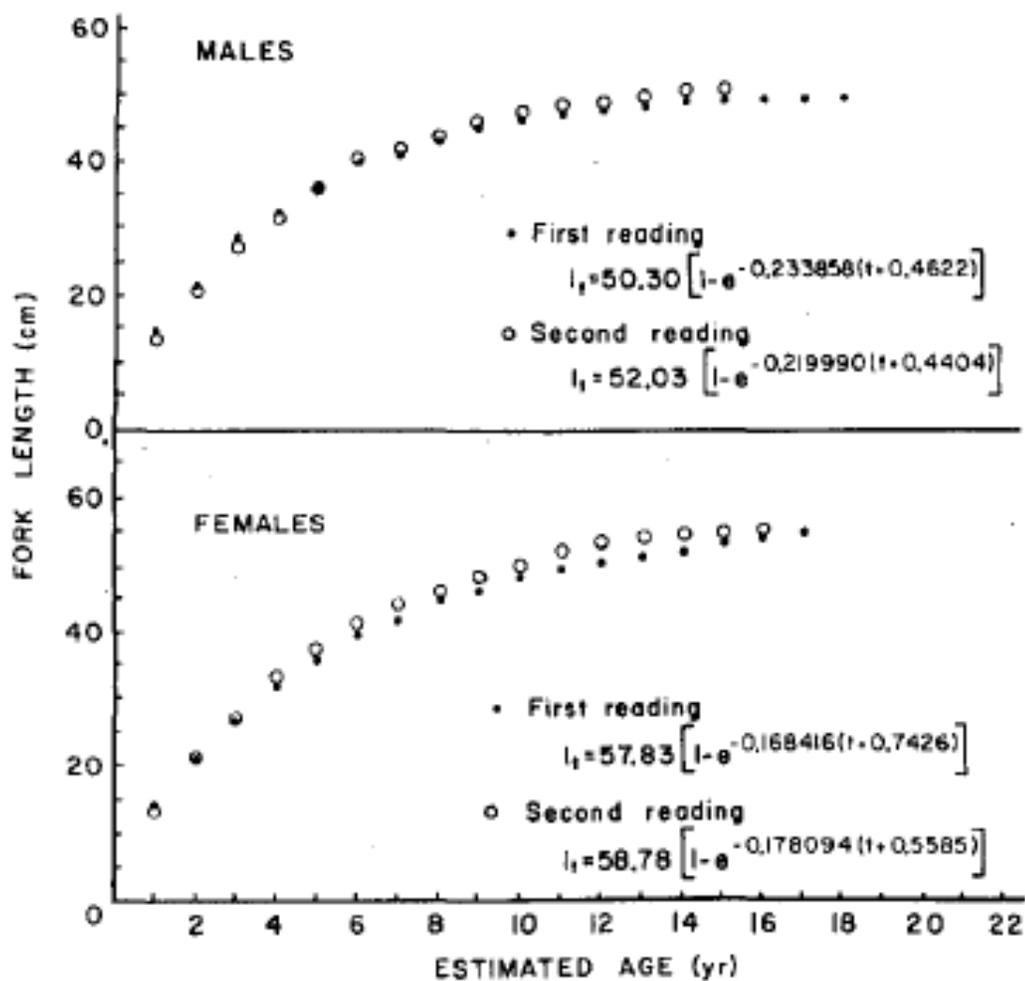
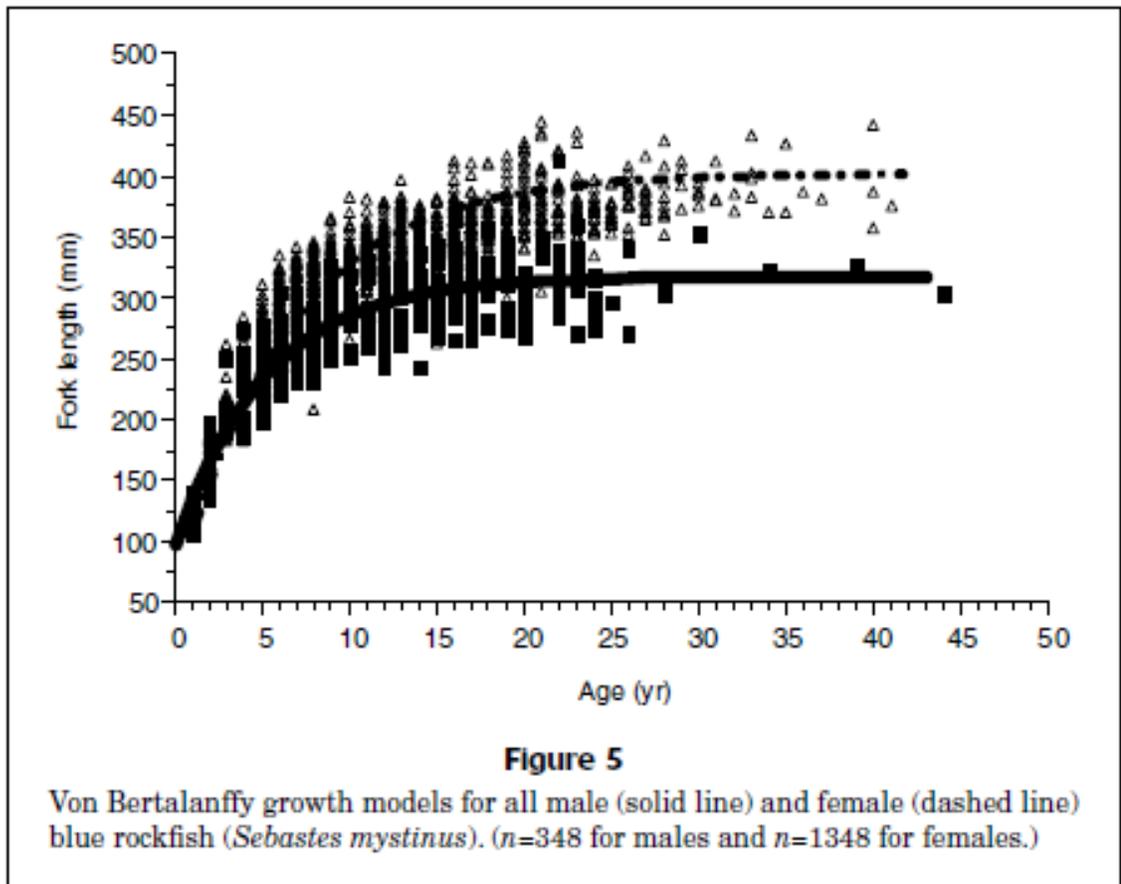


FIGURE 8.—Age-length relationships for black rockfish derived from two independent readings of their otoliths collected from Oregon samples, 1973-75.

Appendix 1. Age-length models used in generating lag period for Black rockfish, from Six and Horton (1977).



Appendix 2. Age-length models used in generating lag period for the Blue rockfish group, from Laidig et al. (2003).

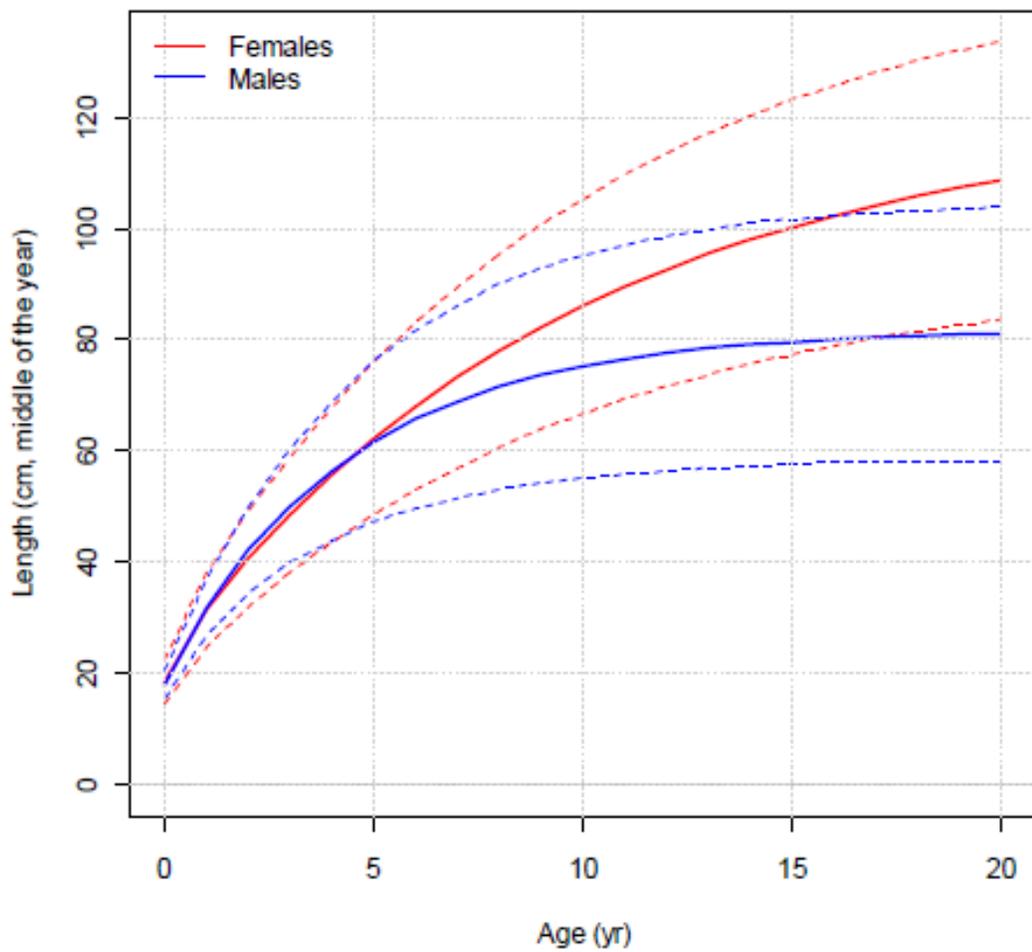
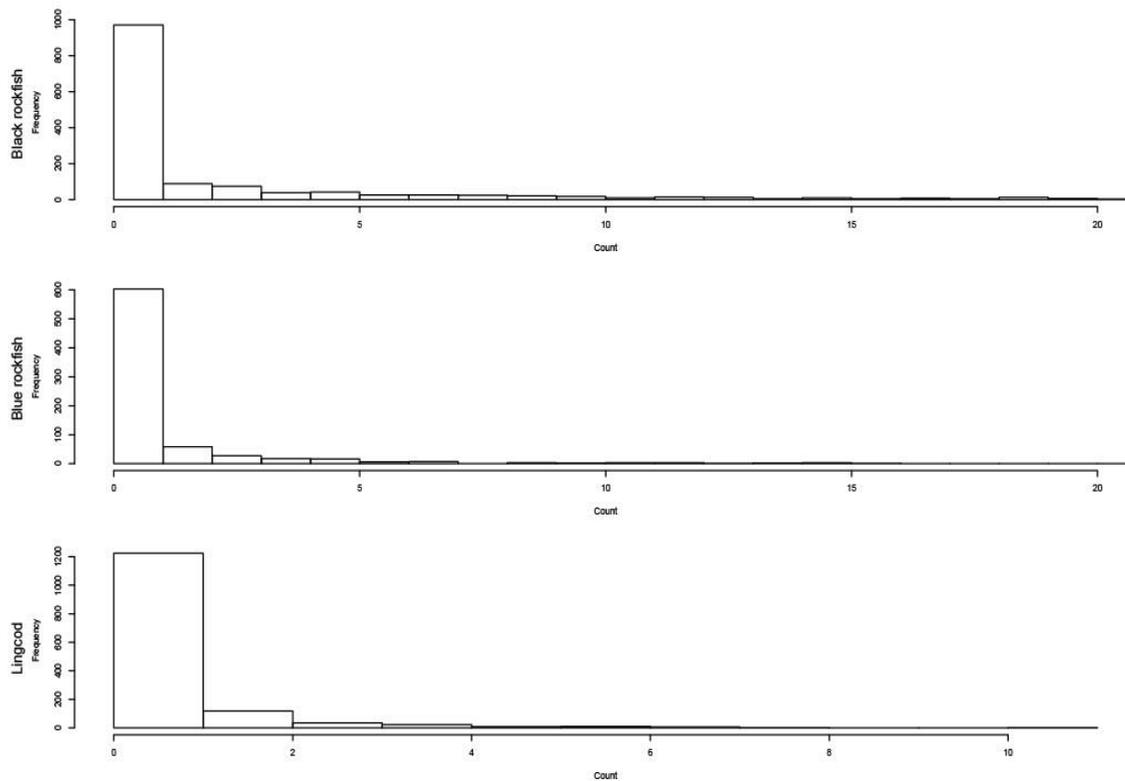


Figure 96. Growth curve for female (upper) and male (lower) lingcod estimated in the California model (length at age 1 and 20 is fixed, but k and cvs are estimated).

Appendix 3. Age-length models used in generating lag period for Lingcod, from Hamel et al. (2009), where the upper curve represents estimated age at length for females, and the lower curve represents the estimated age at length for males..



Appendix 4. Frequency of counts from observations of Black rockfish, Blue rockfish, and Lingcod, utilized in the analysis examining environmental effects on abundance.