Monitoring and Evaluation of Mid-Depth Rock Ecosystems in the California MLPA Marine Protected Area Network

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Project Description and Background

The mid-depth (30–100 m) rock ecosystem in California coastal waters provides a variety of ecosystem goods and services. Populations of species in this ecosystem are greatly affected by the high variability of productivity of the California Current as well as commercial and recreational fishing activities. Many species that live in this ecosystem are slow growing and experience sporadically large fluctuations in survival of young, causing large variations in populations. These natural oscillations in population abundance often make it difficult to quantify population trends. To address how fish and invertebrate populations in mid-depth habitats responded to the implementation of MPAs, we compiled data from a variety of video camera systems, including Remotely Operated Vehicle (ROV), Human Occupied Vehicle (HOV), Baited Remote Underwater Video (BRUV) and Tethered Video Landers. Additionally, we used California's seafloor mapping products to identify habitat characteristics that affect populations of key fish and invertebrate species.

Methods

We compiled data from 2,445 Remotely Operated Vehicle (ROV) transects and 564 Human Occupied Vehicle (HOV) transects across 47 MPAs (20 SMCAs, 27 SMRs) and their associated Reference sites. Additionally, we analyzed data from 360 BRUV surveys and 1,331 Tethered Video Lander drops. Also, we created maps of high-quality rocky habitats in 96 MPAs to show the distribution of high-quality habitats. We calculated density, biomass, and metrics of diversity, community composition, and response ratios (i.e., difference between MPAs and paired Reference sites).

Key Findings

- Neither rocky reef nor high-quality habitat is uniformly distributed across the state. Both Northern and Central California have more high-quality rock habitat than Southern California. Additionally, SMRs have more rock and more high-quality habitat than SMCAs.
- Fish densities have increased over time throughout the state, due to good recruitment years for many species and to the restrictive fishery management regulations in the last 20 years.
- Reserve effects varied across species, MPAs, management regions, and years. However, some species showed clear positive reserve effects. For example, in the South Region, Copper Rockfish densities were consistently higher inside MPAs relative to outside MPAs in all years surveyed.
- Structure-forming invertebrates, such as corals and sponges, were found at greater densities within MPAs than in associated Reference sites.
- Results of MPA and fishery management measures are intertwined; for example, California sea cucumbers showed a positive reserve effect across the South management region due to fishing closures and the Rockfish Conservation Areas helped rebuild rockfish populations across the state.
- Priorities for ROV sampling of mid-depth habitats have been to survey as many MPAs as possible in a given year. This has resulted in inconsistencies in ROV sampling over time and space, making it difficult to compare surveys across years.
- OPC-sponsored work has shown that current ROV sampling levels are sufficient to detect only large statistical differences in fish populations. Sample sizes need to be larger to detect smaller changes.
- Lightweight, relatively inexpensive BRUVs and larger Tethered Video Landers work well for the mid-depth habitat in California and can complement ROV sampling. In addition to MPA monitoring, these tools show promise for collecting data that could be used in fisheries management, invasive or rare species monitoring, and documentation of range extensions.
- Results of the seafloor habitat analyses can be used to distribute survey effort from the three visual tools more effectively throughout MPAs and adjacent reference sites by stratifying by habitat quality and reef patch size.

Conclusions

The Marine Life Protection Act, which was the enabling legislation for the MPA network, listed six broad goals for California's MPAs. This study addresses only a small part of the MLPA goals and for one specific habitat. MPAs can provide benefits beyond the protection of economically or ecologically important species. For some species, we identified differences in fish densities inside MPAs relative to Reference sites. Although this study did not show dramatic MPA effects across all of the organisms sampled or all of the tools used, we note that this does not constitute a failure of MPAs to achieve the many goals set out by the MLPA. For example, we are only beginning to understand the potential for MPAs to provide resilience to climate change including extreme events. Continued monitoring following the marine heatwave of 2014–2016 will allow California researchers to understand the patterns and time scales of recovery, contributing important information on MPA resilience. Similarly, the benefits of protecting biodiversity may be hard to measure from studies using methods that survey only a subset of organisms or habitats. Ongoing efforts to synthesize results from the many long-term monitoring programs across the state will better inform questions about biodiversity.

Recommendations

- A comprehensive plan for sampling mid-depth rock habitats should be developed and be based on specific scientific objectives and appropriate sampling designs. Results of the monitoring program should be evaluated on a regular basis to ensure objectives are being met.
- Quantifiable targets for MPA performance (e.g., a given percent change in fish abundance) should be elucidated so that appropriate sampling levels can be set.
- Future surveys should be designed to more carefully account for habitat and depth differences and be conducted at the same time of year in each management area.
- Reference sites should be evaluated and new or additional ones chosen for mid-depth MPAs to cover the range of depths and habitats used by key species and thus increase chances of detecting changes.
- The number of ROV survey sample units should be increased at MPA and Reference sites to improve the ability to enable detections of significant change of a) all fish combined and b) the most abundant fishes and invertebrate communities. Depending on funds available, this may require monitoring fewer MPAs.
- Surveying the same sites at regular intervals is essential for documenting changes over time. Funding levels will influence how regularly MPAs can be surveyed. We suggest monitoring a few MPAs within each region as often as possible, while monitoring other MPAs less frequently.
- Surveys should be stratified by habitat types and depths. Deeper habitats and SMCAs have been under-sampled and deserve more attention, as they are de facto MPAs for many species. More surveys should occur in habitats deeper than 50 m to encompass the full range of depths inhabited by target species.
- Both shallow and deep stereo-video landers have proven useful for evaluating species and communities inside and outside MPAs. They could be used to complement ROV surveys.
- It is critical to utilize stereo video on all tools (ROV, HOV, BRUV, Lander) to enable a more accurate estimate of fish lengths and thus fish biomass. Stereo cameras need to be calibrated to ensure accuracy of data collected.
- As video technology continues to improve, scientists will need to determine how much the technological improvements have affected apparent changes in MPAs when comparing current and historical data.
- Invertebrate communities appear to be changing on a regional, rather than MPA basis. Sampling 1-2 MPAs per region on an annual basis with more MPAs every 5 years may be sufficient to evaluate changes.
- Fishing pressure and/or fishery removals inside Reference sites and near MPAs are key variables that affect MPA performance and should be monitored along with environmental and biological variables.

Introduction

The California Legislature passed the Marine Life Protection Act (MLPA) in 1999, which required the state to redesign its system of marine protected areas (MPAs) to function as a statewide network in order to protect the abundance, integrity, and diversity of marine life, habitats, and ecosystems. Deep (30–100 m) rocky banks and outcrops, underwater pinnacles, and submarine canyons are important habitats in California waters. These and other continental-shelf habitats represent at least 75% of the area of all marine habitats in California waters, yet far less is known of these habitats and associated fish assemblages than those in waters <30 m deep. Importantly, there is a high diversity of demersal (i.e., associated with the seafloor) fishes in deep rock habitats off Central California (Love and Yoklavich 2006); these areas are home to more than 100 taxa of fishes and clearly dominated by over 50 species of Rockfishes (Allen et al. 2006). All demersal species that were officially designated as overfished in the early 2000's occur in deep-water habitats in California; several of these species also have been identified by the CDFW as those likely to benefit from MPAs. In addition, the likelihood of habitat destruction is much greater in these deep areas than in nearshore habitats due to the use of potentially damaging fishing gears such as trawls, longlines, and gillnets in deep water. These human activities can greatly alter deep-water habitats (NRC 2002, Barnes and Thomas 2005) and associated habitat-forming invertebrate assemblages (Hixon and Tissot 2007, Engel and Kvitek, 2008, Lindholm et al. 2015), compared to natural disturbances, which are relatively uncommon at these depths.

Quantitative assessment of fish populations that live in deeper waters (greater than 30 m) and associate with hard substrate has been difficult and imprecise using traditional sampling methods such as trawl and hook and line (Uzmann et al. 1977, Butler et al. 1991, O'Connell and Carlile 1993, Adams et al. 1995). Over the past three decades, human-occupied submersibles (HOVs), remotely operated vehicles (ROVs), as well as towed camera sleds and video landers, have been used to study fine-scale habitat distribution and association patterns of rockfishes (genus *Sebastes*), behavior of rockfishes, and for studies over rock or cobble where trawling is difficult (Stein et al. 1992, Auster et al. 2003, Busby et al. 2005, Wakefield et al. 2005, Starr et al. 2016). These tools enable observation of fishes in the habitats in which they occur, thus directly establishing species-habitat associations. No other tools provide such direct insight below the depth of SCUBA.

In response to the Ocean Protection Council (OPC), California Department of Fish and Wildlife (CDFW), and California Sea Grant (CASG) request for assistance in summarizing information about deep rocky habitats for the California Fish and Game Commission 2022 review of California's MPA network, we assembled a team of experts in MPA design, monitoring, and evaluation to help the state identify and evaluate changes that have occurred in the deeper, rocky portions of California MPAs (defined by the state as 'mid-depth', 30-100 m). As a group, we have well over 100 years of experience designing, operating, and using deep-water tools to survey fishes and invertebrates, and more than 80 years of experience working with the design, monitoring, and evaluation of MPAs in California and across the world. After gathering and analyzing data for two years, this report provides analyses of existing information about changes in populations of species in mid-depth rocky habitats, discusses reasons for apparent change (or lack of change) in rocky-habitat species, describes characteristics of mid-depth rocky habitats, and provides recommendations for long-term monitoring programs. We based our work on the guidance provided in California's MPA Action Plan (MPA Action Plan 2018), and this report has been designed based on questions and priorities described in the report: Scientific Guidance for California's MPA Decadal Reviews Hall-Arber et al. (2021).

Our work included six primary objectives:

1) Identify changes inside MPAs to-date by compiling and analyzing data that California researchers have collected for fish and invertebrates in the last 25 years inside MPAs and in associated Reference areas using human-occupied submersibles (HOV) and remotely operated vehicles (ROV)
2) Describe information collected from new ROV surveys conducted as part of this project
3) Describe information collected from new video lander surveys and compare results with ROV surveys to evaluate the utility of new, lower-cost video tools that are being used around the world
4) Investigate the importance of habitat composition for understanding differences among MPAs in mid-depth rock ecosystems
5) Provide an estimation of effectiveness of MPAs for protecting species in mid-depth rock ecosystems, and
6) Provide recommendations about future MPA monitoring of mid-depth rock ecosystems.

History of Mid-depth HOV Surveys

From the early 1990s to 2011, the Delta submersible was used to survey fishes and invertebrates in Central and Southern California. Recent HOV surveys have been conducted using the same approach as the Delta surveys, but with Deep Worker submersibles (Nuytco Research Ltd., Vancouver, BC). Most HOV surveys were designed to estimate populations of fishes (Yoklavich and O'Connell 2008) and invertebrates (Tissot et al. 2006) in natural habitats (Yoklavich et al. 2000, Love et al. 2008) and around oil platforms (Love et al. 1999), but HOV surveys have also been used for developing species-habitat associations (Laidig et al. 2009) and MPA analyses (Yoklavich et al. 1997, Starr and Yoklavich 2008, Yoklavich and Starr 2010). Most researchers using submersibles for quantitative surveys have relied upon strip-transect methods that were based on techniques first developed for scuba surveys.

Although researchers using HOV surveys in California have had somewhat different objectives depending on their specific project goals, the sampling approaches have been similar. The transect and resulting area surveyed is the sample unit used for analyses. Transects provided estimates of abundance, size distribution, species composition and habitat associations of adult and juvenile fishes and key invertebrate species. Typically, submersible surveys enumerate more species than ROV or towed-camera gear because a person underwater can more easily identify species than one who is trying to identify species on digital media. This has implications for estimating changes in diversity of species in MPAs, as camera systems used to record transects have transitioned from low-resolution cameras storing images on VHS tapes to high-definition (e.g., 4k) cameras storing digital media. Also, submersible observers improve their ability to identify species with time. These human and technological improvements can affect interpretation of MPA change.

Additionally, as with other visual assessment methods, submersible surveys contain potential issues related to bias and error associated with estimates of density, abundance, and biomass. Scientists conducting submersible surveys have tried to minimize errors by improving transect area calculations by using doppler velocity logs, by training human observers to correctly identify species, by estimating fish size by using artificial targets (in the likeness of fishes) of known length, and by using hand-held sonars to calculate transect widths. More recently, National Marine Fisheries Service scientists have been conducting experiments to estimate the avoidance or attraction of fishes to visual survey tools.

History of Mid-depth ROV Surveys

ROV surveys have been the primary method of evaluating mid-depth MPAs in California. In conjunction with the implementation of the Marine Life Protection Act, CDFW initiated a monitoring program using ROVs to provide data for both MPA assessment and fisheries management. The initial focus of CDFW's ROV research and assessment program was to develop ROV-based visual sampling as a quantitative tool for tracking changes in habitat and abundances of finfish and invertebrates. The program started in 1998 when CDFW purchased a remotely operated vehicle (ROV) using funds provided by California Sea Grant to study the newly implemented Punta Gorda Ecological Reserve. From 1998 through 2002, CDFW developed operational techniques for the deployment of their new ROV, named "ROV Bob".
In 2003, Marine Applied Research and Exploration (MARE) worked with CDFW to deploy ROV Bob in marine reserves around the northern Channel Islands. During that time, CDFW and MARE led a group to develop ROV strip-transect methods and protocols based upon accepted SCUBA diver and ROV sampling protocols previously used (e.g., Parry et al. 2003, Trenkel et al. 2004, Karpov et al. 2012). Following initial testing, ROV configuration, survey design, sampling protocols, data post-processing and analysis techniques were formalized in 2005, and were based on a fixed index-site design. In 2008, MARE received funding to procure a new ROV, a Vector M4 ROV, named "Beagle", to expand data collection and to help support CDFW's monitoring program statewide. In 2014, ROV survey techniques were modified slightly to include the use of a stratified-random approach to sampling survey sites. Also, long, straight ROV transects were used in the north-central MPA Baseline project in 2010 and 2011. Overall, ROV surveys have been implemented at 178 sites statewide since 2005 (Bergen et al. 2006, Karpov et al. 2007, CDFG 2009 [A,B], Karpov et al. 2012, Lauermann et al. 2012, Lauermann et al. 2015 [A,B,C], Lauermann et al. 2017 [A,B]).

History of Video Lander Surveys

Video assessment has become a widely-used tool for non-extractive, fishery-independent monitoring globally. Mobile video camera systems have been towed behind boats (Lauth et al. 2004, Williams et al. 2010, Knight et al. 2014) and installed on remotely operated vehicles (Johnson et al. 2003). However, these mobile video approaches are both logistically complex and expensive to execute, limiting their utility and widespread use. Camera landers (commonly referred to as RUVs (Remote Underwater Video) or BRUVs (Baited Remote Underwater Video) are systems with single or paired cameras fixed to a frame and stationarily deployed on the benthos for a fixed amount of time. These systems have been used extensively for standardized fisheries-independent surveys around the world for estimation of relative abundances and size distributions of fish species (Watson et al. 2005, Harvey et al. 2007, Langlois et al. 2010, Watson et al. 2010, Hannah and Blume 2012, Easton et al. 2015). While single camera systems can measure relative abundance, the simultaneous application of two cameras in stereo camera configuration allows for precise measurements of the lengths of fish (Harvey et al. 2002). Video camera landers can be a cost-effective and logistically simple alternative to mobile systems, especially with an increase in the availability of inexpensive, high-resolution cameras (Langlois et al. 2010, Bicknell et al. 2016). In many parts of the world, lander surveys have become a standard approach for monitoring potentially cautious fish, surveying depths beyond the limits of SCUBA and providing fishery-independent data for MPA and fisheries assessment (Meekan and Cappo 2004, Malcolm et al. 2007, Easton et al. 2015, Starr et al. 2016), especially in high relief rocky areas. We used data from two different Video Lander systems in this project, both are stereo-video systems, but they differ in size, complexity, and cost.

Benthic Observation Survey Systems (BOSS)

With funding external to this project, a partnership with first MARE and later The Nature Conservancy and the Monterey Bay Aquarium Research Institute, we (Starr et al.) developed a lightweight, rapidly-deployable video system to survey fishes in continental shelf and slope habitats. Our original design was a Rotating Lander, used from 2012-2015, which used a stereo-pair of video cameras and high-powered lights on a rotating arm to survey fishes in 360 degrees. In 2017, we updated to a non-rotating version of this video lander, known as the Benthic Observation Survey System (BOSS), which provides us with information about fish species that inhabit high-relief, and therefore untrawlable habitats. The BOSS is equipped with 8 cameras (4 stereo camera pairs), 4 high-powered lights, one downward facing light and camera, and a load-bearing fiber optic cable that allows for real-time monitoring of surveys. The BOSS allows us to conduct surveys over rocky bottoms and measure fish lengths with a high degree of accuracy. We developed and deployed these video landers using private and federal funds to survey rocky habitats from about 50–300 m deep. Between 2012 and 2015, we tested and deployed the Rotating Lander on several different projects. Although we conducted some baited drops with the Rotating Lander, since 2018, we have deployed the BOSS across California without bait to evaluate fish communities. Our work with the BOSS was not funded by this project, but the tool could be used to evaluate MPAs in the future.

[Baited] Remote Underwater Video (BRUV and RUV)

Following the BOSS development, we sought to create an even smaller, cheaper and more easily deployable camera lander system to use in shallower waters and to explore the potential of landers for citizen science use. The BRUV design used here was modified from designs used extensively to monitor a variety of marine habitats in Australia (Willis and Babcock 2000, Goetze et al. 2021, Harvey et al. 2021) and has been used in Southern CA since 2016. Our BRUVs were initially developed with CA Sea Grant funding to Caselle and Starr. These stereo systems consist of a trapezoidal steel frame, two GoPro cameras (medium FOV, 30fps) mounted 65 cm apart in a stereo configuration 50 cm from the benthos. Each BRUV unit is equipped with two underwater dive lights and, when baited, a perforated PVC bait canister located 100 cm in front of the camera array. These systems are not cabled to the vessel, and crab fishing-style floats and trap lines are attached to each BRUV to facilitate remote deployment and recovery. When baited, we use 500 g of whole, moderately scored Pacific Mackerel (*Scomber japonicus*), which is standard BRUV protocol. BRUV units can be retrieved by hand or using a batterypowered trap hauler and can be deployed from very small vessels. BRUVs can be deployed in mid-depth as well as shallow, sandy and rocky habitats.

MPA Habitat Attributes

Benthic habitat features, including physical characteristics of substrates and biogenic structures, have been used to describe the distribution, relative abundance, biomass, and diversity of fishes (e.g., Lough et al. 1989, Pearcy et al. 1989, Hixon et al. 1992, Stein et al. 1992, O'Connell and Carlile 1993, Yoklavich et al. 1997, Auster et al. 2003, Anderson et al. 2009, Walker et al. 2009, Milligan et al. 2016). Consequently, fish associations with benthic habitat features are known for many fish species (e.g., Auster et al. 2001, Love et al. 2002, Love et al. 2006, Anderson and Yoklavich 2007, Young et al. 2010). On the U.S. West Coast, many species such as rockfishes are associated with rocky habitats, whereas other fishes, such as flatfishes and ratfishes, are associated with soft sediments. Most of the published work on species-habitat relationships, however, has focused on relatively fine-scale habitats. Although we know a lot about fine-scale species-habitat relationships, we have learned that habitat scale plays an important role in the definition and use of species-habitat associations (Tagini 2018). Also, the wide variety of habitat scales makes it difficult to establish species-habitat relationships that are meaningful for spatial management purposes at the scale of MPAs or Marine Sanctuaries. The mega-habitat scale described by Greene et al. (1999) is useful for purposes of understanding regional biodiversity, but not as useful for developing adaptive management measures. Similarly, the microhabitat scale is useful for purposes of understanding biological relationships, but also not very useful for resource management purposes.

MPAs are, by design, spatial management tools. This management approach assumes knowledge of habitats and associated species, and importantly, how those associations change or differ in space. In terrestrial environments, these assumptions are reasonably accurate. In the marine environment, however, less is known about how or why species and habitats are distributed in space and consequently what spatial scale is optimal for resource management. We conducted a spatial analysis of rock habitats across the entire MPA system in California to determine if the type, amount, and quality of habitat within MPAs is an indicator of MPA performance. Also, we investigated the use of Hurdle models (Zuur et al. 2009) to investigate potential differences in species-habitat associations inside and outside MPAs, with particular focus on any relationships with structure-forming invertebrates.

While a variety of environmental variables likely influence the presence of rocky reef species in the 30–100 m water depths along California's continental shelf, the presence, diversity, and quality of rock habitat in an MPA can define which fish are present in that MPA. Further, the distribution and contiguous nature of existing reef habitat can determine how species within an MPA are connected with adjacent areas outside the MPA. Ecological, or landscape, connectivity has been defined as the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al. 1993). Currently, our understanding of the temporal and spatial scales of the processes that underlie landscape connectivity continues to be limited (Pittman et al. 2007). The subtidal seascape is very much a spatiotemporal mosaic of habitat patches and species associations within those patches (Greenfield and Johnson 1990, Auster et al. 1995, Anderson and Yoklavich 2007, Anderson et al. 2009, Chang et al. 2010).

Methods

ROV Surveys (Lauermann, Starr, Kahn, & Tissot)

Operations

ROV survey sites were initially identified by MARE and CDFW scientists, using bathymetric bottom maps and then confirmed during exploratory ROV surveys. For efficiency and ease of operations, sampling blocks were created using GIS maps that were 500 m wide and up to 3 km long. Creating blocks with these dimensions enabled us to select sample sites that covered rocky habitats and spanned several depth zones as the sampling blocks were usually placed perpendicular to the prevailing depth contours. The rectangular shapes were also logistically easier to survey because they maximized the time that the ROV was surveying on transects. Both MPA and outside Reference sites were selected for long-term surveys based upon map-based estimations of similarity in the types and amounts of rocky substrate present, proximity to one another, and depth. The number of sites selected inside or outside the MPA was based on the amount of rocky habitat available inside the MPA, with MPAs containing larger amounts of rocky substrates having multiple sites both inside and outside. We treated these sampling blocks as “index sites” that were revisited over time. See Table 1 for a historical review of ROV survey locations from 2005–2020.

MPA and Reference site pairs that were created prior to 2010 were selected using available multibeam hillshades, sidescan sonar backscatter or habitat interpretive layers. These layers were not consistently collected and were only available for limited sections of the state. From 2010 on, Reference sites were selected using the state’s newly collected multibeam data. Hillshade images of the seafloor overlaid with 10 m contour lines were qualitatively evaluated for areas of similar looking rocky structure and depth. Using this approach did not always generate perfectly matched MPA and Reference site pairs. In addition, for some MPAs (such as Gull Island SMR), the only Reference site that could be found with comparable rocky habitat was selected knowing there was a considerable difference in depth.

Table 1. MPA locations surveyed by the ROV between 2003-2020. Shading designates MPA tier status (White – Tier 1, Light gray – Tier 2 and Dark gray – Tier 3).

North Coast	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	# Years Sampled
Point St George SMCA												X	X					X	3
Reading Rock SMR/SMCA												X	X					X	3
South Cape Mendocino												X							1
Mattole Cyn SMR												X	X						2
Sea Lion Gulch SMR												X	X					X	3
Ten Mile SMR												X	X					X	3
MacKerricher SMCA		X										X							2
Point Arena SMR/SMCA									X				X					X	3
Saunders Reef SMCA													X						1
Stewarts Point SMR													X						1
Bodega Head SMR								X	X				X				X	X	5
Bodega Head SMCA								X	X				X				X	X	5
Point Reyes SMR/SMCA							X	X	X										3
Farallon Islands SMR/SMCA								X	X				X				X	X	5
Central Coast																			
Pillar Pt SMCA								X	X				X					X	4
Montara SMR								X	X				X					X	4
Año Nuevo SMR					X	X							X				X		4
Soquel Canyon SMCA														X					1
Portuguese Ledge SMCA													X	X			X		3
Carmel Bay SMCA						X								X					2
Point Lobos SMR/SMCA					X	X	X							X			X		5
Point Sur SMCA/SMR						X				X				X			X		4
Big Creek SMCA/SMR														X				X	2
Piedras Blancas SMR														X				X	2
Point Buchon SMR						X	X			X				X			X		5
South Coast																			
Point Conception SMR												X					X		2
Naples SMCA												X							1
Campus Point SMCA												X					X		2
Harris Point SMR			X	X	X	X	X					X					X	X	8
South Point SMR		X	X	X	X	X	X					X	X				X	X	10
Carrington Point SMR	X	X	X	X	X	X	X					X	X				X	X	11
Scorpion SMR												X							1
Gull Island SMR	X	X	X	X	X	X	X					X				X		X	10
Anacapa Island SMCA	X	X	X	X	X	X	X					X	X				X	X	11
Anacapa Island SMR	X	X	X	X	X	X	X					X	X				X	X	11
Santa Barbara Island SMR												X							1
Farnsworth Offshore SMCA									X	X		X						X	4
Point Dume SMR												X							1
Swami's SMCA												X						X	2
South La Jolla SMR/SMCA												X						X	2

Transect Selection

Within selected MPAs and Reference sites, we used 500-meter long transect lines as a sampling unit. This length was selected for logistical ease of use (Karpov et al. 2010). Prior to 2011, transects were set up as fixed distances along the length of the sampling box. After 2011, a stratified-random design was used, in which a transect was randomly placed in each of the 100 m bins along the long axis of the sampling block. Transect lines were randomly generated and distributed to maximize the area within each site to be sampled, by evenly spacing lines throughout the site and by selecting different lines each year the site was sampled. The number of transects selected at each site was based on the total rocky habitat present (based on multibeam habitat interpretations) and the amount of survey time allotted to each study area. Both ROVs collected video and still imagery while moving along a fixed transect path along the sea floor using a "live boat" technique that employs a 227 kg (600 lb) clump weight. This provides the ROV pilot with sufficient maneuverability to maintain a constant speed (0.5 to 0.75 m/sec) and a straight course down the planned survey line (Lauermann et al. 2017 [B]). The ROV pilot used sonar readings to sustain a consistent transect width by maintaining a constant altitude from the camera to the substrate (at the screen's horizontal mid-point) between 1.5 and 3 m.

Video Post Processing

Video imagery collected was analyzed to characterize substrate types present and to identify and count all demersal and epibenthic finfish and macro-invertebrates. Using a series of non-overlapping video quadrats, the distribution, relative abundance, and density of species were estimated along each transect, as described in Auster et al. (1991) and Lindholm et al. (2004). Using the Coordinated Universal Time (UTC) start and end time code of each independent substrate, "substrate layers" were generated that were subsequently combined to generate habitat types. In total, nine different substrate types were quantified: rock, boulder, cobble, gravel, sand, mud, active asphalt, fresh asphalt, and old asphalt (Greene et al. 1999). Each substrate type was recorded independently, enabling us to capture the often-overlapping segments of substrates. These overlapping substrate segments allowed for the identification of mixed substrate areas along the transect line, which we then combined into four habitat types to characterize the sea floor: hard, hard-mixed, soft-mixed, and soft classifications. This was done by combining the two most predominant substrate types in a hierarchical scheme, in the following order with rock being weighted the highest: rock, boulder, cobble, sand, and mud. Hard substrates were defined by the presence of rock and/or boulder substrates. Hard-mixed was defined by the presence of rock and/or boulder with cobble, sand and/or mud. Soft-mixed was defined by habitats with cobble and/or sand and mud. Soft habitat was defined as sand and/or mud. Active, fresh or old asphalt was not included, as these habitat types only occurred at one study location, Point Conception.

Once substrates were identified, video analysts then counted macro-invertebrates and fishes; each organism was identified to the lowest taxonomic level possible. Fish and invertebrate counts were derived from the forward-facing video camera, which was situated at an oblique angle to the seafloor. All organisms were identified, enumerated, and recorded with UTC timecode and linked to ROV position and sensor files. Forward digital still photographs were used to verify species identifications where high resolution of species characteristics is required.

Colonial invertebrate patches were observed during video review and entered as segments with discrete start and stop points along each transect. Each invertebrate patch was assigned an estimated percent cover between the forward projecting lasers and lower edge of the field of view, thus providing an estimate of the total area of colonial invertebrates along each transect.

Fish were sexed and sized whenever possible. Fish were sized using visual size estimates from the paired lasers. Size estimates made using this rapid method provide a broad qualitative assessment of the size frequency of fish populations within and across MPAs. These sizing methods were consistent across all years. However, Kline et al. (2016) and Denney (2017) showed that video analysts tend to underestimate the lengths of the larger fishes observed. This has implications for MPA change analysis, because fish biomass (calculated from fish lengths) has been shown to be a better indicator of MPA effects than lengths alone (Sciberras et al. 2013). Stereo-video that has been recorded beginning in 2017 is available, but MARE has not calibrated the cameras or analyzed stereo video because of the extra time/cost needed to calibrate the cameras and accurately measure fish. We discuss the differences between laser-based and stereo-video measurements later in the Benthic Observation Survey System (BOSS) section.

Positional Processing

Positional data recorded for each transect were processed to remove outliers and data anomalies caused by acoustic noise and vessel movement, which are inherent in these systems (Karpov et al. 2006). Lauermann et al. (2017) provide more information about the error checking and smoothing protocols for positional data. The end result of navigational data processing produced a positional file, which links the location of the ROV with all habitat, fish and macro-invertebrate observations collected on each transect using UTC timecode.

HOV Surveys (Starr)

Operations

For most HOV surveys, researchers used multibeam maps and/or local knowledge to target specific types of habitats, and then conducted multiple dives consisting of multiple 10-30 min transects at haphazardly or randomly selected sites. The submersible traveled at a speed of about 0.5 kt, most often parallel to an isobath. A pilot operated the submersible while an experienced scientist identified all fish species and estimated their lengths, using paired lasers, set 20 cm apart, as a guide. The submersible pilot maintained a height off the bottom of about 0.5 m (unless the terrain precluded that height), and the observer counted all fish and/or invertebrates seen in a 2 m-wide strip adjacent to the submersible. The length of each transect was determined at first by USBL acoustic systems and in later years was measured accurately using a Doppler velocity log and ring-laser gyrocompass. Transect width was estimated by scientific observers with the aid of a hand-held sonar device. An external camera recorded video of the transect and audio that contained real-time fish identifications and observations by the scientist. Invertebrates and habitats were later counted from the videotape.

Dataset Compilation

We contacted all the researchers who have multi-year datasets from HOV surveys in California and requested access to their information that pertains to fishes observed on their surveys. We obtained databases from the National Marine Fisheries Service (courtesy Tom Laidig), UC Santa Barbara (courtesy Milton Love), and the data we generated for the Central California MPA baseline survey (Starr and Yoklavich 2008, Yoklavich and Starr 2010). Those survey data were compiled and error checked before we obtained the spatially-explicit data. We then mapped the locations of transects, assigned a protection category to each transect (MPA or REF) and exported the data to different files for analyses.

ROV and HOV Fish Statistical Analyses:

Fish, Invertebrates, and Habitats

Fish and Invertebrate communities are greatly influenced by seafloor bottom types and depths. ROV and HOV data were combined to assess changes in populations and communities through time inside and outside MPA areas both before and after implementation. Prior to analysis of faunal data, we examined the distributions of depths sampled by each gear type using a frequency distribution and then binned data by depth range: 30–60 m and 60–130 m to better account for variation in depths among tools, and to evaluate shallow water and deeper water fish assemblages separately. To ensure that ROV transects surveyed comparable proportions of the different substrate types and depth ranges in the MPAs and their associated Reference sites, we assessed average depths and proportions of cover for each region. Habitat types were separated into four major categories: hard, hard-mixed, soft-mixed, and soft. Any site whose MPA and Reference locations had surveyed significantly different substrate types were identified using a chi-square analysis, or Fisher test when assumptions for a chi-square test could not be met. Significantly different depths were identified using a bootstrapped t-test. All these analyses can be found in Appendix A (Fig. A1-27).

Total Fish Community Analysis

Prior to data analysis, we filtered out any data observed in less than 30 m of water and greater than 130 m deep and over soft sediment habitats. We removed any unidentified species, fish complexes that contain species with different life history strategies (e.g., Olive and Yellowtail Rockfish), as well as Señorita (*Oxyjulis californica*), and Halfbanded Rockfish (*Sebastes semicinctus*) from the data set. We removed Señorita because these fish are typically shallow-water and are not well surveyed by the ROV. Although Halfbanded Rockfish are typically found in deeper water habitats, we removed these fish due to patchiness in observations and the high abundance of schooling individuals when observed, which skewed density data through time. Also, we removed any species that were observed less than 100 times across the entire dataset (all sites and years combined). This resulted in a total of 43 species that were consistently sampled and identified for analysis (Table 2).

Table 2. Total counts of all species observed more than 100 times by the ROV between 2005-2020.

	North		Central		South	
Common Name	MPA	Reference	MPA	Reference	MPA	Reference
Black Rockfish	231	265	75	113	1	8
Blacksmith	0	1	30	1	25758	4437
Blue/Deacon Rockfish	2786	6085	6081	4244	20768	12120
Bocaccio	4	6	158	65	327	117
Brown Rockfish	714	405	70	45	8	5
Calico Rockfish	27	60	113	89	433	703
California Lizardfish	0	0	0	0	537	230
California Scorpionfish	1	0	0	0	256	8740
California Sheephead	0	0	36	15	2763	1179
China Rockfish	123	222	39	34	0	0
Combfish complex	87	69	61	53	562	916
Copper Rockfish	289	216	214	145	2910	1035
Flag Rockfish	6	2	43	30	162	235

Gopher Rockfish	179	323	501	536	1253	672
Greenspotted Rockfish	137	31	63	90	82	13
Greenstriped Rockfish	85	16	51	78	24	37
Halfmoon	10	0	0	0	181	5
Kelp Bass	2	2	0	0	668	14
Kelp Greenling	1386	1620	361	243	56	57
Lingcod	1065	1287	938	600	1120	717
Ocean Whitefish	1	0	0	2	1501	485
Opaleye	0	0	0	0	163	4
Painted Greenling	400	1062	715	720	1304	728
Pile Perch	19	158	415	421	1001	852
Pink Seaperch	160	252	241	314	1829	1890
Pygmy Rockfish	716	644	3429	1714	1043	126
Quillback Rockfish	515	456	10	8	3	0
Rock Wrasse	0	0	0	0	209	4
Ronquils	74	172	77	84	87	89
Rosy Rockfish	1238	1856	2370	2214	1001	724
Sablefish	114	0	0	0	0	0
Sharpnose Seaperch	0	0	1	3	145	2
Shortbelly Rockfish	1147	54	6	25	9024	0
Spotted Ratfish	46	13	79	28	18	11
Squarespot Rockfish	32	6	1525	1837	309	1779
Starry Rockfish	26	64	294	221	164	189
Striped Seaperch	18	110	224	173	95	79
Treefish	0	3	8	6	484	161
Tubesnout	0	0	321	0	60	85
Vermilion Rockfish	677	731	775	930	5357	2423
White Seaperch	0	2	109	77	75	17
Widow Rockfish	53	173	72	12	104	179
Yelloweye Rockfish	266	192	46	41	2	0
Total	12,634	16,558	19,551	15,211	81,847	41,067

Due to spatial and temporal gaps in MPA specific data, we grouped all data by region to assess changes in total fish density, species-specific density, biomass, and length relationships (App. Fig. B1-33 show the densities of each species in MPAs and Reference sites). We examined total fish density (no. m^{-2}) inside and outside each MPA and year sampled. To determine if total fish density varied by designation (inside or outside the MPA) or survey year, we conducted serial two-way ANCOVAs for each region. Graphs of length frequency distributions for individual species can be found in Appendix B (Fig. B34-44).

Using density values, a yearly response ratio was calculated to estimate the strength of the MPA effect on fish communities inside relative to outside the MPA. Response ratios were calculated by taking the log of the quotient between both total fish density and biomass inside relative to outside the MPA, calculated by Log ($Metric_{MPA}/Metric_{REF}$). A response ratio above 0 indicates a positive effect of the MPA on total fish density or biomass and below zero indicates a negative effect or lack of an effect of MPAs on total fish density. Using the calculated response ratios, we examined the differences in fish density between SMRs and SMCAs with one-way ANOVAs. Individual density response ratios by species and MPA can be found in Appendix B (Fig. B45-47). We also examined the relationship between fish density and the amount of rock habitat (km^2), high-quality rock habitat (km^2) and the percentage of high-quality rock within a MPA with linear regression.

For each year sampled, we evaluated fish diversity inside and outside each MPA. We calculated multiple diversity metrics: Species Richness (Fisher's alpha) and Shannon-Weiner diversity. We then examined how each diversity metric changed, both inside and outside each MPA and across years sampled. We examined changes in community structure in MPAs and associated Reference sites through time with a permutational analysis of variance (PERMANOVA) and a non-metric multidimensional scaling ordination (NMDS) with a Bray Curtis dissimilarity matrix, to visually examine changes in communities across space and time for each management region independently (North, Central, and South). Also, we categorized species as targeted by fisheries (or not) and by trophic category (App. Table B1).

Species-Specific Analysis

For the North Coast we examined 11 focal species: Blue/Deacon Rockfish (*Sebastes mystinus* and *Sebastes diaconus* combined), Black Rockfish (*Sebastes melanops*), Brown Rockfish (*Sebastes auriculatus*), China Rockfish (*Sebastes nebulosus*), Copper Rockfish (*S. caurinus)*, Kelp Greenling (*Hexagrammos decagrammus)*, Lingcod, (*Ophiodon elongatus*) Quillback Rockfish (*Sebastes malige*r), Rosy Rockfish (*Sebastes rosaceus*), Vermilion Rockfish (*Sebastes miniatus)* and Yelloweye Rockfish (*Sebastes ruberrimus)*. For the Central Coast we focused on 11 species: Blue/Deacon Rockfish, China Rockfish, Copper Rockfish, Gopher Rockfish (*Sebastes carnatus*), Kelp Greenling, Lingcod, Painted Greenling (*Oxylebius pictus*), Pile Perch (*Rhacochilus vacca*), Pink Seaperch (*Zalembius rosaceus*), Striped Seaperch (*Embiotoca lateralis*) and Vermilion Rockfish. For the South Coast, we focused on 13 species: Blacksmith (*Chromis punctipinnis*), Blue/Deacon Rockfish, Bocaccio (*Sebastes paucispinis*), California Sheephead (*Semicossyphus pulcher)*, Copper Rockfish, Gopher Rockfish, Kelp Greenling, Lingcod, Ocean Whitefish (*Caulolatilus princeps*), Painted Greenling, Pile Perch, Treefish (*Sebastes serriceps*), and Vermilion Rockfish. These species were chosen because they are present across most MPAs and years sampled within a given region and are either economically or ecologically important. For each species, we examined density, density response ratios, mean lengths, proportion of fish observed with lengths greater than the length at 50% maturity, biomass, and biomass response ratios. To obtain estimates of biomass, we converted lengths of fishes to biomass based on published length-weight relationships. Note that Blue and Deacon Rockfishes were analyzed as a group because currently video analysts cannot differentiate those two species and they are managed as a group. ROV analysts are also often unable to differentiate between Yellowtail Rockfish and Olive Rockfish and they are often reported as a species complex. Due to large differences in life histories between Yellowtail and Olive Rockfish, this grouping was excluded from the species-specific analyses.

For each species, we examined mean density through time by current MPA management regions because many species had low sample sizes when evaluated at the MPA level. Specifically, we assessed changes in length and biomass between MPAs and Reference sites within a MLPA management region across all years surveyed. Using data on length at 50% maturity, we examined the proportion of individuals that were greater than 50% maturity in both MPAs and Reference sites by region and for each focal species (all years combined). Lastly, we examined changes in biomass through time for each focal species and region. We were unable to calculate biomass for Pink Seaperch due to insufficient information on length-weight relationships. We conducted serial two-way ANCOVAs for all response variables (i.e., mean length, >50% maturity and biomass) to investigate whether there were differences among MPAs and Reference sites for each region through time.

ROV Invertebrate Statistical Analyses:

Responses to MPAs by individual focal taxa

To assess whether the statewide network of marine protected areas affected invertebrate focal species of interest, we calculated response ratios for particular invertebrate species as well as higher-level taxonomic groups. Upon initial review, invertebrate communities differed at the regional level (similar to what we observed with fish, above), so some analyses were done at the statewide level and some were grouped into the Northern, Central, and Southern California MPA management regions. Response ratios were calculated using counts and density measured from ROV transects conducted statewide between 2005 and 2019. For each species or functional group, we calculated response ratios as described above, by dividing the log of the mean density of that species in the MPA by the log of the mean density of that species in the corresponding Reference site.

Focal species were selected based on taxa that had strong economic or ecological significance. These included the California sea cucumber (*Apostichopus californicus*) as a commercially important species, sponges and corals of several morphotypes and red urchins (*Mesocentrotus franciscanus*) as foundation species, and sunflower sea stars (*Pycnopodia helianthoides*) as keystone species. We also surveyed taxa that were abundant statewide and so could be good indicators of MPA function across the statewide network (Table 3).

Responses of higher taxonomic levels or functional groups

ROV surveys encountered so many different invertebrate taxa that it was difficult to assess any patterns of response at the scale of individual species (but see focal species, above). Taxa were therefore combined into higher taxonomic groups or by functional groups related to mode of feeding, and in the future could be assessed by differences in habitat or lifestyle (App. Table C1). We assessed response ratios of higher taxonomic levels for some groups of invertebrates such as corals and sponges since in many cases there was poor taxonomic resolution, but these groups in general are important for their role as foundation species by creating three-dimensional structure in benthic habitats.

Table 3. Focal invertebrate species with statewide abundance assessed for suitability for statistical comparisons across the whole state. Numbers represent unique counts of each species from ROV surveys of MPAs and Reference sites in the North, Central, and South management regions of California. Species marked with an asterisk were determined to have good coverage across the state and were assessed individually.

Species	North	Central	South
Sponges (Phylum Porifera)			
Craniella arb	413	426	1453
Tethya californiana	621	2035	10138
Unidentified Porifera (branched)	610	2266	10459
Unidentified Porifera (nipple)	516	4945	7103
Unidentified Porifera or Bryozoa	323	12025	4830
Sea whips, anemones (Cnidaria)			
Halipteris californica (sea whip)	1095	416	34502
Metridium farcimen (anemone)	33367	17313	287
Urticina columbiana (anemone)	682	1128	5602
Urticina piscivora (anemone)	502	5377	128
Stylaster californicus	2586	5153	181
*Stylatula elongata** (sea pen)	2265	3569	48980
Moss animals (Bryozoa)			
Unidentified Bryozoa (branched)	103	6785	43977
Echinoderms (Echinodermata)			
Sea stars (Class Asteroidea)			
Dermasterias imbricata	421	804	1200
*Mediaster aequalis**	3777	10216	22852
Pycnopodia helianthoides	35	264	5877
Unidentified Asteroidea	300	441	842
Unidentified Henricia sp.	1719	2950	1838
Sea urchins (Class Echinoidea)			
*Mesocentrotus franciscanus**	1744	9144	19664
Strongylocentrotus purpuratus	37	7839	1178
Sea cucumbers (Class Holothuroidea)			
*Apostichopus californicus**	22050	22043	19633
Cucumaria piperata	1054	30	1837
Psolus chitinoides	27483	1221	711

Invertebrate Community Metrics

Invertebrate community metrics (Shannon diversity, richness, and Pielou's evenness) were assessed using direct counts of species present during ROV transects from various sites surveyed between 2005 and 2019. Each unique species observed along a transect was documented along with the cumulative distance traveled and seafloor surface area covered.

Richness was assessed at several points along a transect, then averaged across all transects from a given site and year. A natural log curve fitted to those points resulted in a species-area curve. Data were analyzed in R v4.0.5. Species accumulation curves provide three different pieces of information (App. Fig. C1-3): 1) A steeper initial slope is indicative of a denser habitat with more fauna present and commonly encountered; 2) The asymptote at which a curve levels off is a measure of species richness; and 3) a curve that does not level off is a strong indication that sampling was insufficient to capture the full diversity of a region. Slopes of species accumulation curves were also calculated and compared between MPAs and associated Reference sites. First curves were fitted for each year of sampling, then averaged into a single average curve, and finally the derivative of the averaged curve was plotted for the MPA and its associated Reference site.

To assess beta diversity at the level of sites within the North, Central, and South regions, ROV data were divided into regions and furthermore into MPAs sampled more than 2 years. The MPAs with more than 2 years of sampling were Bodega Bay and the Farallon Islands in the Northern CA region (2011, 2015, 2019), Point Buchon, Point Lobos, and Point Sur in the Central CA region (2008, 2016, 2019), and Carrington Point, Gull Island, Harris Point, and South Point in the Channel Islands (2005, 2006, 2007, 2008, 2009, 2014, 2015). We randomly selected 5 transects with lengths of up to 350 m^2 from those MPAs and their corresponding Reference sites to create unified areas from each MPA. The species counts of these transect data were summed, resulting in a matrix of sampled species abundances for the MPA and Reference sites each year of sampling (which changed region to region). The matrix used MPAs as 'plots', in the alpha (local) scale, and regions (Central CA and the Channel Islands) as the gamma (regional) scale, with designation consisting of two levels, MPA or Reference, as the treatment.

Beta diversity in deepwater MPAs within a region was assessed using the mobr package in R and methods of McGlinn et al. (2019). The regional matrices for each year were converted to 'mob_in' objects with attached latitude and longitude data. We calculated total invertebrate abundance (N), invertebrate species richness (S), rarefied richness (S_n), and the 'effective' number of species (S_{PIE}) at the alpha scale for each MPA and corresponding Reference site for a single year in a region. The gamma and beta scales for these statistics were also calculated. One-way ANOVAs were performed to test differences in these statistics both between samples and groups. Three beta statistics, β_S, β_{Sn}, & β_{Spie} were calculated for each MPA and Reference site within each region every year of sampling and compiled into a matrix. For all three beta statistics, a larger value indicates greater species turnover between gamma and alpha scales, but each relies on different reasons for that turnover. β_S indicates turnover due to aggregation, density or species abundance distribution (SAD) effects. β_{Sn} by contrast indicates turnover and emphasizes cause due to aggregation of common and rare species. β_{Spie} indicates turnover with emphasis on aggregation of common species only.

A similarity percentage breakdown (SIMPER) analysis was applied to determine which taxa accounted for the greatest differences between the Northern, Central, and Southern management regions, and between MPA and Reference sites, both statewide and at the regional level. Species densities were arranged in a matrix with species as columns and transects as rows. We used the simper() function in the vegan package to run SIMPER analysis in R v4.0.3. Species were ranked by highest cumulative contribution until a threshold of 0.7 cumulative contribution was reached.

Combined fish and invertebrates

Using the ROV dataset collected by MARE, we examined total fish and invertebrate densities (no. m^{-2}) inside and outside each MPA and year sampled. We ran a four-way interactive analysis of variance (ANOVA) to determine if there were differences in densities between MPA locations, designation (MPA and REF), years and between fish and invertebrate taxa. Response ratios were calculated by taking the log of the quotient between either total fish density or invertebrate density inside relative to outside the MPA. To examine the difference in fish and invertebrate response ratios across years and habitat type, we used a four-way interactive ANOVA for data collected between 30–60 m and 60–130 m independently. These analyses can be found in Appendix A (Text and Fig. A28-34)

For each year sampled, we assessed combined fish and invertebrate diversity inside and outside each MPA. We calculated multiple diversity metrics: Species Richness (fisher's alpha), Shannon-Weiner, Simpson and Pielou's evenness. We then examined how each diversity metric changed across years sampled both inside and outside each MPA. Also, we examined shifts in community composition in MPAs and associated Reference sites through time. We ran a permutational analysis of variance (PERMANOVA) to assess whether community composition varied by MPA location, designation (MPA vs. REF), and survey year. We then ran a non-metric multidimensional scaling ordination (NMDS) with a Bray-Curtis dissimilarity matrix, to visually examine changes in communities across space and time for each management region independently (South, Central and North). To determine which species drove the differences in community composition across years, we ran a similarity percentages breakdown procedure (SIMPER), which provides the average percent contribution of each species to the dissimilarity matrix.

Baited Remote Underwater Video (BRUV) (Caselle)

Study locations and sampling design

We sampled two MPAs in the Santa Barbara Channel, Carrington Point State Marine Reserve (SMR) on Santa Rosa Island and Anacapa Island SMR/State Marine Conservation Area (SMCA) on Anacapa Island (Fig. 1). Both of these MPAs are in Tier 1 in the California MPA Monitoring Action Plan (2018). These two marine protected areas are characteristically distinct, occupying opposite ends of a strong environmental gradient that exists across the Northern Channel Islands. The most notable variation along the gradient is in sea surface temperature, although other factors such as productivity, wave exposure and algal species diversity and persistence also vary along the gradient of SST (Harms and Winant 1998, Blanchette et al. 2006, Hamilton et al. 2010, Caselle et al. 2015, Fewings et al, 2015). Anacapa SMR/SMCA, in the Eastern channel is characterized by warmer water, lower productivity and lower wave exposure, while Carrington Pt. SMR, in the Western portion of the Santa Barbara Channel historically experiences colder water conditions from exposure to the California current, greater productivity and higher wave exposure. These two MPAs and associated Reference areas also differ in their distance to the nearest port, with Anacapa and Carrington Pt. approximately 15 km and 50 km away, respectively. Proximity to ports and generally more favorable ocean conditions make Anacapa more accessible to fishing charters and personal vessels, potentially resulting in greater fishing pressure for some fishing sectors relative to Santa Rosa Island (Zellmer et al. 2018).

Anacapa is divided into three management zones defined by two natural breaks in the island (Caselle et al. 2018): State Marine Reserve (SMR; no-take), State Marine Conservation Area (SMCA; commercial and recreational take of CA spiny lobsters and recreational take of pelagic finfish allowed), and Reference area (open to fishing; Fig. 1). A portion of the SMR, north of the eastern island, has been closed to fishing since 1978 (Old SMR) and was extended in 2003 to include the north side of the middle island (New SMR). The SMCA was also established on the north side of the western island in 2003. Because the BRUV surveys do not survey lobsters and generally do not survey pelagic finfish, we treat the SMCA together with the SMR for most analysis. We also combine the Old SMR and New SMR for most analyses and indicate when we have separated those zones.

We deployed BRUVs using a stratified random approach, using geological habitat maps and bathymetry. We created a fishnet grid of 100 m x 100 m cells (in ArcGIS Pro2.1), applied across each MPA and its respective Reference area (Fig. 2). Habitat maps from the California Seafloor Mapping Program were used to calculate the amount of hard bottom within each grid cell. Grid cells were then allocated into three depth bins (30–50 m, 50–70 m, and 70–100 m). Grid cells that contained >15% hard bottom for the two shallowest depth bins and >5% hard bottom for the deepest depth bin were selected as potential sampling locations. Deeper grid cells (70–100 m) at both target MPAs contained considerably less hard bottom and required the lower criteria to ensure an even number of potential sampling grid cells across the depth bins. The mean depth of surveys differed between the two islands but there was no difference between MPA and Reference areas at each island (Mean depth (SE): Anacapa – MPA = 52.7 m (1.5), Reference = 54.5 m (1.8). Carrington Pt. – MPA = 38.0 m (0.8), Reference = 41.7 m (0.9)).

BRUVs were deployed on each survey day within haphazardly selected grid cells that met the criteria described above. The center point of each grid cell was used to begin “searching” for rocky habitat utilizing the on-vessel fathometer, and a BRUV was deployed by hand once appropriate habitat was detected. Each BRUV was deployed for a minimum of 30 min (Harasti et al. 2015). We averaged approximately 12 deployments per day and the sampling effort included both MPA and Reference sites on any single day to control for daily environmental variability. All BRUVS were set at a minimum distance of 250 m between units to minimize the effects of bait plumes and reduce the likelihood of fish being re-sampled. Sampling took place from August to October in 2019 and 2020. In 2020, we also sampled in June at Anacapa Island as a response to a shutdown of fishing at that location due to COVID-19.

Video Processing

Video files were analyzed using observation logging and 3D measurement software SeaGIS EventMeasure (www.seagis.com.au). All fishes observed were identified to the lowest taxonomic group. In order to quantify fishes, we recorded the maximum number of individuals of a species present in a single frame (MaxN) (Willis and Babcock 2000). Without the ability to discern individuals or distinguish multiple sightings of the same fish, MaxN is a conservative estimate of relative abundance that has become the standard metric for BRUVs (Shortis et al. 2009, Langlois et al. 2020).

We also measured the total length for every fish observed in the MaxN video frame. To ensure accurate length measurements in EventMeasure, cameras were calibrated before and after each sampling season following the procedures outlined in (Harvey and Shortis 1998) and using CAL v1.32 (www.seagis.com.au) software. In some instances, not all individuals in a particular MaxN frame were able to be accurately measured due to the camera angle or obstructions. In this case, we measured as many individuals as possible from the MaxN frame. The biomass of individual fishes was estimated using an allometric length-weight conversion: $W = aTL^b$, where parameters a and b are species-specific constants, TL is total length in cm, and W is weight in grams. Length-weight fitting parameters were obtained from the literature and from FishBase (Froese and Pauly 2000). The sum of all individual weights in the MaxN frame for each individual species was used to estimate biomass. Species were classified as targeted by fishing or not targeted by fishing using information from the CA Department of Fish and Wildlife as well as local knowledge of the authors. We summed MaxN and biomass for all Targeted and Non-targeted species and separately for all Targeted and Non-targeted Rockfish species (App. Table B1).

Statistical Analyses:

We completed 156 and 204 BRUV surveys at Carrington Pt. and Anacapa Island, respectively, for a total of 360 surveys (App. Table D1). Of those 360 surveys, 264 were classified as 'usable' (73% usable) and were included in analyses below. In order to inform recommendations about the future utility of BRUV surveys as a monitoring technique for California's MPAs, we quantified the 'usability' of each video. All videos were assigned a "usability" score that considered the amount of visible substrate and video length (Table 4). Any videos that did not remain upright for the entire 30 min (i.e., scores of 3 or 4) were removed from analyses. In general, two conditions resulted in unusable video; these were highly rugose habitat and/or very strong currents causing the BRUV system to not land upright, or tip over at some point in the video survey. The percentage of unusable surveys varied at the two locations with the highest percentage (38%) at the Anacapa Reference area (App. Table D1). This location, on the South side of Anacapa island, is known for extremely strong currents and although care was taken to not survey when currents were obvious, there were occasions where the initial drop appeared successful and the currents increased during the survey period. These conditions will need to be considered when designing future BRUV surveys.

Table 4. Description of the categories used to classify BRUV surveys as usable or unusable.

"Usability" Score	Criteria
1	BRUV lands upright Benthos and open water visible (ideally 1/3 benthos, 2/3 water) Remains upright for at least 30 minutes
2	BRUV lands upright Primarily looking at benthos or open water, but is not actually tipped over Remains upright for at least 30 minutes
3	BRUV lands upright Tips over before 30 minutes or camera dies before 30 minutes
4	BRUV lands and immediately tips over

Among the usable surveys only, we scored the habitat type that was most prominent in the view of the video (App. Table D2A). Anacapa Island habitats contained more soft (i.e., sandy) habitat than Carrington Pt. In particular, the MPA at Anacapa (north side of the island) is characterized by a very narrow, fringing rocky reef against the shoreline and extending to depths of 15-20m. At the depths of our sampling at that site, rocky habitat was more patchy and mixed. We tested for MPA effects on MaxN or Biomass for both targeted and non-targeted species groupings between surveys classified as 'soft versus all other habitats combined using two-way Analysis of Variance (App. Table D2B), as well as testing levels of protection zones at Anacapa (App. Table D3).

We observed a total of 53 species on the BRUV surveys across two years and both locations (App. Table D4A). A single species, Ocean whitefish (*Caulolatilus princeps*) accounted for 42% of the summed MaxN values. Ocean white fish were abundant at both islands and had the highest frequency of occurrence overall, and at each island (70-74% of all BRUV surveys). Ocean whitefish are large-bodied, benthic schooling species and are well suited for identification on BRUVs. Two species, Copper Rockfish (*Sebastes caurinus*) and CA Sheephead (*Semicossyphus pulcher*) had both high MaxN values and high frequency of occurrence at both islands. Copper Rockfish occurred on 30-62% of surveys while CA Sheephead occurred on 36-44% of surveys. Blue Rockfish (*Sebastes mystinus*), also abundant, had a similarly high occurrence at Carrington Pt. (35%). Three schooling species (Jack mackerel (*Trachurus symmetricus*), Blacksmith (*Chromis punctipinnis*) and Halfbanded Rockfish (*Sebastes semicinctus*) were abundant when observed but occurred much less frequently (2-16% of all surveys). The BRUVs were able to observe species rarely seen in other surveys (e.g., SCUBA, ROV, HOV). These included Giant sea bass (*Stereolepis* *gigas*) (37 individuals), Bocaccio (*Sebastes paucispinis*) (37 individuals) and Bat Rays (*Myliobatis californica*) (8 individuals) as well as various species of flatfishes (including CA halibut [*Paralichthys californicus*] and Pacific sanddabs [*Citharichthys sordidus*]). Although many species were documented by only a single individual, this type of presence-only data can be useful for documenting climate-induced range shifts, invasions, and habitat associations. Total MaxN and Frequency of Occurrence for each species are shown in App. Table D4A. Total Biomass for each species by island is shown in App. Table D4B, and Mean Biomass at each MPA (Anacapa Island SMR & SMCA and Carrington Point SMR) and Reference site is shown in App. Table D5.

In order to understand the effects of habitat on MPA effectiveness and because we cannot control the precise location of the BRUV drops (i.e., with ~50 m radius), we classified habitat based on substrate characteristics within the field of view of the camera(s). The four habitat classifications were "Hard", "Mixed-Hard", "Mixed-Soft", and "Soft". We defined "Hard" habitat as any substrate that primarily consists of rock, boulder, or bedrock, with little to no soft (sand/mud) habitat present. We defined "Mixed-Hard" habitat as any substrate where rock or boulders were present in combination with sand or mud (>25% sand/mud). We defined "Mixed-Soft" habitat as any substrate consisting of low relief bedrock or cobble in combination with sand or mud (>25% sand/mud). We defined "Soft" habitat as any sand or mud substrate with little to no bedrock, cobble, rock, or boulders.

Although all BRUV drops were targeted for rocky habitat as described in the sampling strategy above, once the BRUV is dropped, it is impossible to ensure that it lands on rock habitat. Many BRUV drops had only sand in the view and were scored as such. We visually inspected the patterns of MaxN and Biomass for targeted and non-targeted species across MPA and Reference areas, including all surveys and with soft habitat surveys excluded. We also tested for MPA effects on MaxN or Biomass for both targeted and non-targeted species groupings between surveys classified as 'soft versus all other habitats combined using two-way Analysis of Variance (ANOVA). We found that while there was an effect of habitat (soft versus hard/mixed) on both MaxN and biomass for several combinations of island location and species grouping (App. Table D2B), we found no significant interactions between MPA status and habitat for any species grouping at either island location, indicating no consistent differences between the MPA responses with or without the soft habitat surveys. Based on these results, and the fact that all surveys 'targeted' rocky reef habitat (i.e. if sand was present, it was likely that some mixed or rocky habitat was nearby), we use all the drops in the dataset unless specifically noted in the methods.

We tested for differences in mean MaxN, biomass, diversity, and species richness between MPAs and associated Reference areas using a Bootstrapped resampling means comparison approach. All bootstrapped resampling was done in R version 4.0.3 using the 'boot' package and was done with replacement. We calculated the difference in the mean for two randomly bootstrapped samples. We then repeated this process 9,999 times to build a distribution of all the possible differences in the mean, independent of treatment (i.e., independent of MPA vs Reference). We then tested our actual, observed difference between MPA and Reference against the resulting distribution. Any observed value that fell outside of the 95% CI was considered significant and the resulting p-value was reported. We employed a resampling approach because it is a distribution-independent method and our observed data were positively skewed (i.e., mostly data with few fish but with the occasional large school). All surveys were combined for both years.

To justify combining all surveys over years and sampling periods, we conducted ANOVAs to test for differences in the sampling period (Aug-Oct 2019, June 2020, Aug-Oct 2020) on MPA effects. Analyses indicated that there were no consistent differences in MPA effects on MaxN or Biomass for targeted or non-targeted species groups between sampling periods and so these data were combined in all analyses (App. Table D6).

Species richness and diversity (Shannon diversity index) were calculated in R using the Vegan package V2.5-6, and results are shown in Appendix Table D7. Non-metric multidimensional scaling (nMDS) techniques were used to visualize differences in the fish community at fished and unfished areas and Anacapa and Carrington Pt. nMDS plots were made in R version 4.0.3 using the 'metaMDS' package (Vegan package V2.5-6). In order to focus on the dominant fish community at each MPA and Reference area, we removed rare species from the analysis by selecting only species that were present on more than 5 separate surveys and had more than 10 individuals in the entire data set. Additionally, we only used surveys that had at least 3 different species present. We used this filtered dataset to calculate a Bray-Curtis dissimilarity matrix using the square root of the MaxN values. To measure the amount of overlap between the communities we ran an analysis of similarity using the 'anosim' function in the Vegan package. The analysis of similarity provides an R value between 1 and 0 to measure the amount of overlap between groups. Generally, R values from 1 - 0.75, 0.75 - 0.5, and 0.5 - 0.25 indicate the groups are highly different, different, and different with some overlap, respectively. To measure the influence of each particular species within the Bray-Curtis dissimilarity matrix we ran a Similarity of Percentage analysis using the 'simper' function in the Vegan package. Appendix Tables D8A and D8B display the results of an Analysis of Similarity (comparing the level of differentiation or overlap between groups) and a Similarity of Percentages analysis used to rank each species contribution to the Bray-Curtis dissimilarity matrix.

ROV and BRUV Comparison

ROV and BRUV surveys each occurred at two MPAs within the South Coast region (Carrington Pt. and Anacapa Island SMR/SMCA) during the same general time period (2019 and 2020). We used these overlapping data to briefly compare the general findings of the two tools, keeping in mind that ROV data were analyzed as a yearly time series while BRUV data from 2019 and 2020 were pooled. Additionally, the ROV and BRUV surveys did not necessarily survey the same exact reference area. Results of both ROV and BRUV surveys showed that overall fish density was generally greater at the Carrington MPA, with the exception of ROV fish density data from Carrington Pt. in 2019 (Fig. 3; App. Fig. B51). At Anacapa we found that both tools agreed and that overall fish density was slightly larger in the reference area. The Anacapa result is most likely due to the reference area containing more rock at deeper depths that is favored by certain rockfishes. *See BRUV discussion section for more information*.

Interestingly, the Anacapa and Carrington SMR biomass results from the two different tools were somewhat different. The 2019 ROV data from Carrington Pt. showed greater biomass in the Reference site, and in 2020 the biomass data were similar between the Reference site and MPA (App Fig. B56). However, the pooled biomass data from BRUV surveys at Carrington Pt. in 2019 and 2020 showed significantly larger biomass inside the reserve (Fig. 3). At Anacapa, the

ROV biomass data showed greater biomass in the Reference site than in the MPA, while the BRUV data did not show a significant difference between the MPA and Reference site (Fig. 3; App. Fig. B56). This conflicting result could be due to the different methods used to measure fishes and particularly the underestimation of the largest fishes by paired lasers (ROV) versus the stereo calibrated cameras (BRUV). See ROV Video Post Processing for further discussion.

Benthic Observation Survey System (BOSS) (Starr)

We developed stereo-video camera systems to survey rockfishes and other species that inhabit high-relief, and therefore untrawlable habitats, because state and federal management agencies manage fisheries based on stock assessments that are created from data from research trawls, which have been shown to poorly survey high relief rock habitats (Yoklavich and O'Connell 2008, Starr et al. 2016). The work we have done to evaluate high-relief rocky areas is pertinent to MPA monitoring, because the deeper portions of California MPAs have been under-surveyed. The analyses we discuss here are intended to show that video landers can be used in deep water to assess changes in fish and invertebrate populations, and can be used to complement ROV surveys, because we have shown that there is little difference between mean Lander and ROV densities for the most common species (App. Fig. E1, Denney 2017). Results of our work with the BOSS and Rotating Lander are presented in Appendix E. We are including the information in this report to show how the data collected from these tools can help understand MPA effects and for general knowledge of nearshore ecosystems in California.

We found that using the BOSS system enabled us to achieve a high level of precision in our density estimates in less than 2 days of sampling. We typically can complete 30 surveys a day and precision in BOSS density calculations begins to level off at around 50 surveys for both Central and Southern California (Fig.4; more information on this analysis can be found in App. E). Furthermore, the BOSS video lander utilizes stereo-video technology which allows us to accurately measure the length of fishes, which we have shown to be important for MPA evaluation, because paired-lasers used currently on ROV tools underestimate the actual length of fishes (App. Fig. E2). After a cruise, we use EventMeasure software (SeaGis, Australia) to analyze collected video in order to provide information about densities and length distributions of fishes. This software, along with our calibrated stereo cameras, allows us to measure lengths and distances with a high degree of accuracy (errors in length are typically 2%). For each drop, we take a Max N for each species (as described above in the BRUV section). This method eliminates any possibility of double-counting fishes. These counts are later converted to density using an area calculation based upon the field of view of our cameras and water visibility. We also measure the lengths of as many fish within that MaxN frame as possible.

To date, we have conducted over 1300 rotating lander and more than 1000 BOSS surveys along the California coast (Fig. 5). In the Fall of 2018, we spent 24 days at sea surveying the California coast from Half Moon Bay to the Channel Islands to demonstrate how our system can be used to conduct broad-scale surveys of high-relief habitats. We demonstrated that the BOSS video lander can be deployed rapidly in untrawlable rocky habitats at large geographic scales to collect data on density and size of demersal fishes, including stocks of important commercial fishes such as Cowcod (*Sebastes levis*), Yelloweye Rockfish (*S. ruberrimus*), Canary Rockfish (*S. pinnig*er) and Lingcod (*Ophiodon elongatus*). Importantly, for MPA analysis, we also demonstrated that there are different fish communities in different rocky banks along the continental shelf (App. Fig. E3), a factor to account for when monitoring MPA changes. Similarly, we showed significant differences occur in fish densities among hard, mixed, and soft substrate types (App. Fig. E4).

We are continuing to use the BOSS to conduct visual surveys in the untrawlable parts of the Cowcod and Rockfish Conservation Areas (CCAs, RCAs). Our goal is to determine how well visual surveys can be combined with hook and line surveys to improve stock assessments. In September 2021, we conducted 12 days of video surveys in conjunction with NMFS hook and line surveys in the Channel Islands. Our primary objective was to survey sites selected by NMFS scientists at fishing sites around the Channel Islands using our BOSS video lander. Our video data will be used to compare frequency of occurrence, density, length-frequency distributions, and calculated biomass of important species with information from NMFS hook and line surveys that occurred closely in time and space to our data collection. NMFS scientists were conducting hook and line surveys using commercial fishing boats and crew members to catch fish during standardized time periods.

We have also used the BOSS in collaboration with California State University Monterey Bay and the US Navy to conduct surveys at San Clemente Island to explore fish-habitat interactions and build upon previous ROV surveys. The military presence at the island has created a de facto MPA, which gives us the opportunity to study fishes and habitats removed from fishing pressure. We conducted four cruises at the island in October 2019, February 2020, March 2021, and June 2021.

MPA Habitat Attributes (Lindholm)

Objectives

The primary objectives of this portion of our project were to leverage high-resolution topographic maps of the seafloor for much of the coastline to:

a) Quantify the performance of individual State Marine Reserves (SMRs) and Conservation Areas (SMCAs) with respect to the abundance of rocky reef and high-quality habitat within the 30–100 m isobaths.
b) Quantify habitat-based connectivity within MPA clusters across the state and with the adjacent unprotected areas around those clusters.
c) Quantify the extent to which seafloor habitat, both rocky reef and high-quality habitat within the 30-100 m isobaths, contributes to the abundance, density, and species composition inside and out of MPAs.

Literature Review

We first conducted a literature review of peer-reviewed publications and graduate theses that employed any form of habitat-based modeling to study fish communities (23 papers). Ultimately, we focused on eight of those papers that specifically focused on habitat suitability models for fishes along the California coast. Habitat attributes that commonly featured as metrics in these models included: vector ruggedness measure (VRM), topographic or benthic position index (TPI/BPI), slope, depth, curvature (slope of slope), aspect, and distance from rock. Common challenges to any modeling effort are two-fold: making sense of the output from a normally large number of individual models and determining the extent to which the lessons learned by a particular model on a particular species can be extrapolated to other species and other locations. To minimize the potential impact of those challenges on our analyses, we conducted a meta-review of significant variables across the models produced by 11 papers (Table 5). The eight papers featured a total of more than 40 fish species, across multiple locations, ranging from Point Arena in the north to the Channel Islands in the south.

Table 5. List of papers from the California coast that used habitat suitability models for demersal and benthic fish species, including the authors, location of the study, and list of fish species addressed in the models.

Source	Location	Fish Species
Basset et al. (2018)	Central California (Point Arena to Point Buchon)	Lingcod (*Ophiodon elongatus*)
Bolton, H. (2014)	Bodega Head	Vermilion Rockfish (*Sebastes miniatus*); Canary Rockfish (*Sebastes pinniger*); Yelloweye Rockfish (*Sebastes ruberrimus*)
Caselle et al. (unpublished)	Northern Channel Islands, CA	Twenty-four species, including rockfishes, Perches, other species.
Iampietro et al. (2005)	Del Monte Shale Beds, Monterey, CA	Canary Rockfish (*Sebastes pinniger*); Brown Rockfish (*Sebastes auriculatus*); Vermilion Rockfish (*Sebastes miniatus*); Blue Rockfish (*Sebastes mystinus*); Olive Rockfish (*Sebastes serranoides*); Rosy Rockfish (*Sebastes rosaceus*); Flag Rockfish (*Sebastes rubrivinctus*); Gopher Rockfish (*Sebastes carnatus*)
Hamilton et al. (2009)	Northern Channel Islands, CA	Thirty species, including rockfishes, Perches, and others.
Martel, G. (2020)		Squarespot Rockfish (*Sebastes hopkinsi*); Rosy Rockfish (*Sebastes rosaceus*); Pygmy Rockfish (*Sebastes wilsoni*)
Tagini, A. (2018)		Canary Rockfish (*Sebastes pinniger*); Copper Rockfish (*Sebastes caurinus*); Greenspotted Rockfish (*Sebastes chlorostictus*); Greenstriped Rockfish (*Sebastes elongatus*); Vermilion Rockfish (*Sebastes miniatus*); Pacific sanddab (*Citharichthys sordidus*)
Young & Carr (2015)	Pigeon Point to Point Conception, CA	Tubesnout (*Aulorhynchus flavidus*); Black perch (*Embiotoca jacksoni*); Striped perch (*Embiotoca lateralis*); Olive Rockfish (*Sebastes serranoides*); Kelp Rockfish (Sebastes atrovirens); Gopher Rockfish (*Sebastes carnatus*); Black and Yellow Rockfish (*Sebastes chrysomelas*); Black Rockfish (*Sebastes melanops*); Blue Rockfish (*Sebastes mystinus*); Kelp greenling (*Hexagrammos decagrammus*)

Topographic Analyses
From those eight papers, a list of four key habitat attributes was identified for their consistent importance to multiple fishes across each of the surveyed projects. The key attributes included:

Bathymetry: a measurement of water depth.
Substrate: the geologic material on the seafloor with which fish associate.
Substrate slope: a measure of the steepness of a substrate.
Complexity: a measure of the rugosity of a substrate.

Each of the reviewed papers featured models that identified these habitat attributes as significant predictors of demersal fish-habitat associations across multiple species.
All seafloor topographic data were obtained from the California Mapping Project through the California Undersea Imagery Archive (csumb.edu/undersea). The highest resolution data available were at two-meter horizontal resolution. All data rasters were uploaded into ArcMap 10.8.1. and were merged with contiguous rasters where necessary to obtain complete coverage of a given MPA.

Merged data layers, including all four attributes, were reclassified according to categories used by Greene et al. (1999), Iampietro et al. (2008), and Young (2014). The categories are depicted in Table 6 below. This approach provided an aggregate habitat assessment (aggregated across species and locations). A quartile analysis conducted on each habitat attribute was used to identify a measure of 'high-quality habitat,' which was quantified as data in the fourth quarter (above the third quartile). All subsequent analyses for Objectives 1a and 1b were based on this high-quality habitat.

To address the substrate attribute, all analyses were conducted on rocky substrates identified in the topographic maps, excluding any area that was primarily unconsolidated sediments. The bathymetry attribute was addressed by constraining all analyses to the area between the 30–100 m isobaths (which is the focal area of the larger grant). **Note**: for Objective 1c bathymetric data were further apportioned into bins of 30–60 m and 61–100 m for inclusion in a separate modeling effort conducted by other PIs on the project.

Table 6. Four habitat attributes derived from literature review of habitat suitability models and subsequently categorized based on Greene et al. (1999) and Young (2014).

Attribute	Category
Bathymetry	0 – 30 m 31–100 m 101 m+
Substrate Type	0: unconsolidated sediment 1: rocky reef

Substrate Slope	0°-5°: flat 5°-30°: sloping 30°-60°: steeply sloping 60°-90°: vertical > 90°: overhang
Substrate Complexity	Low Low to moderate Moderate Moderate to high High

A quartile analysis was conducted on each category of the substrate slope and complexity attributes. Attribute tables were used to obtain pixel counts of each category. These counts were then apportioned into four quarters. Given the demonstrated fish-habitat associations with steep topographic highs and highly-complex microhabitats, those two categories were selected for subsequent analyses.

The rasters for the slope and complexity attributes were reclassified to include only steeply sloping features (30°–60°) and high complexity. Using the raster calculator tool, steep slope and high complexity rasters were combined to obtain overlapping features in a new raster. Individual pixel values were used to calculate the total surface area covered by the raster of combined features. A raster calculator was used to obtain the overlap of data in the fourth quarter for both attributes. The resultant combined rasters were used to determine the areal extent of high-quality habitat within individual MPAs and in adjacent unprotected areas.

MPA-based Analysis

A total of 69 MPAs, both SMRs and SMCAs, were included for analysis (see App. F). The focus on rocky, subtidal habitat located within the 30–100 m isobaths resulted in several MPAs being excluded from our analysis (Table 7) due to their shallow depth. An additional few MPAs were excluded due to the absence of topographic coverage at the 2-meter resolution (e.g., Anacapa Island SMR and SMCA), which was required for this analysis. The resultant distribution of MPAs extended from the Pyramid Point SMCA in the north to the South La Jolla SMCA in the south.

Table 7. Summary of MPA classifications and the total number of each type across the state and the reduced number included in this study.

MPA Classification	Total #	# Included for Analysis
State Marine Reserve (SMR)	48	28
State Marine Conservation Area (SMCA)	70	40

The total area of rocky reef occurring within the 30–100 m isobaths was calculated for each MPA, as was the total area of high-quality habitat. In the context of this analysis, Reference areas were identified by selecting a comparable area (equivalent to the entire MPA) immediately adjacent to an MPA or MPA cluster to the north or south along the coast. In several cases the same Reference area was used to compare the performance of an SMR and an adjacent SMCA. **Note**: with rare exception, the Reference areas identified for this analysis also included the Reference locations for the ROV transects conducted as part of the larger project.

Results

We organized the results of our work around the specific OPC Decadal Evaluation Working Group (DEWG) questions that our investigations could address. In all monitoring programs, additional information is collected that can help improve our understanding of how ecosystems function. Analyses conducted on mid-depth fish and invertebrate communities that are not directly related to the DEWG questions or MPA responses have been placed in the Appendices to this report. These include examining fish and invertebrate interactions with zero-inflated hurdle models from ROV surveys, information about the rotating lander, benthic observation survey system (BOSS), and the depth distributions of ROV and HOV surveys.

DEWG Question 1**: Do focal and/or protected species inside of MPAs differ in size, numbers, and biomass relative to Reference sites?**

Q1a. Does the difference between MPAs and Reference sites in the size of individuals of a focal and/or protected species increase over time?

HOV and ROV fish data:

Mean Length

We examined the changes in body size of fishes from the North, Central, and South Coasts for all years of sampling, using mean lengths from the top focal species from each region. Across all regions we detected changes in mean length of fish among MPAs and Reference sites and across years for certain focal species. However, the differences in mean lengths of fishes between MPA and Reference sites did not show a clear positive or negative trajectory through time (Fig. 6-8). For the North Coast, we found that there were differences in body size for 2 of the 11 focal species (Kelp Greenling and Quillback Rockfish) between MPA and Reference sites and across years (Fig 6; App. Table B2). On average, Kelp Greenling were 0.81 cm smaller and

Quillback Rockfish were 2.62 cm smaller in MPAs compared to areas open to fishing. For the Central Coast, statistical differences in mean lengths among MPA and Reference sites across sampling years were apparent for 6 of 11 focal species (Blue/Deacon Rockfish, Gopher Rockfish, Lingcod, Painted Greenling, Pink Seaperch, and Vermilion Rockfish) (Fig. 7; App. Table B3). On average, Blue/Deacon Rockfish were 0.48 cm larger, Gopher Rockfish were 0.28 cm larger, Lingcod were 1.82 cm larger, Painted Greenling were 0.23 cm smaller, Pink Seaperch were 0.21 cm larger, and Vermilion Rockfish were 0.87 cm smaller in MPAs compared to associated Reference sites. For the South Coast, 5 of 13 species (Blacksmith, Blue/Deacon Rockfish, California Sheephead, Kelp Greenling, and Vermilion Rockfish) showed differences in mean body size among MPAs and Reference sites across years (Fig.8; App. Table B4). On average, Blacksmith were 0.52 cm smaller, Blue/Deacon Rockfish were 1.65 cm larger, California Sheephead were 0.29 cm larger, Kelp Greenling were 4.20 cm smaller, and Vermilion Rockfish 1.82 cm larger in MPAs compared to associated Reference sites.

Proportion of fish with lengths >50% Maturity

Using published information about size at maturity for focal fish species, we assessed how the proportion of individuals larger than the mean length at 50% maturity for a species varied inside MPAs compared to their Reference sites for each management region. In the North, we had sufficient lengths to conduct this analysis for 9 of the 11 focal species (we excluded Quillback and Brown Rockfish). For the Central Coast, 7 of 11 focal species were analyzed (excluding Painted Greenling, Pile Perch, Pink Seaperch, and Striped Seaperch). For the South Coast, 8 of 12 focal species were analyzed for proportion greater than the length at 50% maturity (excluding Blacksmith, Painted Greenling, Pile Perch and Treefish). Across all regions and focal species analyzed, there was no statistical difference in the proportion of individuals greater than 50% maturity inside MPAs compared to associated Reference sites (Fig. 9; App. Fig. B48). There were non-significant trends of increased proportion of individuals greater than 50% maturity for Copper Rockfish, China Rockfish, and Gopher Rockfish in the North Coast, Lingcod, China Rockfish, and Blue/Deacon Rockfish for the Central Coast, and Copper Rockfish in the South Coast.

BRUV data: We tested for reserve effects on MaxN for individual focal species that were abundant in the BRUV surveys (Fig. 10, App. Table D5). Copper Rockfish (*Sebastes caurinus*), a heavily fished species showed the strongest reserve effect with greater MaxNs inside the MPA at Anacapa and Carrington. Additionally, the heavily targeted Blue Rockfish showed positive reserve effects for MaxN at Carrington Pt. However, the Rosy Rockfish, which is targeted, had significantly greater MaxN outside the MPA at Anacapa. The heavily Targeted Non-rockfish species, Ocean Whitefish, had significantly greater MaxNs inside the Anacapa MPA. Interestingly, California Sheephead showed significantly larger MaxNs outside of the MPA at Anacapa, most likely due to more favorable habitat in the shallower depth zones favored by that species. (All focal species plots and statistics are shown in Fig. 10, Fig. 11, and App. Table D5).

We calculated the average log response ratios for MaxN for 10 focal species that were abundant and included both targeted and non-targeted species (Fig. 12). Response ratios were calculated as log (MPA/Ref) and varied over the two years. At Anacapa, eight of the ten species evaluated showed negative response ratios, including some targeted species. At Carrington Pt., seven species had positive response ratios for MaxN. Notably, Copper Rockfish and Blue Rockfish, both presumed to be heavily fished at Carrington Pt. showed positive and larger response ratios.

The Carrington Pt. SMR and associated Reference areas are adjacent to one another with continuous, rugose habitat connecting the fished and unfished areas (Fig. 2). The different trends observed for Rockfish and non-Rockfish abundance and biomass could be related to species-specific movement patterns. For example, Copper Rockfish are relatively resident with small home ranges (<10 m^2) over high relief habitat, and Blue Rockfish fitted with acoustic tags have shown residence times >365 days (Love et al. 2002, Green et al. 2014). Ocean whitefish have considerably larger home range sizes (average 95% KUD of 20,439 +/- 28,49 2m^2) compared to most Rockfish species and have been shown to freely move across sandy low relief habitats (Bellquist et al. 2008). Lingcod have been shown to have a wide array of movement patterns, with individuals being highly resident at times but also exhibiting inshore and offshore migrations to nesting habitats (Starr et al. 2015). These differences in movement most likely result in more frequent MPA boundary crossing and expose species like Ocean Whitefish and Lingcod to consumptive fishing compared to resident rockfishes inside the SMR.

Q1b. Does the difference between MPAs and Reference sites in density (or proportionate cover) of a focal and/or protected species increase over time?

ROV fish data: Along the North Coast, for all 11 focal species there was no difference in the trajectory of densities among MPA and Reference sites through time (App. Table B5). All focal species had higher densities in 2020 in both the MPA and Reference sites than initial sampling in 2011 (Fig. 13). For 4 of the 11 species, Brown Rockfish, Quillback Rockfish, Vermilion Rockfish, and Yelloweye Rockfish, there were higher densities inside the MPAs compared to Reference sites in the most recent sampling year (2020). There were no clear differences in densities among MPA and Reference sites in 2020 for 7 of 11 species: Black Rockfish, Blue/Deacon Rockfish, China Rockfish, Copper Rockfish, Kelp Greenling, and Lingcod and Vermilion Rockfish. One species, Rosy Rockfish, had lower densities inside the MPA compared to the Reference sites in 2020. Along the Central Coast, 9 of 11 species showed increasing densities through time however, there were no statistical differences among MPAs and Reference sites with the exception of higher densities in the Reference sites for Pink Seaperch (Fig. 14; App. Table B6). Lingcod and Kelp Greenling densities peaked in 2014-2015, however densities drastically declined after that time in both MPA and Reference sites. In the most recent sampling year (2020), 1 of 11 species (Striped Seaperch) showed higher densities in MPAs compared to Reference sites. Conversely, 8 of 11 species showed lower densities inside MPAs compared to Reference sites, while there were no differences in densities among MPAs and Reference sites for the remaining 2 focal species. For the South Coast between 2005 and 2020, 9 out of 13 species showed increasing densities through time, 3 species (Bocaccio, Kelp Greenling, Lingcod) showed little change in density between 2005 and 2020, and 1 species (Pile Perch) experienced a decline in density through time (Fig. 15; App. Table B7). For both Copper Rockfish and California Sheephead, the difference in densities between MPA and Reference sites increased through time with statistically higher densities in the MPAs in 2020. Interestingly, densities of some species such as Kelp Greenling and Lingcod increased inside MPAs and Reference sites until 2014-2015 and then declined resulting in little observed change between initial and recent sampling.

BRUV data: We used MaxN as a proxy for fish density and tested for reserve effects on density and biomass for focal and/or protected species that were abundant in the BRUV surveys; these results are discussed in section *BRUV Q1a* above.

ROV invertebrate data: The California sea cucumber, *Apostichopus californicus*, is harvested as a fishery in Southern California. Sea cucumber numbers were significantly lower in Reference sites in Southern California compared to within MPAs (Fig. 16), while California sea cucumber densities were comparable between Reference sites and MPAs in Central and Northern California, where there is no substantial harvest (Fig. 17). We conducted a regional analysis to study the effects of MPAs on sea cucumber distributions across different years, between MPAs and non-MPAs, and within particular sites. Southern California sea cucumber densities were most affected by year, and surprisingly did not show significantly different population sizes among the Reference sites and the protected sites. However, California sea cucumber density in MPAs was generally greater in Southern California MPAs than in Reference areas, by a regular and consistent margin (Fig. 17D). Across the state and within the Northern and Central regions, there was also sometimes a pattern of greater densities in MPAs, but not as consistently as where they are fished (Fig. 17A-C). We conclude that there was a positive MPA effect on California sea cucumbers in general, and that this was mainly a factor of fishery protections where they are fished.

California sea cucumbers are commercially harvested by trawl in Southern CA and, to a smaller extent, by divers in Northern CA with peak landings of 600,000 lbs. in 1993, but recent landings reduced to tenfold by 2018 (CA Marine Species Portal 2020). The Southern CA trawl fishery was established in 1978 and primarily harvests sea cucumbers in mid-depths, from 45-130 m (CA Marine Species Portal 2020). ROV surveys indicated the lowest cucumber densities in Southern CA, where commercial harvest occurs, compared to Central and Northern CA. Given the fishing pressure at mid-depths in Southern CA, it is unsurprising that, with positive response ratios suggesting that California sea cucumbers occurred in greater densities within the MPAs than outside of them. Protections from fishing may be the main driver of this positive MPA effect. Positive response ratios for Northern and Central CA cucumbers are more of a mystery because diver collections primarily occur shallower than mid-depths (between 12 and 26 m; CA Marine Species Portal 2020). There is no way to know why numbers might be lower if divers are likely not harvesting at these deeper depths, but one hypothesis may be spillover from protections in nearby shallow waters. What was surprising, however, was that despite there being known fishing restrictions in marine protected areas there was no statistically significant difference in their numbers in MPAs compared to Reference sites at mid-depths, either in Southern CA alone or across the whole state. This may be due to the significant changes in cucumber numbers between years, which might mask any effect by the MPAs.

In contrast to what we observed with sea cucumbers, density of the ecologically important sea urchin species *Mesocentrotus franciscanus* was lower in MPAs than in Reference sites statewide as well as in each region when considered separately (Fig. 18). The exception to this is in the northern region, where urchin densities were relatively unchanged between MPAs and References in some years, and lower in others (Fig. 18B). This species, along with the purple urchin *Strongylocentrotus purpuratus*, can have population explosions that shift regions from kelp forests to urchin barrens in shallow waters. While kelps are not expected to grow in much of the depth range of the deepwater MPAs, the urchins can still persist and, where numbers are high, have potential to act as source populations for shallower cohorts that would coexist with kelps. Given explosions of urchins and a history of creating urchin barrens throughout CA (reviewed by Filbee-Dexter and Scheibling 2014), including barrens forming and spreading throughout Central CA since 2013 (Rogers-Bennett and Catton 2019), it was surprising to see differences in urchin densities and raised several questions. Firstly, why were urchin populations lower inside of MPAs than outside? One possible explanation is if fishing protections in the MPA had indirect effects because either more or larger fish that could act as predators and keep urchin populations down (Cowen 1983). Another possibility is that there is more competition for food if communities are more diverse in MPAs, including with herbivorous fish or invertebrate taxa that could occupy similar niche spaces. The former model seems more likely – there was no clear pattern of there being more herbivores, at least in terms of invertebrates, within MPAs based on response ratios of herbivores as a functional group.

The sunflower star *Pycnopodia helianthoides* is a generalist benthic predator whose role in shaping benthic communities is becoming increasingly recognized, potentially as a keystone species. Sunflower star densities were generally greater in Central California MPAs than in their associated Reference sites (Fig. 19C) but lower in Northern and Southern California regions. Densities were generally low for this predator and no *P. helianthoides* were observed in any ROV surveys, from any deepwater MPA or Reference site, since 2015, when sea star wasting syndrome (SSWS) decimated all sea star populations along the west coast of North America and especially affected *P. helianthoides*.

We also assessed two additional species that were neither particularly commercially nor ecologically important, but that were abundant across the state of California and therefore good candidates to assess populations across the entire MPA network. As non-fished, non-targeted species, we infer these two species to be suitable indicators of invertebrates in general across the state. Statewide, there was no clear difference in density of the vermilion star, *Mediaster aequalis,* between MPAs and Reference sites, with no clear pattern statewide nor in Central or Southern California (Fig. 20). Sea star densities were lower in Northern California MPAs than in their Reference sites (Fig. 20B). There was also no clear change in vermilion star populations after 2015, unlike what was observed for the sunflower star. Densities of the slender sea pen, *Stylatula elongata,* did not differ between MPAs and Reference sites in Northern or Central California, or when considered statewide (Fig. 21A), but densities were greater in Southern California MPAs (Fig. 21D).

Q1c. Does the difference between MPAs and Reference sites in biomass of a focal and/or protected species increase over time?

ROV fish data: Along the North Coast, there were statistical differences in biomass between MPAs and Reference sites across survey years for 3 of 11 focal species (Copper Rockfish, Kelp Greenling and Yelloweye Rockfish) (Fig. 22; App. Table B8). For example, Copper Rockfish changed very little in biomass inside the MPAs through time, in contrast Copper Rockfish biomass in the Reference sites increased until 2015 and then declined in 2019 and 2020. None of the 11 focal species increased in biomass inside the MPA through time more so than the Reference sites. Along the Central Coast, total biomass varied across survey years for 5 of 11 focal species (Blue/Deacon Rockfish, Gopher Rockfish, Lingcod, Painted Greenling, and Vermilion Rockfish); however, there were no differences in biomass among MPAs and Reference sites (Fig. 23; App. Table B9). In contrast to density, no focal species along the Central Coast showed higher biomass in MPAs in the most recent sampling year (2020). For the South Coast, 6 out of 13 species (Blue/Deacon Rockfish, California Sheephead, Copper Rockfish, Gopher Rockfish, Lingcod, and Vermilion Rockfish) displayed varying biomass through time (Fig. 24; App. Table B10). In 2020, biomass of 3 of 13 species was higher inside the MPA than the Reference site (Bocaccio, Kelp Greenling, and Pile Perch); however, these differences were not statistically significant.

ROV invertebrate data: We are unable to calculate differences in invertebrate biomass because there are few length:weight relationships available for invertebrate species.

BRUV data: We tested for reserve effects on biomass for individual focal species that were abundant in the BRUV surveys (Fig. 10, App. Table D5). Copper Rockfish (*Sebastes caurinus*), a heavily fished species, showed the strongest reserve effect with greater biomass inside the MPA at Anacapa and Carrington. Additionally, two heavily fished Rockfish species, Blue and Vermilion, showed positive reserve effects for biomass at Carrington Pt.

At the Anacapa MPA, the heavily Targeted Non-rockfish species, Ocean Whitefish, showed a significant reserve effect for biomass. Similar to our MaxN result, California Sheephead had a significantly larger biomass outside the Anacapa MPA. (All focal species plots and statistics are shown in Fig. 10-11 and App. Table D5).

We calculated the average log response ratios for Biomass for 10 focal species that were abundant and included both targeted and non-targeted species (Fig. 12). Response ratios were calculated as log (MPA/Ref) and errors varied over the two years. At Anacapa, seven of the ten species shown had negative response ratios, including some targeted species. At Carrington Point, most species showed positive response ratios for biomass. Notably, large, positive response ratios were observed for Copper Rockfish and Blue Rockfish, both presumed to be heavily fished at Carrington Pt.

Q1f. Does the difference between MPAs and Reference sites in the size and age structure of populations of a focal and/or protected species increase over time?

ROV fish data: Currently, the use of paired lasers to estimate fish lengths is not sufficiently accurate to answer the DEWG question about differences in size and age structure (i.e., frequency distributions). The use of stereo-video analysis would increase the ability to statistically distinguish between size structures of fish; however, growth rates of older fishes are slow enough that it is difficult to estimate the maximum ages of larger fish without using lethal means of fish collection.

BRUV data: Our stereo-video BRUVs allow for individual fish length measurements. We plotted length frequency histograms for the three most numerous Targeted Rockfish (family *Sebastes*) in our study; Blue Rockfish (*Sebastes mystinus*, n = 171), Copper Rockfish (*Sebastes caurinus*, n = 211), and Vermilion Rockfish (*Sebastes miniatus*, n = 126) (Fig. 25B). Copper Rockfish are notably larger inside the MPAs at both Anacapa Island and Carrington Pt., likely driving the strong reserve effects on overall biomass discussed in section *BRUV Q1g*. Vermilion Rockfish, another large-bodied, heavily fished Rockfish, were larger at the MPA at Carrington Pt. Smaller-bodied Blue Rockfish were similar in size across protection zones at Carrington Pt. and we excluded this species from Anacapa Island because they were not observed in high enough numbers to accurately reflect a size distribution.

We also plotted the size structure for two additional large-bodied, Targeted Non-rockfish species that were abundant in BRUV surveys; Ocean Whitefish (*Caulolatilus princeps*, n = 1109) and California Sheephead (*Semicossyphus pulcher*, n = 120), from fished and unfished areas at Anacapa and Carrington Pt (Fig. 25A). Similar to the Rockfish species, larger individuals of both Ocean Whitefish and California Sheephead were found inside MPAs at Anacapa and Carrington Pt.

ROV invertebrate data: We are unable to calculate age differences because there are few length:age relationships available for invertebrate species.

Q1g. Does the difference between MPAs and Reference sites in overall density and biomass of focal and/or protected species increase over time?

ROV Fish data: We examined total density (no. m^{-2}) trends for all MPAs combined within a region and each individual MPA sampled for 3 or more years at both MPA and Reference sites. For the North Coast, total density showed an overall positive trajectory through time in both MPAs and Reference sites with peak density occurring in 2014 (Fig. 26). However, there were no statistical differences in total density among MPAs and Reference sites in any year sampled (Fig. 26). One MPA surveyed (Point St. George SMCA) had total densities greater inside the MPA compared to the associated Reference sites. In contrast, 7 MPAs (Bodega Head SMCA, Bodega Head SMR, Point Arena SMR, Reading Rock SMR, SE Farallon Islands SMR, Sea Lion Gulch SMR, and Ten Mile SMR) showed lower total average densities in the MPAs or no difference in total density between MPAs and Reference sites (App. Fig. B49). Interestingly, in 2020 the total fish density in both Bodega Head SMR and SMCA exceeded total density in the associated Reference site for the first time during sampling. For the Central Coast, total density increased through time, peaking in 2019 and then declining drastically in 2020. In 2012, 2015, and 2016, MPAs contained higher total fish density than associated Reference sites. In all other years sampled there were no statistical differences in total density among MPAs and Reference sites (Fig. 26). Two Central Coast MPAs, Point Lobos SMR and Point Buchon SMR, showed increasing total densities through time in both MPA and Reference sites (App. Fig. B50). In the most recent sampling years (2019) there was no difference in density between the MPA and Reference sites at Point Buchon SMR. Point Lobos and Point Sur SMRs experienced increasing densities through time in both the MPAs and Reference sites; however, the densities at the Reference sites for both Point Lobos and Point Sur SMRs were much higher than densities inside the MPA in the most recent sampling year (2019; App. Fig. B50). For the South Coast, total fish densities showed a positive trajectory through time, peaking in 2014 for both MPAs and References sites. MPAs had higher total density than Reference sites in 2015 and 2019; however, in 2020 Reference sites had substantially higher densities than inside MPAs (Fig. 26). Four South Coast MPAs and associated Reference sites were sampled 3 different years: Carrington Point SMR, Gull Island SMR, Harris Point SMR and South Point SMR. All four MPAs showed increasing total densities through time inside and outside the reserve (App. Fig. B51). However, Harris Point was the only site where total density was statistically greater in the MPA compared to the Reference site during the most recent year of sampling (2020).

We examined total biomass (kg m^{-2}) trends for all MPAs combined within a region and each individual MPA sampled for 3 or more years at both MPA and Reference sites. For the North Coast, total biomass showed an overall positive trajectory through time in both MPAs and Reference sites, with peak biomass occurring in 2014. However, there were no statistical differences in total biomass among MPAs and Reference sites (Designation: $F_{1,267} = 1.71$, p=0.19; Fig. 27). Along the North Coast, for 4 of 7 MPAs (Bodega Head, SE Farallon Islands, Sea Lion Gulch, and Ten Mile) total biomass varied across years but there was no difference in biomass among MPAs and Reference sites (App. Fig. B52-53). For the Central Coast, total biomass increased through time, peaking in 2016 in the Reference sites and 2019 in the MPAs (Year: $F_{1,273} = 49.49$, $p < 0.001$); however, there were no statistical differences between MPAs and Reference sites (Designation: $F_{1,273} = 0.011$, p=0.92; Fig.27). Along the Central Coast, total biomass in 3 MPAs (Point Buchon, Point Lobos, and Point Sur) varied across years, but did not differ among MPA and Reference sites (App. Fig. B54, App. Fig. B55). For the South Coast, total biomass displayed a positive trajectory through time, peaking in 2014 for both MPAs and Reference sites (Year: $F_{1,702} = 36.77$, $p < 0.001$). MPAs had higher total biomass than Reference sites in 2015 and 2019; however, in 2020 Reference sites contained substantially higher biomass than MPAs (Designation: $F_{1,702} = 5.66$, p=0.001; Fig. 27). Along the South Coast, 4 of 4 MPAs varied in total biomass across years sampled (Carrington Point, Harris Point, South Point and Gull Island), 2 of 4 MPAs (Carrington Point and Harris Point) showed statistically different biomass between MPA and Reference sites (App. Fig. B56, App. Fig. B57). Additionally, at Harris Point there was an interactive effect of year and designation on total biomass.

ROV invertebrate data: Structure-forming invertebrates, such as corals and sponges, were both found at greater densities within MPAs than in associated Reference sites (Fig. 28, Fig. 29). Coral densities as a group (Phylum Cnidaria, Class Anthozoa, Subclass Octocorallia) had the strongest, most consistent positive density response ratio calculated each year. All regions and time periods were consistently greater than zero, meaning that MPAs contained denser communities than their Reference sites (Fig. 28). Sponges (Phylum Porifera) also showed greater densities in MPAs compared to their Reference sites (Fig. 29), although response ratios from the most recent surveys (2019) showed lower densities of sponges in MPAs compared to Reference sites in all regions except Southern California (Fig. 29A-D). We calculated response ratios for different feeding functional groups. Across the state, densities of suspension feeders and sessile predators were enriched in MPAs compared to Reference areas (Fig. 30). There were no clear patterns for herbivores or scavengers, and a generally weak but negative effect on mobile predators.

BRUV data: Using MaxN as a density proxy***,*** we tested the overall effect of fished (Reference) and protected (MPA) areas at Anacapa and Carrington Pt. by summing the MaxN for all targeted and non-targeted species observed on a particular BRUV survey for all habitats for both years (Fig. 3). For this analysis we excluded one species, a pelagic schooling baitfish Jack mackerel (*Trachurus symmetricus*), that had significantly larger MaxNs than any other species in our study, and for which we do not expect to show a reserve effect due to their large home ranges and short lifespans. We found a significant reserve effect for targeted species at Carrington Pt., with the observed summed MaxN for the MPA and Reference area being 20.44 and 14.03 fish, respectively ($p = 0.004$; Fig. 3, App. Table D9A). We also found a slightly significant reserve effect for non-targeted species at Carrington Pt., with the observed summed MaxN for the MPA and Reference area being 8.06 and 3.53 fish respectively ($p = 0.04$; Fig. 3, App. Table D9A).

We also summed MaxN for Targeted and Non-targeted Rockfish species and found a significant reserve effect for Targeted Rockfishes at Carrington Pt., with the observed MaxN for the MPA and Reference area being 11.84 and 5.93 fish respectively ($p < 0.001$; Fig. 31, App. Table D9B. We also found a significant effect of Targeted Rockfishes at Anacapa Island, however the trend favored the Reference area with mean summed MaxN of 5.4 and 2.1 observed in the Reference area and MPA respectively ($p = 0.001$; Fig. 31, App. Table D9B).

Similar to MaxN, we tested for reserve effects on total biomass at Anacapa and Carrington Pt. for all targeted and non-targeted species (Fig. 3, App. Table D9C), as well as Targeted and Non-targeted Rockfishes (Fig. 31, App. Table D9D). We excluded two species for the biomass calculation, Giant Sea Bass (*Stereolepis gigas*) and Yellowtail Amberjack (*Seriola lalandi*), because they are considerably larger in size than any other species in our study and exhibit large movements. Similar to total MaxN for all species, we found a significant difference in total biomass between fished and non-fished areas at Carrington Pt., with estimated mean biomass of 8.39 kg and 5.36 kg inside the MPA and Reference area respectively ($p = 0.003$; Fig. 3, App. Table D9C). We found a significant difference between the non-targeted biomass between the MPA and Reference at Anacapa, however the trend favored the Reference area with mean estimated biomass of 0.14 kg and 0.07 kg in the Reference area and MPA respectively ($p = 0.005$; Fig. 3, App. Table D9C).

For biomass of Targeted and Non-targeted Rockfishes, the only significant reserve effect detected was for Targeted Rockfishes at Carrington Pt., with a mean biomass of 4.33 kg and 1.83 kg in the MPA and Reference area, respectively ($p = 0.001$; Fig. 31, App. Table D9D). Note that the biomass of Non-targeted Rockfish species at Carrington Pt. was too low to run a valid statistical model.

DEWG Question 2**: Does community structure and/or functional diversity differ in MPAs relative to Reference sites?**

Q2a. Does the difference between MPAs and Reference sites in community structure and/or species diversity within any given functional group increase over time?

ROV fish data: For this analysis, we examined changes in species richness, Shannon-Weiner diversity, and community composition through time for MPAs and associated Reference sites. We focused our analyses on 9 MPAs spanning the entire coast of California (3 from each management region): Reading Rock SMR, Bodega Head SMR, SE Farallon Islands SMR, Point Lobos SMR, Point Sur SMR, Point Buchon SMR, Carrington Point SMR, Harris Point SMR and South Point SMR. We removed Starry Rockfish, Rosy Rockfish and Greenspotted Rockfish from these analyses to account for the fact MARE did not distinguish these species prior to 2014.

To determine if community composition differed across MPAs and Reference sites, across years, and among regions, we conducted a three-way interactive permutational analysis of variance (PERMANOVA) and a non-metric multidimensional scaling ordination (NMDS). We found there was an effect of survey year ($F_{1,90}$=15.84, p <0.001), region ($F_{2,90}$=26.23, p <0.001) and an interactive effect of the two ($F_{2,90}$=5.72, p = 0.002) on community composition. Interestingly, there was no difference in community composition among MPAs and Reference sites ($F_{1,90}$=1.50, p = 0.19). The NMDS explained 99.2% of the dissimilarity among fish communities. Three-dimensional axes were utilized to visually examine community composition across all three regions with a stress of 0.05. In both the North and Central regions, the 95% CI ellipses expanded in more recent years (while still overlapping) indicating the communities, while still similar in both MPAs and Reference sites, are starting to change. In contrast, on the South Coast there is a visual expansion and shift in the communities (both inside and outside MPAs) after 2014 (Fig. 32). This could potentially be due to the marine heatwave; however, due to the patchiness in the data directly following the heatwave, we do not feel confident in this conclusion.

Observed species richness across all MPAs ranged from an anomalously low 6 species at Point Sur SMR in 2008 to 21 species at Harris Point SMR in 2020. Overall, there was no difference in species richness through time for MPAs or associated Reference sites with the exception of the Reference sites at both Bodega Head SMR and Point Sur SMR (Fig. 33). Shannon diversity differed slightly from species richness and ranged from 0.093 at Point Sur in 2008 to 1.03 at South Point SMR in 2015. There were increases in diversity through time for all sites both inside the MPA and in associated References (Fig. 34). For the three MPAs along the South Coast with the longest time series, Shannon Diversity increased through time in both MPA and Reference sites. There was a large jump in diversity in 2014 after a gap in sampling between 2009-2013. Harris Point SMR was the only site with substantially higher diversity inside the MPA compared to the Reference sites across all years of sampling.

HOV/ROV fish Diversity Comparison: We found large differences in species diversity and species richness at the same MPAs and Reference sites in the same year between the HOV and ROV. On average, more species and more diverse communities were observed with the HOV than the ROV in both MPAs and Reference sites. The lowest species richness surveyed by the HOV was 23 species at Point Sur SMR and the highest richness was 60 species at Soquel Canyon SMCA in both 2007 and 2008. For a direct comparison, the ROV surveyed 6 species at Point Sur SMR in 2008 while the HOV surveyed 26 different species at Point Sur SMR in the same year. Similarly, there were large differences among the ROV and HOV for species diversity. The highest Shannon-Weiner diversity sampled by the ROV was 1.03 in contrast the highest diversity captured by the HOV was 3.38. These substantial differences among sites may be due to differences in survey design, ROV avoidance, differences in capabilities of tools to work in poor weather, or issues with species identification in the earlier years of ROV surveying. These differences among species richness among gear types highlight that using one tool to survey mid-depth communities may not be sufficient to capture all fishes in this depth range.

ROV invertebrate data: Species richness, diversity, and evenness varied little between MPAs and their associated Reference sites, although some individual sites had significant differences, as outlined below. Intermediate and higher latitudes corresponded with greater community diversity and richness (Fig. 35). Diversity was greater at higher latitudes up to a point, then dropped slightly. This shape is not surprising given that Central California is a region with significant range overlap of more southerly species and northerly species. A second-power curve fits the data best, with diversity increasing to a greater extent (greater slope) in MPAs than in Reference areas (Fig. 35A). Richness also increased at higher latitudes but in a linear relationship, with northern communities generally containing more species than southern communities. Richness within MPAs increased slightly more than richness in Reference areas with increasing latitudes (a greater slope), but differences in richness were greatest between MPA and Reference areas in lower latitudes (Fig. 35B). Species evenness followed a similar pattern as diversity, with middle latitudes having the greatest evenness compared to lower and higher latitudes (Fig. 35C). There were no clear changes in diversity or evenness over time, although species richness increased in more recent years for both MPAs and Reference sites (Fig. 36). Without spatial and temporal regularity to sampling, however, it is impossible to determine whether any changes in richness were attributed to how many surveys were carried out in a given year, or in particular regions.

Species richness across the network of MPAs for the state of California was 15.0 ± 4.28 (mean ± SD) and outside (from Reference sites) it was 15.4 ± 2.7. Species richness significantly differed between regions (ANOVA, $F = 4.25$, df = 2, $p = 0.021$), with Southern California surveys yielding fewer species than Northern California (Tukey's HSD, $p=0.033$), and no difference from Central California surveys (combined MPA + Reference: North: 16.7 ± 5.0, Central: 16.1 ± 5.8, South: 13.1 ± 3.8. Variability was high across sites and regions, and each region had different complements of species. Richness in northern MPAs was 16.3 ± 5.1 (mean ± SD) and from outside (Reference) sites it was 17.0 ± 4.9, with no significant difference between richness within and outside of each MPA and its Reference site (Table 8, App. Fig. C1-3) (paired t-test, df = 7, $t = 0.27$, $p = 0.79$). There were no significant differences among richness in MPAs and Reference areas in Central California (paired t-test, df = 4, $t = 0.26$, $p = 0.80$) or in Southern California (paired t-test, df = 8, $t = 0.088$, $p = 0.93$) (Fig. 37).

Table 8. Species richness and Shannon diversity of marine protected areas and their associated Reference sites across all years of ROV surveys.

Site	Richness		Diversity		Evenness	
	MPA mean ± SD	Reference mean ± SD	MPA mean ± SD	Reference mean ± SD	MPA mean ± SD	Reference mean ± SD
North	**16.3 ± 5.1**	**17.0 ± 4.9**	**1.66 ± 0.39**	**1.54 ± 0.35**	**0.57 ± 0.13**	**0.55 ± 0.13**
Point St. George	18.9 ± 4.1	21.7 ± 4.5	1.57 ± 0.17	1.48 ± 0.22	0.54 ± 0.08	0.49 ± 0.07
Reading Rock	17.5 ± 3.1	19.0 ± 4.2	1.65 ± 0.20	1.25 ± 0.43	0.58 ± 0.07	0.42 ± 0.13
Sea Lion Gulch	20.2 ± 3.8	18.6 ± 4.6	1.81 ± 0.31	1.52 ± 0.57	0.61 ± 0.10	0.52 ± 0.19
Ten Mile	16.2 ± 3.5	14.6 ± 4.1	1.45 ± 0.24	1.56 ± 0.21	0.52 ± 0.06	0.59 ± 0.04
Point Arena	15.1 ± 3.4	15.2 ± 2.9	1.68 ± 0.20	1.56 ± 0.31	0.63 ± 0.09	0.58 ± 0.13
Bodega Head	15.2 ± 5.3	16.9 ± 2.6	1.10 ± 0.83	1.56 ± 0.33	0.59 ± 0.13	0.57 ± 0.12
Farallon Islands	16.3 ± 6.1	16.5 ± 5.5	1.56 ± 0.42	1.60 ± 0.30	0.55 ± 0.13	0.57 ± 0.12
Pillar Point	20.0 ± 1.2	15.0 ± 2.3	1.48 ± 0.35	1.51 ± 0.26	0.53 ± 0.05	0.58 ± 0.13
Central	**16.0 ± 6.0**	**16.1 ± 5.4**	**1.66 ± 0.39**	**1.69 ± 0.41**	**0.62 ± 0.12**	**0.62 ± 0.13**
Ano Nuevo	16.9 ± 2.6	16.2 ± 6.8	1.10 ± 0.83	1.65 ± 0.44	0.39 ± 0.27	0.58 ± 0.15
Portuguese Ledge	23.5 ± 6.1	17.4 ± 5.0	1.90 ± 0.32	1.61 ± 0.41	0.61 ± 0.09	0.57 ± 0.12
Point Lobos	18.9 ± 6.5	18.3 ± 5.5	1.74 ± 0.48	1.63 ± 0.39	0.61 ± 0.14	0.57 ± 0.14
Point Sur	14.8 ± 4.2	17.3 ± 6.6	1.75 ± 0.26	1.88 ± 0.40	0.66 ± 0.07	0.67 ± 0.09
Big Creek	11.8 ± 6.7	13.4 ± 2.7	1.39 ± 0.49	1.55 ± 0.49	0.63 ± 0.11	0.60 ± 0.17
Piedras Blancas	8.9 ± 2.3	N/A	1.31 ± 0.26	N/A	0.62 ± 0.16	N/A
Point Buchon	14.1 ± 4.8	14.7 ± 5.0	1.50 ± 0.33	1.73 ± 0.36	0.58 ± 0.12	0.65 ± 0.10
South	**13.1 ± 3.9**	**13.0 ± 3.6**	**1.43 ± 0.42**	**1.42 ± 0.47**	**0.57 ± 0.15**	**0.56 ± 0.17**
Point Conception	12.3 ± 5.1	13.3 ± 3.9	1.25 ± 0.71	1.15 ± 0.67	0.51 ± 0.26	0.45 ± 0.25
Campus Point	13.9 ± 5.7	10.8 ± 3.1	1.49 ± 0.43	1.55 ± 0.37	0.58 ± 0.11	0.67 ± 0.16
Harris Point	15.0 ± 3.2	10.0 ± 3.6	1.64 ± 0.37	1.40 ± 0.42	0.61 ± 0.13	0.62 ± 0.15
Carrington Point	11.9 ± 3.6	12.7 ± 2.7	1.26 ± 0.40	1.18 ± 0.29	0.52 ± 0.14	0.47 ± 0.10
South Point	15.4 ± 3.0	14.6 ± 3.4	1.53 ± 0.32	1.84 ± 0.33	0.56 ± 0.11	0.69 ± 0.11
Gull Island	13.5 ± 2.6	13.2 ± 3.2	1.54 ± 0.37	1.47 ± 0.40	0.60 ± 0.14	0.58 ± 0.14
Anacapa Island	11.5 ± 4.3	N/A	1.35 ± 0.39	N/A	0.58 ± 0.16	N/A
Farnsworth	13.9 ± 2.1	14.5 ± 3.8	0.93 ± 0.60	0.85 ± 0.53	0.36 ± 0.23	0.32 ± 0.20
Swami's	12.3 ± 3.9	15.4 ± 2.0	1.33 ± 0.31	0.77 ± 0.52	0.54 ± 0.13	0.29 ± 0.19
South La Jolla	13.5 ± 3.1	16.5 ± 3.9	0.84 ± 0.47	1.06 ± 0.42	0.34 ± 0.20	0.38 ± 0.15

A Shannon diversity index, calculated across the network of MPAs for the state of California, was 0.58 ± 0.15 (mean ± SD) inside MPAs and was 0.57 ± 0.16 from outside (Reference) sites. Species diversity significantly differed between regions (Type I ANOVA, F = 10.9, df = 2, p = <0.001), with Southern California surveys having lower diversity than Northern and Central California (Tukey's HSD, p=0.55), and no difference from Central California surveys. As with richness, variability was high across sites and regions. Diversity did not significantly differ between each MPA and its Reference site (Table 8) (Type I ANOVA, F = 0.58, df=1, p = 0.45). There was no significant difference among richness in MPAs and Reference areas in Central California (paired t-test, df = 4, t = 0.26, p = 0.80) or in Southern California (paired t-test, df = 8, t = 0.088, p = 0.93) (Fig. 37).

Pielou's evenness across the network of MPAs for the state of California was 0.58 ± 0.15 (mean ± SD) and from outside (Reference) sites it was 0.57 ± 0.16. Species diversity significantly differed among regions (Type I ANOVA, F = 4.91, df = 2, p = 0.013). Evenness did not significantly differ between each MPA and its Reference site (Table 8) (Type I ANOVA, F = 0.065, df=2, p = 0.937). There were no significant differences among evenness in MPAs and Reference areas in any of the regions (Fig. 37).

Beta Diversity: There were not enough MPAs within a single region surveyed in one year to provide sufficient alpha-scale replicates to statistically test whether there were differences in species turnover or beta diversity at the level of regions. For each region, however, beta statistics were calculated from 2 (North), 3 (Central), and 4 (Southern region) MPA sites (App. Fig. C4). Within all three regions, species turnover was most heavily influenced by changes (turnover) based on aggregation of the most common species (β_{Spie} values were greater than β_S and β_{Sn}). While beta statistics differed between regions, there was no clear effect of MPA protection on species turnover (no difference in beta statistics between MPAs and their associated Reference areas; one-way ANOVA; β_S F=0.538, p=0.480; β_{Sn} F=0.181, p=0.680; β_{Spie} F=0.594, p=0.459).

The strongest determinant of variability in beta statistics came from differences among sites within a region. There was no difference in species turnover between the two northern sites, Bodega Bay and Farallon Islands by any metric (one-way ANOVA; β_S F=0.000, p=0.998; β_{Sn} F=0.000, p=0.989; β_{Spie} F=0.594, p=0.459). In Central California, species turnover was significantly different at different sites based on β_S but not the other beta diversity metrics, which means turnover relied the most on density or species abundance distribution (one-way ANOVA; β_S F=15.657, p<0.001; β_{Sn} F=0.458, p=0.641; β_{Spie} F=0.005, p=0.945). Beta diversity and species turnover was most variable between sites in Southern California (one-way ANOVA; β_S F=6.265, p=0.001; β_{Sn} F=5.551, p=0.002; β_{Spie} F=8.086, p=<0.001).

Community Structure: Differences between Northern (N), Central (C), and Southern (S) California invertebrate communities were driven by several echinoderm taxa (N-C contribution = 38.2%, C-S contribution = 16.3%, N-S contribution = 50.3%). Within the echinoderms, sea urchins were responsible for the greatest differences between regions, 4-21% (N-C contribution = 4.6%, C-S contribution = 21.4%, N-S contribution = 16.9%), followed by sea stars and cucumbers, which were each responsible for 3-6% (sea stars: N-C contribution = 3.0%, C-S contribution = 6.2%, N-S contribution = 3.4%; sea cucumbers: N-C contribution = 3.0%, C-S contribution = 6.2%, N-S contribution = 3.4%). Several individual taxa were also identified as relevant to differences in community composition between all three regions: California sea cucumbers (*Apostichopus californicus*), red sea urchins (*Mesocentrotus franciscanus*), and unidentified branched bryozoans. Other relevant groups included suspension feeders as a functional group (N-C contribution = 41.4%, C-S contribution = 39.0%, N-S contribution = 31.1%). This is unsurprising, since suspension feeders are a well-known functional group in deep water ecosystems, and the spread of taxa within this group doesn't point to a more specific trend.

A statewide SIMPER analysis also showed that echinoderms were responsible for the greatest differences among MPAs and Reference communities, making up a cumulative contribution of 42%. The single species with the highest contribution was the white urchin (*Lytechinus anamesus*) with a contribution of 14.7%. Here too, suspension feeders played an important role in differentiating communities in MPAs and non-MPA areas (contribution = 36.4%).

An assessment of MPA and Reference areas within the three different regions maintained most of the above trends, including strong contributions from urchins, sea cucumbers. and suspension feeders, but no single taxon with a high contribution made a critical difference in communities between MPAs and Reference sites within all three regions. However, many species, such as the California sea cucumber (*Apostichopus californicus*), red sea urchin (*Mesocentrotus franciscanus*), California hydrocoral (*Stylaster californicus*), white sea urchin (*Lytechinus anamesus*), and the short red gorgonian (*Swiftia spauldingi*) were present in SIMPER outputs in at least 2 regions.

ROV combined fish and invertebrates: *Community Structure*: For the combined fish and invertebrate analyses, we only used data from 2005–2019 because 2020 data were not yet available. The differences in community composition of the combined fish and invertebrate communities across the statewide MPA network were driven by MPA location ($F_{25,217}$ = 5.34, R^2 = 0.44, p = 0.001) and survey year ($F_{10,217}$ = 3.13, R^2 = 0.10, p = 0.001). However, there was no difference in community composition between MPAs and associated Reference sites ($F_{1,217}$ = 1.15, R^2 = 0.003, p = 0.29) or any interaction among variables; indicating no reserve effect. In the South region, The NMDS explained 85.2% of the dissimilarity among communities. Two-dimensional axes were utilized to visually examine community composition across the south region with a stress of 0.19. Axis 1 accounted for 77.9% of the variance in community structure while Axis 2 accounted for 57.9% of the variation in community structure. There were clear differences in community composition across years and between MPAs and associated Reference sites. After 2014, the communities inside and outside the MPAs became more homogeneous or similar. (Fig. 38). In the Central Region, the NMDS plot explained 96.8% of the dissimilarity among communities. Two-dimensional axes were utilized to visually examine community composition across the Central region with a stress of 0.12. Axis 1 accounted for 28.9% of the variance in community structure while Axis 2 accounted for 21.2% of the variation in community structure. There were clear differences in community composition across years; however, there were no differences in community composition between MPAs and associated Reference sites. Community composition both inside and outside the MPAs were highly clustered all years prior to 2016. However, in 2016 and 2019, the communities shifted and became more dissimilar, as indicated by an expansion of the 95% confidence intervals (Fig. 38). In the North region, the NMDS explained 99.3% of the dissimilarity among communities. Two-dimensional axes were utilized to visually examine community composition across the Central region with a stress of 0.06. Axis 1 accounted for 36.7% of the variance in community structure, while Axis 2 accounted for 20.3% of the variation in community structure. There were clear differences in community composition across years, but there were no differences in community composition among MPAs and associated Reference sites, although 2014 was an exception. Community compositions, both inside and outside the MPAs, were highly clustered in 2011. However, in 2014 and 2015, the communities shifted and became more dissimilar, as indicated by an expansion of the 95% confidence intervals. In 2019, communities once again became highly clustered, indicating similar communities across MPAs and Reference sites. (Fig. 38).

Species Diversity: Within the South region (Carrington Point, Gull Island, Harris Point, and South Point), combined fish and invertebrate diversity was higher in the MPA compared to the associated Reference sites across all years sampled. There was a clear positive relationship between survey year and diversity metrics: species richness (R^2_{adj} = 0.22, $F_{1,91}$ = 26.26, p < 0.001), Shannon diversity (R^2_{adj} = 0.46, $F_{1,91}$ = 79.11, p < 0.001), and evenness (R^2_{adj} = 0.38, $F_{1,91}$ = 56.29, p < 0.001) (Fig. 39). In the Central region, diversity metrics were variable across sites. Across the entire Central region, survey year was positively correlated with species richness (R^2_{adj} = 0.07, $F_{1,45}$ = 4.64, p = 0.037), Shannon diversity (R^2_{adj} = 0.28, $F_{1,45}$ = 18.47, p < 0.001), and evenness (R^2_{adj} = 0.30, $F_{1,45}$ = 20.51, p < 0.001) (Fig. 39). In the North region there was no relationship between survey year and diversity metrics: species richness (R^2_{adj} = 0.022, $F_{1,39}$ = 0.1.89, p = 0.18), Shannon diversity (R^2_{adj} = -0.014, $F_{1,39}$ = 0.45, p = 0.51), and evenness (R^2_{adj} = -0.009, $F_{1,39}$ = 0.61, p = 0.44) (Fig. 39).

BRUV data: *Community Structure:* Carrington Pt. and Anacapa MPAs are subject to different oceanographic conditions and previous work in shallow water has documented strong geographic variation in fish community structure at the islands as well as differences in and out of MPAs (Freedman et al. 2020; Caselle et al. 2018; Hamilton et al. 2010). For these deeper water surveys, we plotted fish community structure in multidimensional space to ask a) if the fish community differs between Anacapa and Carrington Pt. and b) if the fish community structure differs in and out of MPAs. Overall, we did not find strong evidence for differences in community structure across our study. The analysis of similarity found an R value of 0.31 when comparing Anacapa to Carrington, indicating that the two communities differ slightly with a considerable amount of overlap (Fig. 40, App. Table D8A). We compared the 4 MPA and Reference communities (e.g. Anacapa MPA and Ref, Carrington Pt. MPA and Ref) and found an R value <0.25, indicating that the communities do not differ and have a high amount of overlap (Fig 40, App. Table D8A). The similarity of percentages analysis showed that 10 out of the 24 species from our refined species list were responsible for 75% of the species contributions and these are species plotted in Fig. 40 and App. Table D8B.

Species Diversity: We tested for differences in species richness and diversity between fished and unfished areas at Anacapa and Carrington Pt. (App. Table D7). We found a clear statistical difference in mean species richness and Shannon diversity indices when comparing the MPA and Reference areas of both Anacapa and Carrington Pt. However, it is notable that the direction of the relationship differs at Anacapa and Carrington Pt. At Anacapa, both species richness and diversity were greater in the Reference area than the MPA (*Species Richness: MPA=3.79, Ref=4.65; p = 0.002; Diversity MPA=0.71, Ref=0.95; p = 0.001;* App. Table D7). At Carrington Pt., both metrics were greater in the MPA compared to the Reference area (*Species Richness: MPA=6.38, Ref=5.07; p = 0.003; Diversity MPA=1.32, Ref=1.08; p = 0.003;* App. Table D7).

Not surprisingly, species diversity was strongly related to habitat type (Fig. 41). There was a clear trend towards increasing diversity with increasingly more complex rock habitats. We conclude that diversity may be more strongly related to habitat than to protection level (Fig. 41). The Anacapa MPA site had greater amounts of soft surveys (App. Table D2A) which may in part drive the lower diversity values we measured.

DEWG Question 3**: Do MPAs that include multiple habitat types harbor higher species abundance or more diverse communities than those that encompass a single habitat type or less diverse habitat types?**

Q3a. Is there a positive relationship between the density of any given focal species and habitat diversity across MPAs of similar protection levels?

ROV Fish data: For this question, we focused on examining the influence of habitat diversity inside the MPAs on fishes using information on the amount of rock and high-quality rock calculated for DEWG Question 21. Specifically, we examined how total density response ratios across all years sampled and response ratios of focal species related to the amount of rocky habitat (km^2), high-quality rock habitat (km^2) and the percent of high-quality rock (%) inside each MPA. We found no significant relationship between the total density response ratios and any metric of rocky habitats inside MPAs (Fig. 42; rock: $F_{1,94} = 0.027$, $p = 0.87$; high-quality rock: $F_{1,90} = 0.27$, $p = 0.61$; % high-quality rock: $F_{1,95} = 1.46$, $p = 0.23$)

Q3b. Is there a positive relationship between species diversity and habitat diversity across MPAs of similar protection levels?

ROV Fish data: For 9 sites spanning the entire coast of California (Reading Rock SMR, Bodega Head SMR, SE Farallon Islands SMR, Point Lobos SMR, Point Sur SMR, Point Buchon SMR, Carrington Point SMR, Harris Point SMR and South Point SMR), we examined how species richness and Shannon-Weiner diversity related to the amount of rocky habitat (km^2), high-quality rock habitat (km^2) and the percent of high-quality rock (%) inside each MPA. We found no significant relationship among species richness and any metric of rocky habitats inside MPAs (Fig. 43; rock: $F_{1,94} = 3.19$, $p = 0.63$; high-quality rock: $F_{1,50} = 0.34$, $p = 0.56$; % high-quality rock: $F_{1,50} = 2.80$, $p = 0.10$). However, there was a slight positive relationship between the amount of rock and species richness for the MPAs examined. Similarly, we did not find any statistically significant relationships between the amount of rock habitat, the amount of high-quality rock habitat or the percent of high-quality rock habitat within the MPA and Shannon-Weiner diversity (Fig. 43; rock: $F_{1,94} = 1.01$, $p = 0.32$; high-quality rock: $F_{1,50} = 3.49$, $p = 0.06$; % high-quality rock: $F_{1,50} = 3.37$, $p = 0.07$).

ROV invertebrate data: There were strong, positive MPA effects on structure-forming invertebrates (sponges and corals). Response ratios, however, neither increased nor decreased over time across the decade of sampling. Since these species are slow growing (e.g. Love et al. 2007), it is possible that our observations have not spanned a timescale that would include population-level changes (but see Kahn et al. 2012, although this relates to species thousands of meters deep). A positive MPA effect since the beginning of sampling in 2005 might be more reflective of the placement of the MPAs in high relief areas with structure-forming invertebrates already, given their long lifespans, sensitivity to environmental change, and ecosystem function as essential fish habitat.

With so many different invertebrate taxa observed, often only at low frequencies, during ROV surveys, using functional groups allowed us to address two measurable questions within MLPA Goal 1: “Does structural and functional diversity differ in MPAs relative to Reference sites?” and “Do the abundance, size/age structure, and diversity of predator and prey species differ inside MPAs, or outside areas of comparable habitat?” Functional diversity did differ between the MPAs relative to Reference sites, with MPAs having a positive effect on densities of suspension feeders (which included sponges, tunicates, bryozoans, corals, and a few crustaceans) and sessile predators (which were mainly sea anemones) while there was a negative MPA effect on mobile predators (which included crustaceans, echinoderms, and molluscs). That there are several invertebrate taxa that at least fell within these feeding functional groups suggests there may be moderate functional redundancy within the MPA network. More focused sampling could assess whether functional diversity metrics are affected by MPAs as they have been for fish (e.g. Rincón-Díaz et al. 2018).

SIMPER analysis confirmed that echinoderm groups and suspension feeders were enriched in MPAs. Echinoderms were responsible for the greatest differences between MPA and Reference communities. SIMPER does not indicate whether their densities are higher or lower but response ratios for individual species suggest that densities of California sea cucumbers and sunflower stars were enriched in MPAs while those of red sea urchins were not.

DEWG Question 5**: Does the nature or timing of recovery of natural communities from disturbance events differ in different types of MPAs relative to outside areas?**

ROV Fish data: To assess this question, we were interested in determining the effect of the 2014–2016 marine heatwave on densities of mid-depth fish communities inside and outside of MPAs. Due to the patchiness of the ROV data with large temporal gaps between 2009–2014 and 2016–2019, it was difficult to determine the effects of the marine heatwave across the entire coast. We focused on the four MPAs in the Channel Islands (Carrington Point, Gull Island, Harris Point, and South Point SMRs) with the longest time series of MPA monitoring. We examined the change in slope of annual mean densities for all species in the MPAs before and after the marine heatwave (Fig. 44a). For this analysis, we had sufficient data to evaluate densities of 16 species, both before and after the heatwave along the Channel Islands. Prior to the heatwave, 13 species showed positive slopes in density, indicating an increase in density through time. Following the heatwave, only 7 of 16 species showed positive slopes, and 9 of the species that initially displayed increasing densities had negative slopes following the heatwave (Fig. 44b). Surprisingly, 2 of the 3 species (Squarespot Rockfish and Kelp Bass) that initially showed negative slopes in density, displayed positive slopes following the heatwave. Six species appeared to change little in the slope of densities relative to the heatwave (slope remained positive: Blacksmith, California Sheephead, Gopher Rockfish, Ocean Whitefish and Pink Seaperch; slope remained negative: Flag Rockfish). As stated earlier, however, the substantial data gaps make us hesitant to assert that the trends we saw are real changes. This is one reason why we suggest that MPA surveys be consistent over time and space.

ROV invertebrate data: Sunflower stars (*Pycnopodia helianthoides*) were hit hard by the sea star wasting syndrome (SSWS) epidemic, which began in 2013 with the anomalous warm “blob” in the northeast Pacific (Eisenlord et al. 2016). Densities were generally greater in Central CA MPAs than in Northern and Southern CA regions, but across the state sunflower stars disappeared from ROV surveys after the onset of SSWS, with no individuals observed after 2015. Given that, we assessed the SSWS epidemic across the ROV surveys. While we did find that the SSWS epidemic was detectable in deep water and especially affected sunflower stars (App. Fig. C5), its effect varied across different species, much as it does in shallow water. We could not detect any changes, for example, to populations of the vermilion star *Mediaster aequalis*, even though a previous epidemic of wasting disease affected 25% of individuals of *M. aequalis* at the same time that only 10% of the population of *P. helianthoides* was affected (Eckert et al. 1999). It is known that sea stars exposed to higher temperatures became more stressed by the marine heat wave and were therefore more susceptible to disease (Bates et al. 2009) so we hypothesized that the outbreak occurred more rapidly and killed more individuals in the southern end of the sunflower star’s range, as was found from shallow water (Hamilton et al. 2021). However, we could not discern any pattern of infection due to the spatial and temporal patchiness of sampling (App. Fig. C6).

DEWG Question 6**: How does spatial variability in fishing effort and fishing mortality rates prior to and after MPA implementation affect the abundance and/or size/age structure of harvested species in MPAs?**

The microblock fishing effort data collected from recreational boat anglers by CDFW are at the scale that will be useful for these analyses. Unfortunately, the scale and positional accuracy of fishing effort collected from Commercial Passenger Fishing Vessels and commercial fishing boats are too patchy. We felt it would be inappropriate to conduct analyses comparing ROV surveys with fishing effort data at this time. This DEWG question is important, and may be a major factor affecting mid-depth and deepwater fish communities; however, we cannot evaluate this question without new socio-economic data streams.

DEWG Question 7**: How do species differ in their rate of response to MPA implementation?**

Q7a. How does the mean rate of response in abundance and size/age structure differ among species?

ROV Fish data: For this analysis, we focused on the Channel Islands MPAs (South Point, Harris Point. Carrington Point and Gull Island SMRs) as these sites have the longest most cohesive time series. The rates of response for individual species in the MPAs and Reference sites showed significant variability among species (Fig. 45a). Inside the MPAs, a few species exhibited dramatic increases in density (e.g., Blue/Deacon Rockfish), while most other species increased much more gradually. Of the 29 species in this analysis, 22 of them (76%) displayed positive slopes (increases in abundance), while seven of them had negative slopes (24%), indicating decreases in abundance on average (Fig. 45a). Thus, the flat or negative slopes of these species over the full time series are not fully representative of their true dynamics inside the MPAs. In the Reference sites, we only observed rapid increases in abundance in one species (Blue/Deacon Rockfish). Overall, 16 of the 29 species (55%) had positive slopes, indicating that density increased over time in the Reference areas, while 9 species had negative slopes (31%) indicating declines in abundance and 4 had slopes of zero (14%) indicating no change through time (Fig. 45a). In comparing species between the MPA and References sites, in general the increases in abundance were more dramatic in the MPA and density values were higher for more species inside the MPA (Fig. 45b).

ROV invertebrate data: One of the strongest patterns we observed was that there are distinct communities that behave differently in different regions across California. As was observed for mid-depth fish species, the greatest source of variation between invertebrate communities occurred between Northern, Central, and Southern California regions, regardless of year or MPA protections. While alpha and beta diversity, species richness, and evenness were only slightly different, if at all, between MPAs and Reference sites, there were clear differences in these metrics across the three regions. Differences in beta diversity were most heavily influenced by aggregations of the most common species, which our SIMPER analysis identifies as various echinoderm groups.

The sheer scale of monitoring the waters of California means that some regions were only surveyed two or three times across the decade, and since each site had its own variations it was impossible to discern the signal from the noise in the data. As an example, as mentioned previously sea star wasting syndrome did not hit every species equally. Sunflower stars (*Pycnopodia helianthoides*) were hit hardest, with none observed past 2015. Other families were affected less, or not at all. Despite knowing there were strong die-offs of sea stars following the onset of SSWS, however, we were unable to perform any tests that resulted in statistical significance. This points to a shortcoming of the research approach so far, with a known, strong, and very visible effect (SSWS) still not achieving sufficient statistical power due to the survey strategy. The scale of monitoring across the state means that some regions were only surveyed two or three times across the decade, and it was impossible to detect the very significant losses of sea stars over the study period. We therefore must raise the question of what other analyses may have type 2 error due to limited statistical power. As one example, we attempted to assess whether SSWS spread from north to south, or if we could see a spread of its impact over time. We constructed a basic map of coverage of which sites, from north to south, were surveyed each year and there was not enough even spread across space to assess that, with surveys in Northern CA only occurring in certain years (App. Fig. C6).

DEWG Question 20**: Are the size/age structure of recreationally valued species increasing in MPAs over time?**

Many of the focal fish species examined by the ROV and BRUV tools are considered recreationally valued species (e.g., Rockfish, Lingcod, California Sheephead, etc.). Thus, the answers to this question and all related sub-questions about recreationally important species can be addressed by any of the species-specific analyses we present in the report.

DEWG Question 21: **Have unique habitats been adequately represented and protected by the current distribution and designation of MPAs?**

Habitat Objective 1a: *Quantify the performance of individual State Marine Reserves (SMRs) and Conservation Areas (SMCAs) with respect to the abundance of rocky reef and high-quality habitat within the 30–100 m isobaths.*

The 69 MPAs included in this study protect a total area of 94.4 km^2 of rocky reef within the 30–100 m isobaths. See Appendix F (App. Fig. F1-62) for maps of each location. Forty of those 69 MPAs surveyed (58%) contained less than 1 km^2 of rocky reef. Table 9 below provides the list of all MPA sites (both SMRs and SMCAs) included in the study as well as the relative abundance of rocky reef and high-quality habitat found at each site. The total area of rocky reef within the 69 individual MPAs averaged 1.37 km^2 per site, with three sites approaching 10 km^2 total rocky reef at the site, including South Cape Mendocino SMR at 9.2 km^2, Bodega Head SMR at 8.6 km^2, and Richardson Rock SMR at 8.3 km^2. A total of six sites had no discernable rocky reef within the depth zone.

Table 9. List of MPA sites included in the study, including designation, location, and amount of rocky reef and high-quality habitat for each site.

MPA Name	Designation	Bioregion	Rocky Reef (30-100m) (km2)	High Quality Habitat (km2)	% High Quality Habitat
Pyramid Point	SMCA	NorCal	0.0000	0.0000	0.00%
Point St. George Reef Offshore	SMCA	NorCal	1.0363	0.0029	0.28%
Reading Rock	SMCA	NorCal	0.0022	0.0020	0.00%
Reading Rock	SMR	NorCal	0.6268	0.0014	0.22%
Samoa	SMCA	NorCal	0.0000	0.0000	0.00%
South Cape Mendocino	SMR	NorCal	9.2011	0.0181	0.20%
Mattole Canyon	SMR	NorCal	0.0719	0.0018	2.50%
Sea Lion Gulch	SMR	NorCal	0.3475	0.0059	1.70%

Big Flat	SMCA	NorCal	0.0018	0.0001	5.56%
Double Cone Rock	SMCA	NorCal	0.2769	0.0005	0.18%
Ten Mile	SMR	NorCal	1.4478	0.0036	0.25%
Ten Mile Beach	SMCA	NorCal	0.0000	0.0000	0.00%
Russian Gulch	SMCA	NorCal	0.0263	0.0001	0.38%
Point Arena	SMR	NorCal	2.2690	0.0063	0.28%
Point Arena	SMCA	NorCal	0.3707	0.0013	0.35%
Saunders Reef	SMCA	NorCal	2.2998	0.0055	0.24%
Stewarts Point	SMCA	NorCal	0.5607	0.0012	0.21%
Stewarts Point	SMR	NorCal	1.0548	0.0041	0.39%
Salt Point	SMCA	NorCal	1.1630	0.0035	0.30%
Bodega Head	SMR	NorCal	3.4498	0.0041	0.12%
Bodega Head	SMCA	NorCal	8.6000	0.0125	0.15%
Point Reyes	SMR	NorCal	0.0000	0.0000	0.00%
Point Reyes	SMCA	NorCal	0.0254	0.0000	0.00%
North Farallon Islands	SMR	NorCal	1.5732	0.0041	0.26%
Southeast Farallon Island	SMR	NorCal	3.4010	0.0073	0.21%

Southeast Farallon Island	SMCA	NorCal	5.9286	0.0092	0.16%
Montara	SMR	CenCal	0.8185	0.0019	0.23%
Pillar Point	SMCA	CenCal	0.7362	0.0015	0.20%
Año Nuevo	SMR	CenCal	2.6330	0.0052	0.20%
Greyhound Rock	SMCA	CenCal	0.0976	0.0002	0.20%
Soquel Canyon	SMCA	CenCal	0.5529	0.0095	1.72%
Portuguese Ledge	SMCA	CenCal	0.3371	0.0005	0.15%
Carmel Pinnacles	SMR	CenCal	0.7698	0.0014	0.18%
Carmel Bay	SMCA	CenCal	0.4377	0.0039	0.89%
Point Lobos	SMR	CenCal	4.1065	0.0176	0.43%
Point Sur	SMR	CenCal	2.4995	0.0127	0.51%
Point Sur	SMCA	CenCal	2.1176	0.0106	0.50%
Big Creek	SMR	CenCal	0.1589	0.0007	0.44%
Big Creek	SMCA	CenCal	0.0194	0.0020	10.31%
Piedras Blancas	SMR	CenCal	1.8421	0.0041	0.22%
Piedras Blancas	SMCA	CenCal	6.0620	0.0186	0.31%
Cambria	SMCA	CenCal	0.0054	0.0047	86.48%
White Rock	SMCA	CenCal	0.3605	0.0004	0.11%

Point Buchon	SMR	CenCal	2.2776	0.0046	0.20%
Point Buchon	SMCA	CenCal	1.7874	0.0016	0.09%
Vandenberg	SMR	CenCal	0.2802	0.0003	0.11%
Point Conception	SMR	SoCal	1.5477	0.0001	0.01%
Naples	SMCA	SoCal	0.2992	0.0001	0.03%
Campus Point	SMCA	SoCal	0.4131	0.0000	0.00%
Richardson Rock	SMR	SoCal	8.2843	0.0053	0.06%
Harris Point	SMR	SoCal	2.3011	0.0014	0.06%
Carrington Point	SMR	SoCal	1.5937	0.0033	0.21%
South Point	SMR	SoCal	1.0226	0.0033	0.32%
Gull Island	SMR	SoCal	1.9851	0.0026	0.13%
Point Dume	SMR	SoCal	0.4099	0.0002	0.05%
Point Vicente	SMCA	SoCal	0.3664	0.0000	0.00%
Abalone Cove	SMCA	SoCal	0.1085	0.0000	0.00%
Arrow Point to Lion Head Point	SMCA	SoCal	0.0268	0.0000	0.00%
Blue Cavern Onshore	SMCA	SoCal	0.0369	0.0000	0.00%
Blue Cavern Offshore	SMCA	SoCal	0.0000	0.0000	0.00%

Farnsworth Onshore	SMCA	SoCal	0.0436	0.0000	0.00%
Farnsworth Offshore	SMCA	SoCal	1.3267	0.0021	0.16%
Crystal Cove	SMCA	SoCal	0.0000	0.0000	0.00%
Laguna Beach	SMR	SoCal	0.0047	0.0000	0.00%
Laguna Beach	SMCA	SoCal	0.0202	0.0000	0.00%
Dana Point	SMCA	SoCal	0.0062	0.0000	0.00%
Swami's	SMCA	SoCal	0.3177	0.0000	0.00%
South La Jolla	SMR	SoCal	1.0564	0.0002	0.02%
South La Jolla	SMCA	SoCal	1.5609	0.0002	0.01%

The total area of high-quality rocky reef habitat protected by the 69 MPAs was considerably lower across the state, with only 0.21 km^2 high-quality habitat within the 30–100 m isobaths. See Appendix F (Fig. F1-62) for maps of each location. Only six sites (9%) contained 0.01 km^2 (average of 0.003 km^2) or more of high-quality rocky reef habitat. These sites included the South Mendocino SMR at 0.02 km^2, Bodega Head SMCA 0.01 km^2, Point Lobos SMR 0.02 km^2, the Point Sur SMR and SMCA both at 0.01 km^2, and the Piedras Blancas SMCA at 0.02 km^2. When the total area of high-quality habitat at each MPA was compared to the total area of rocky reef at each site, only six sites showed high-quality habitat as greater than 1% of rocky reef. It is interesting to note that the six sites with the highest percentage of high-quality habitat were not the same six with the highest total area of rocky reef, including Mattole Canyon SMR 2.5%, Sea Lion Gulch SMR 1.7%, Big Flat SMCA 5.6%, Soquel Canyon SMCA 1.72%, Big Creek SMCA 10.31%, and Cambria SMCA 85.5%. It is also interesting to note that all 13 MPAs described above are north of Point Conception.

Three sites showed a demonstrably higher percentage of high-quality habitat than the rest of the MPAs, including Big Flat SMCA (5.6%), Big Creek SMCA (10.3%), and Cambria SMCA (86.5%). The distribution of rocky reef and high-quality habitat varied considerably across sites. At the Cambria SMCA, for example (Fig. 46), much of the SMCA is shallower than the 30 m upper threshold for inclusion in this study, while rocky reef is considerably more abundant in the adjacent Reference area (see discussion below under Objective 1b). However, while small in total area, the rocky reef within the SMCA that is within the 30–100 m isobaths is nearly all high-quality habitat.

The regional distribution of total rocky reef and high-quality habitat is provided in Fig. 47, with summary totals for each region included in Table 10. Overall statewide, there was no significant difference across regions with respect to the amount of rocky reef (Kruskal-Wallis, p = 0.36) in the 30–100 m depth zone. The Northern California region had the highest cumulative total rocky reef, with 42.2 km^2 spread across the twenty-six MPAs included in the study (Table 10). The Central California region had a lower total amount of rocky reef (27.9 km^2), however with fewer total MPAs included from the region, the mean rocky reef per site was higher at 2.42 km^2. The Southern California region had the least total rocky reef (22.7 km^2) but averaged more per site than Northern California (2.38 km^2).

Table 10. Summary information on the distribution of deep rocky reef and high-quality habitat in MPAs across the three bio-regions in the state, including the total for each in the three regions, as well as the mean per MPA in each region.

Region	Rocky Reef (km^2)	High-Quality Habitat (km^2)
North	42.2	0.09
Mean (26 MPAs)	1.69	0.004
Central	27.9	0.1
Mean (20 MPAs)	2.42	0.006
South	22.7	0.02
Mean (23 MPAs)	2.38	0.006

The relative abundance of high-quality habitat also skewed toward the two regions to the north of Point Conception. The Central California region led with a total of 0.1 km^2, with Northern California slightly behind at 0.09 km^2. Southern California contained the least amount of high-quality habitat overall (0.02 km^2), but averaged 0.006 km^2 per site, which equaled the mean for Central California. Results of a Dunn's Multiple Comparison Test indicated that high-quality habitat differed between North and South (p = 0.000) and Central and South (p = 0.0008).

Habitat Objective 1b: *Quantify habitat-based connectivity within MPA clusters across the state and with the adjacent unprotected areas around those clusters.*

Across the state, SMRs contained significantly more rocky reef (Mann-Whitney, p-value = 0.0024) and high-quality habitat (Mann-Whitney, p = 0.0016) when compared to SMCAs. The total amount of rocky reef and high-quality habitat protected by each of the 69 MPAs in the study is provided in Table 11 below, along with the rocky reef and high-quality habitat present in the adjacent, unprotected areas.

A total of 14 sites among the 69 MPAs surveyed for this project included coupled SMRs and SMCAs. Of those sites, in seven cases (50%) the SMR outperformed the SMCA with respect to the amount of high-quality habitat contained within. In five cases (36%), the SMCA contained a larger total area of high-quality habitat, and in two cases the SMR and SMCA were equivalent. However, it is important to note that, with one exception (Big Creek), the differences between SMRs and SMCAs were less than 1%. In the Big Creek SMR and SMCA, the total area of high-quality habitat was low, 0.0007 and 0.002 km^2, respectively.

Figures 48-50 depict maps of three separate SMR/SMCA pairings from across the state. Note: any rocky reef present in the study area shallower than 30 m was not included in the analysis and was thus not included in any of the maps. In the cases of SE Farallon Island and Bodega Head, the deep rocky reef in the vicinity of the MPAs was contiguous between the SMRs and the SMCAs, also connecting the MPA pairs to the adjacent Reference areas. In South La Jolla, the rocky reef is less contiguous, with two discernable patches within the SMR, only one of which is connected to the SMCA.

Table 11. List of MPAs, including the amount of rocky reef (30–100 m) and the percentage of high-quality rocky habitat within MPAs and adjacent Reference areas, as well as the differences between inside and out of MPAs for both.

MPA Name	Type	MPA Rocky Reef (30-100m) (km^2)	REF Rocky Reef (30-100m) (km^2)	Difference (MPA – REF)	MPA % High Quality Habitat	REF % High Quality Habitat	Diff. (MPA – REF)
Pyramid Point	SMCA	0.0000	0.0000	0.0000	0.00%	0.00%	0.00%
Point St. George Reef Offshore	SMCA	1.0363	0.4577	0.5786	0.28%	0.13%	0.15%
Reading Rock	SMCA	0.0022	0.0273	-0.0251	0.00%	0.00%	0.00%
Reading Rock	SMR	0.6268	2.9701	-2.3433	0.22%	0.25%	-0.02%
Samoa	SMCA	0.0000	0.0000	0.0000	0.00%	0.00%	0.00%
South Cape Mendocino	SMR	9.2011	3.4452	5.7559	0.20%	0.21%	-0.02%
Mattole Canyon	SMR	0.0719	0.1460	-0.0741	2.50%	1.23%	1.27%
Sea Lion Gulch	SMR	0.3475	0.0750	0.2725	1.70%	2.40%	-0.70%

Big Flat	SMCA	0.0018	0.0011	0.0007	5.56%	0.00%	5.56%
Double Cone Rock	SMCA	0.2769	2.4978	-2.2209	0.18%	0.19%	-0.01%
Ten Mile	SMR	1.4478	0.4238	1.0240	0.25%	0.21%	0.04%
Ten Mile Beach	SMCA	0.0000	0.0386	-0.0386	0.00%	0.26%	-0.26%
Russian Gulch	SMCA	0.0263	0.0099	0.0164	0.38%	0.00%	0.38%
Point Arena	SMCA	2.2690	2.5007	-0.2317	0.35%	0.85%	-0.50%
Point Arena	SMR	0.3707	0.3533	0.0174	0.28%	0.34%	-0.06%
Saunders Reef	SMCA	2.2998	1.2864	1.0134	0.24%	0.23%	0.01%
Stewarts Point	SMCA	0.5607	0.0000	0.5607	0.21%	0.00%	0.21%
Stewarts Point	SMR	1.0548	1.4531	-0.3983	0.39%	0.25%	0.13%
Salt Point-new	SMCA	1.1630	0.9650	0.1980	0.30%	0.25%	0.05%
Bodega Head	SMR	3.4498	3.4498	0.0000	0.12%	0.10%	0.01%
Bodega Head	SMCA	8.6000	4.5363	4.0637	0.15%	0.15%	-0.01%
Point Reyes	SMR	0.0000	1.2464	-1.2464	0.00%	0.00%	0.00%
Point Reyes	SMCA	0.0254	0.6755	-0.6501	0.00%	0.00%	0.00%
North Farallon Islands	SMR	1.5732	6.0526	-4.4794	0.26%	1.81%	-1.55%
Southeast Farallon Island	SMR	3.4010	0.8023	2.5987	0.21%	0.27%	-0.06%
Southeast Farallon Island	SMCA	5.9286	6.1766	-0.2480	0.16%	0.25%	-0.08%

Montara	SMR	0.8185	0.8185	0.0000	0.16%	0.05%	0.11%
Pillar Point	SMCA	0.7362	1.2966	-0.5604	0.20%	0.05%	0.15%
Año Nuevo	SMR	2.6330	2.6540	-0.0210	0.20%	0.23%	-0.03%
Greyhound Rock	SMCA	0.0976	0.7805	-0.6829	0.20%	0.18%	0.03%
Soquel Canyon	SMCA	0.5529	0.0019	0.5510	1.72%	5.26%	-3.54%
Portuguese Ledge	SMCA	0.3371	0.0000	0.3371	0.15%	0.00%	0.15%
Carmel Pinnacles	SMR	0.7698	0.6848	0.0850	0.18%	0.64%	-0.46%
Carmel Bay	SMCA	0.4377	1.2516	-0.8139	0.89%	0.26%	0.64%
Point Lobos	SMR	4.1065	1.4639	2.6426	0.43%	0.36%	0.07%
Point Sur	SMR	2.4995	2.1818	0.3177	0.51%	0.49%	0.02%
Point Sur	SMCA	2.1176	0.0000	2.1176	0.50%	0.00%	0.50%
Big Creek	SMR	0.1589	1.3782	-1.2193	0.44%	0.15%	0.30%
Big Creek	SMCA	0.0194	0.4586	-0.4392	10.31%	0.17%	10.13%
Piedras Blancas	SMR	1.8421	0.6883	1.1538	0.22%	0.22%	0.00%
Piedras Blancas	SMCA	6.0620	2.1809	3.8811	0.31%	0.13%	0.18%
Cambria	SMCA	0.0054	0.5027	-0.4973	86.48%	0.00%	86.48%
White Rock	SMCA	0.3605	0.3427	0.0178	0.11%	0.38%	-0.27%
Point Buchon	SMR	2.2776	2.8090	-0.5314	0.20%	0.20%	0.00%
Point Buchon	SMCA	1.7874	5.8222	-4.0348	0.09%	0.16%	-0.07%

Vandenberg	SMR	0.2802	0.5331	-0.2529	0.11%	0.02%	0.09%
Point Conception	SMR	1.5477	0.7044	0.8433	0.01%	0.04%	-0.04%
Naples	SMCA	0.2992	0.0000	0.2992	0.03%	0.00%	0.03%
Campus Point	SMCA	0.4131	0.8596	-0.4465	0.00%	0.00%	0.00%
Richardson Rock	SMR	8.2843	9.7519	-1.4676	0.06%	0.07%	0.00%
Harris Point	SMR	2.3011	5.8624	-3.5613	0.06%	0.09%	-0.03%
Carrington Point	SMR	1.5937	1.7149	-0.1212	0.21%	0.15%	0.06%
South Point	SMR	1.0226	1.1413	-0.1187	0.32%	0.12%	0.20%
Gull Island	SMR	1.9851	0.3648	1.6203	0.13%	0.05%	0.08%
Point Dume	SMR	0.4099	0.2896	0.1203	0.05%	0.00%	0.05%
Point Vicente	SMCA	0.3664	0.5837	-0.2173	0.00%	0.00%	0.00%
Abalone Cove	SMCA	0.1085	0.1183	-0.0098	0.00%	0.00%	0.00%
Arrow Point to Lion Head Point	SMCA	0.0268	0.0063	0.0205	0.00%	0.00%	0.00%
Blue Cavern Onshore	SMCA	0.0369	0.1318	-0.0949	0.00%	0.00%	0.00%
Blue Cavern Offshore	SMCA	0.0000	0.0191	-0.0191	0.00%	0.00%	0.00%
Farnsworth Onshore	SMCA	0.0436	0.0310	0.0126	0.00%	0.00%	0.00%
Farnsworth Offshore	SMCA	1.3267	0.4783	0.8484	0.16%	0.08%	0.07%
Crystal Cove	SMCA	0.0000	0.3106	-0.3106	0.00%	0.00%	0.00%

Laguna Beach	SMR	0.0047	0.0000	0.0047	0.00%	0.00%	0.00%
Laguna Beach	SMCA	0.0202	0.0000	0.0202	0.00%	0.00%	0.00%
Dana Point	SMCA	0.0062	0.0148	-0.0086	0.00%	0.00%	0.00%
Swami's	SMCA	0.3177	0.7688	-0.4511	0.00%	0.00%	0.00%
South La Jolla	SMR	1.0564	1.6550	-0.5986	0.02%	0.01%	0.01%
South La Jolla	SMCA	1.5609	1.2243	0.3366	0.01%	0.03%	-0.02%

Overall, statewide, neither SMRs (Mann-Whitney, $p = 0.57$) nor SMCAs (Mann-Whitney, $p = 0.47$) contain significantly more rocky reef than an equivalently sized adjacent area. A total of thirty-five (51%) MPAs, including both SMRs and SMCAs, have a larger area of rocky reef (km^2) contained within their boundaries when compared to adjacent Reference areas. The advantage in favor of the MPAs increases to 72% with respect to the percentage of high-quality habitat inside the MPAs. However, statewide there were no significant differences with respect to high-quality habitat inside and out of MPAs. Figures 51-54 depict the variety of cases observed when comparing MPAs to Reference areas.

A review of the patterns with respect to differences between MPAs and Reference areas, for both the total area of rocky reef as well as the percentage of high-quality habitat, resulted in six broad categories (MPA to Reference):

1) Equivalent: MPA and Reference area had similar values, either positive or negative.
2) Equivalent rocky reef – greater high-quality habitat
3) Less rocky reef – equivalent high-quality habitat
4) Less rocky reef – greater high-quality habitat
5) Greater rocky reef – less high-quality habitat
6) Greater rocky reef – equivalent high-quality habitat.

The differences between MPA and Reference areas were equivalent in 41% of the sites, meaning that the area of rocky reef and the percentage of high-quality habitat were either both positive or both negative. Sites that had equivalent differences with respect to rocky reef, but either equivalent or greater high-quality habitat accounted for 35% of MPA/Reference pairs, whereas sites with more rocky reef, but equivalent or less high-quality habitat accounted for 21% of MPA/Reference pairs (Fig. 55). This indicates that the regional MPA design teams did a good job of including “typical” habitat in the MPAs; our results do not support the concept that the regional MPA design teams chose to protect the “best” sites available in a region.

The latitudinal distribution of differences between MPAs and References sites was not uniform with respect to the total area of rocky reef (Fig. 56) nor the percentage of high-quality habitat (Fig. 57). Northern California had the widest range of variation in the distribution of rocky reef, with the total area protected by South Cape Mendocino SMR exceeding the area in the unprotected Reference by 5.8 km^2, and the Reference area for the North Farallon Islands SMR exceeding the rocky reef within the MPA by 4.5 km^2. The distribution of rocky reef inside and out of MPAs was more uniformly distributed along the Central Coast, with eight MPA sites protecting more rock area than References, and nine Reference sites protecting more rock area than associated MPAs. The distribution of rocky reef at the Southern California sites was clustered closer to zero for most sites. The distribution of high-quality habitat as a percentage of rocky reef (Fig. 57) varied much less latitudinally, with the Southern California sites clustered tightly around zero, Northern and Central California showed more variation across sites, with a greater number of Central California sites (both SMRs and SMCAs) showing a higher percentage of high-quality habitat protected in MPAs.

Habitat: *Moving Forward.* Three questions that emerge from the habitat analysis are a) what is the full extent of deep rocky reef and high-quality habitat across the state within the 30–100 m isobaths? b) how much of that area is captured by MPAs across the state (including SMRs, SMCAs, and de facto MPAs)? and c) to what extent, and at what locations, are deep reefs connected to shallower reefs inside and adjacent to MPAs? These are questions that we will be working on in the near future.

DEWG Question 23**: Have endangered species and/or culturally significant species benefited from the presence of California's MPAs?**

Q23a. Has the difference between MPAs and Reference areas in the abundance of endangered species or species of concern for management increased over time?

ROV Fish data: For this analysis we focused on 3 species of current management concern: Copper Rockfish, Quillback Rockfish and Yelloweye Rockfish. We conducted an interactive two-way ANCOVA to determine if the slopes between the MPAs and Reference sites were different for each management region (Fig. 58). Copper Rockfish densities increased through time in both MPAs and Reference sites for all three regions. Additionally, in the South region, Copper Rockfish densities were higher inside the MPAs compared to Reference sites and the difference among MPAs and Reference sites increased through time. For both Quillback Rockfish and Yelloweye Rockfish, these species were most abundant along the North Coast but were also observed in the other two management regions. For the South region, there were few observations of these two species, resulting in very low densities and no change through time. In the Central region, both Quillback and Yelloweye Rockfish densities were low but showed small increases in density through time in both MPAs and Reference sites. For the North region, both Quillback and Yelloweye Rockfish exhibited increasing densities through time in both the MPAs and Reference sites. While not statistically significant, the differences among the MPAs and Reference sites have begun to diverge for both species, with slightly higher densities inside the MPAs compared to the Reference sites in the most recent year of sampling.

BRUV Fish data: Similar to the results of ROV surveys, Copper Rockfish, a heavily fished species that is currently of concern, showed the strongest reserve effect with greater biomass inside the MPAs at Anacapa Island and Carrington Pt.

DEWG Question 32**: Do State Marine Reserve (SMR)/State Marine Conservation Area (SMCA) clusters provide greater protection than stand-alone SMRs?**

Q32c. Is there an increase over time in the difference between MPAs and Reference sites in abundance (density, cover, biomass) of focal species and if so, are there differences between SMR and SMCAs of similar size?

ROV fish data: In many cases SMCAs encompass deeper depth and therefore may provide protection for larger individuals that have undergone ontogenetic migrations to deeper water. We were unable to provide much information about this question, however, because few ROV surveys occurred in the SMCA portions of MPA clusters containing a shallow SMR and a deeper SMCA. We were able to compare density response ratios through time at Bodega Head SMCA and SMR because they were both in shallow water and were both surveyed using ROVs. Overall, we found that fish densities in both Bodega Head SMCA and SMR had fairly similar trajectories (Fig. 59). There was no difference in the trajectory of density response ratios through time between the SMR and SMCA for 3 of 10 species (Blue/Deacon Rockfish, Kelp Greenling, and Vermilion Rockfish). Quillback Rockfish and Brown Rockfish both had higher response ratios in the SMR compared to the SMCA, however density response ratios at both MPAs increased through time. Lingcod response ratios decreased through time in both the SMCA and SMR, however Lingcod had higher density response ratios in the SMR compared to the SMCA. Rosy Rockfish, Black Rockfish, and China Rockfish did not have sufficient temporal coverage with response ratios to accurately assess the difference between the SMR and SMCA. Copper Rockfish response ratios decreased through time in both the SMCA and SMR, however density response ratios were higher at the SMCA compared to the SMR.

HOV Fish data: Using data from the Delta submersible, we assessed the differences in the density of fishes between SMCAs and SMRs from Big Creek, Point Lobos and Point Sur in the years directly following MPA implementation (2007–2008; Fig. 60). We found a difference in total fish density among SMRs and SMCAs at Point Lobos ($F_{1,1098}$=19.499, $p<0.001$) and Point Sur ($F_{1,36}$=8.41, $p=0.004$). However, there was no statistical difference in fish density among the Big Creek SMR and SMCA ($F_{1,618}$=2.506, $p=0.11$) directly following implementation. For species-specific analyses with HOV data, we calculated response ratios for 6 species inside both SMCAs and SMRs (Fig. 61). We observed differences in response ratios for Kelp Greenling at Point Lobos and Point Sur. Kelp Greenling had positive response ratios inside the SMR and response ratios of 0 at the SMCA. This indicates that there were higher densities of Kelp Greenling inside the SMRs compared the Reference sites while no difference between Reference site and SMCA. At Point Sur we observed the opposite trend for Kelp Greenling with a positive response ratio in the SMCA and a negative response ratio in the SMR. We also observed a large difference in response ratio for Lingcod at Big Creek where there was a response ratio of zero at the SMR and a negative response ratio (~ -5.0) at the SMCA. This indicates that Lingcod densities did not differ at Big Creek SMR from the Reference sites; however, there were significantly lower densities in the SMCA compared to the associated Reference sites. For all other species and sites there were no significant differences in response ratios among SMRs and SMCAs indicating these MPA types are functioning similarly for our focal species.

BRUV data: BRUV surveys at Anacapa were done at all four different protection zones (Old SMR, new SMR, SMCA and fished Reference area (Fig. 1). We tested whether the differences in protection level-age combination affected MaxN and biomass for targeted or non-targeted species using one-way ANOVA for each group and island separately (Fig. 62). We found no significant difference among protection zones for either species grouping for either metric (ANOVA: MaxN Targeted F = 0.44, p = 0.72; MaxN Non-targeted F = 0.68, p = 0.56; Biomass targeted F = 1.66, p = 0.18, Biomass non-targeted F = 1.34, p = 0.26; App. Table D3).

DEWG Question 38**: How do other stressors impact the management of MPAs over time?**

There are a variety of environmental stressors that could influence MPAs such as changing oceanographic conditions (e.g., temperature, currents), increased frequency of storms, and species range shifts. The mid-depth survey data unfortunately are not robust enough temporally to determine how these stressors affect marine communities inside and outside MPAs. For instance, the spatio-temporal gaps in data collection surrounding the 2014–2016 marine heat wave and subsequent 2016 El Niño event prevented us from determining the effects of those climatic events on mid-depth fish communities. This lack of essential data indicates there need to be changes to the sampling design of mid-depth surveys. There needs to be a) a more frequent replication of ROV sampling effort across the same MPAs through time, b) a more consistent ROV sampling time frame (every 1–2 years), and/or 3) the supplementation of ROV surveys with video landers to assess mid-depth fish and invertebrate communities.

Discussion

The main body of this report provided a description of the methods, results, and interpretation of results of the MPA analysis work our group has conducted in the past few years. A large Appendix provides more detailed information. The analyses we conducted using data collected from mid-depth rocky habitats provided valuable information about species, habitats, and marine protected areas (MPAs) in California. We assessed response variables (e.g., differences in density and biomass between MPAs and Reference sites) over time, and were able to identify differences in densities between MPAs and associated Reference sites for some fish and invertebrate species.

In California's North Coast, total fish density from ROV surveys showed an overall positive trajectory through time in both MPAs and Reference sites with peak density occurring in 2014. This peak in fish density occurred just before the marine heatwave that occurred from 2014–2016. Similarly, along the Central Coast, 9 of 11 species showed increasing densities through time, and in the South Coast, density of 9 of 13 species increased with time. In 2020, ROV sampling indicated that the total fish density in both Bodega Head SMR and SMCA exceeded total density in the associated Reference site for the first time during the years sampled. These increases were probably due to the successful recruitment of rockfish species that occurred coastwide from 2013–2017 (Schroeder et al. 2019; Field et al. 2021). The response ratios we calculated, however, showed that although fish densities increased along the coast, there was no widespread evidence that MPAs were performing better than Reference sites. A notable exception is that fish densities calculated from BRUV surveys showed that Copper Rockfish, a heavily fished species, exhibited a strong reserve effect with greater MaxNs inside the MPA at Anacapa Island and Carrington Pt. Additionally, BRUV surveys showed that the heavily targeted

Blue Rockfish showed positive reserve effects for MaxN at Carrington Pt. Also, ROV surveys indicated there were strong, positive MPA effects on structure-forming invertebrates (sponges and corals). This is important because these taxa create habitat that attracts fish and can act as nursery habitat or 3D substrate (Buhl-Mortensen et al. 2010). Indeed, Tissot et al. (2006) and Henderson et al. (2020) found that corals and sponges can attract fish species to them, so their presence in MPAs could affect both fish abundance and diversity.

The decade-long dataset of annotated ROV surveys conducted across the state between 2005 and 2020 showed that MPA effects were specific to each taxon; however, in most cases variation between years and regions overshadowed any potential MPA effects. Certain functional groups (suspension feeders, sessile predators, and structure-forming invertebrates) benefitted from MPA presence but the response ratios varied on a per-species basis. Most notably, the fished species (California sea cucumber) showed strong benefits to protections in Southern CA MPAs where fishing occurs, but not further north where there is no fishing pressure. In general, echinoderms such as sea stars, urchins, and sea cucumbers were responsible for the greatest variation between MPAs and Reference areas and across regions. Beyond assessing MPA effectiveness, we also assessed statewide and regional community-scale metrics such as alpha diversity, species richness, and evenness, and we observed some geographic and temporal trends. Statewide, the greatest species diversity occurred in Central California, possibly due to range overlaps by species with loci further south or north. Over time, we were able to recognize the onset and extent of the sea star wasting syndrome (SSWS) epidemic but the patchiness of sampling across sites and years limited the types of analyses that could be undertaken, for this and other analyses. Indeed, even though the SSWS event had a visibly clear and broad-reaching effect along the California coastline, the epidemic was not detectable through statistical analyses of ROV surveys, which raises questions of the statistical power that could be achieved from intermittent and irregular ROV surveys across space and time. We cannot rule out whether type 2 statistical errors from low statistical power may have obscured any potential MPA effects or results of other analyses.

The 69 MPAs included in this study protect a total area of 94.4 km^2 of rocky reef within the 30–100 m isobaths. Forty of those 69 MPAs surveyed (58%) contained less than 1 km^2 of rocky reef habitat. Also, the total area of high-quality rocky reef habitat protected within MPAs is considerably lower across the state, with only 0.21 km^2 high-quality habitat within the 30–100 m isobaths. This is important because the presence of high-quality rocky reef habitat has been shown to be a significant predictor of demersal fish-habitat associations across multiple species (see Table 5 for a list of references).

We did not detect widespread differences in population trends between MPAs and associated Reference sites. Also, neither environmental conditions nor recruitment indices fully explained the patterns in density or biomass for focal species across MPAs or Reference sites. What then could be driving the patterns observed in fish populations from video surveys? We suggest there are four main possibilities for the unexpected results:

A) The California Current is too dynamic to enable us to differentiate short-term from long-term changes in short periods of time and MPAs are not old enough for the expected changes to have occurred;

B) There are differences between MPAs and Reference sites, but we were unable to detect them with the sampling designs and tools that have been used to date;

C) Fishery management actions have been sufficiently effective so that populations of fishes in both MPAs and Reference sites have increased; or

D) There are no real differences, MPAs have not provided the expected level of resource protection.

With respect to the four possible reasons why we did not see widespread statistically significant differences in density or biomass of focal species between MPAs and Reference sites, we provide the following insights:

A) The California Current ecosystem is extremely dynamic, with physical, chemical, and biological characteristics changing on daily to decadal time scales (e.g., Beas-Luna et al. 2020, Osborne et al. 2020, Deutsch et al. 2021). This ever-changing environment may make it more difficult for populations of invertebrates and fishes to come to the equilibrium state that is commonly expected, based on the marine reserve literature. Ocean water temperatures, productivity, and timing of upwelling conditions all influence the success of incoming year-classes of fishes and the latitudinal and depth distributions of species in the California Current ecosystem. Since the first placement of the MPAs in Southern California, we have experienced several periods of anomalously warm water and resulting biological changes (e.g., Sydeman et al. 2013, Kintsch 2015, Leising et al. 2015, Lavaniegos et al. 2019, Chiu et al. 2021), the largest of which occurred from 2014–2016 as California waters experienced a dramatic marine heatwave. These large fluctuations provide a variety of challenges when trying to statistically detect differences in abundance, biomass, and size structures of species among years. For example, in conjunction with these warming periods, Blue/Deacon Rockfish populations experienced a significant recruitment event (Dick et al. 2017) that led to shifts in the community composition along the entire California coast, which could have major implications for food web dynamics and community resiliency into the future. Marine communities are still feeling the effects of the heatwave and these changes may overshadow any MPA effects. Some of the MPAs we surveyed are more than 20 years old, however, and although we were unable to detect a significant difference in trends in those older MPAs, fish density inside those MPAs was greater than nearby Reference areas. This may indicate that species in older, more established MPAs are more resilient than Reference areas, and may be better suited for “weathering” changes in short-term environmental anomalies.

Both empirical and modeling studies have indicated that it might take 20 years or more to see changes between MPAs and Reference sites in California (e.g., Moffit et al. 2013, Starr et al. 2015, Nichols et al. 2019). Given that MPAs created in the MLPA process are all less than 20 years old, this possibility cannot be ruled out. The scientific literature, however, contains information to suggest that at least three of those older MPAs (Point Lobos SMR, Carrington Pont SMR, Anacapa Island SMR) have shown reserve effects in shallower water (Hamilton et al. 2010, Caselle et al. 2015, Starr et al. 2015). Because we do not have data from the time of implementation of the very old MPAs, we don't know whether they started with higher biomass, or are at some kind of carrying capacity now. Of note is that, theoretically, in very old MPAs, we might not expect response ratios increase over time, because an MPA will theoretically build up biomass at first and then level out at a carrying capacity. After that, spillover rates should increase, and lead to increased fish biomass in adjacent areas relative to the stable MPA biomass. If that happens, Response Ratios of biomass inside reserves to biomass in Reference sites should actually decrease.

B) Monitoring of fishes and invertebrates has occurred somewhat haphazardly over the last 20 years, with a variety of survey tools being used at different MPAs, different time frames, and for different purposes. At least three workshops have been held in the past 15 years for scientists to discuss the use of different kinds of deep-water survey tools. Discussions in those workshops have included the use of HOVs, ROVs, tethered video landers, camera sleds, and BRUVs. The consensus of each of the workshops has been that each kind of tool is useful and has strengths, weaknesses, and costs of operation. Similarly, there have been multiple scientific workshops to discuss monitoring approaches for MPAs. The consensus of those workshops has been that MPA monitoring programs are most effective if the sampling is systematic, balanced, and consistent over long time periods.

To date, the sampling approach in mid-depth rock habitats has been unbalanced in time and space. Some video tools have been used for a small number of years and in few MPAs, such as submersibles, BRUVs, and Tethered video landers. ROV surveys have been geographically and temporally scattered. Because a CDFW priority for ROV surveys has been to sample as many MPAs as possible, less sampling time was devoted to areas that were logistically difficult to sample, so that more survey time could be allocated to areas with high probability of survey completion in a given time window. As a result of a choice to focus on surveys in MPAs, the number of ROV transects conducted is greater in MPAs than Reference sites. Also, relative to large MPAs located in more easily sampled regions (i.e., Southern California), the number of ROV transects conducted is lower in SMCAs and Reference sites than SMRs with less rocky habitat and in MPAs that have a higher total rocky habitat but are considered more remote. This unbalanced sampling design has made it more challenging to determine trends in relative abundance, especially before 2014, when many fewer fishes were identified to species.

Some MPAs have been surveyed with ROVs for multiple years, but were not paired with surveys in appropriate Reference sites; this prevents the use of response ratios as a tool for evaluating MPA performance. Some years, ROVs were used to sample MPAs and Reference sites, but sampling occurred in very different oceanographic seasons (surveys occurred from June through January). We know that fish distributions can change seasonally, so differences in numbers of fish observed at different times of the year can confound MPA evaluations. Also, the approach of ROV surveys to date has been to survey as many MPAs a year as is logistically feasible. This approach has led to a low sample size, in terms of days sampled and sample units at the same time of year, which increases variability in estimates of fish abundance. ROV surveys have occurred primarily in shallow-water MPAs, while the deeper areas (such as SMCAs and offshore SMRs) have been poorly surveyed, if at all. The inconsistency in sampling levels, time of year sampled, and variability in depths and habitats sampled confounds our ability to detect significant MPA changes and answer the DEWG questions.

Changes in fish biomass in MPAs are typically easier to detect than fish density because small increases in fish lengths result in exponentially greater fish weights. The methods used to estimate fish lengths using paired lasers on ROV and submersible surveys have provided only coarse estimates of fish lengths, as analysts estimate lengths to the nearest 5 or 10 cm. This approach, which might have an error exceeding 5 cm, can greatly reduce the accuracy of estimates of size distribution and biomass for certain species, and has caused biases in estimates of fish length in ROV surveys (Kline et al. 2016). Many of the fishes of concern in California's MPAs may grow less than 1 cm per year, thus making it difficult to get accurate changes in biomass using the lengths derived from coarse-scale fish observations. The use of stereo-video analysis tools to more accurately estimate fish lengths will make it easier to detect changes in fish size distributions and biomass over time. The measurement of fish lengths using stereo-video methods will also help when the data are used for stock assessments.

A subcommittee of the Pacific Fisheries Management Council Scientific and Statistical Committee recently recommended to CDFW that they increase the depth range of habitats surveyed and increase the accuracy of fish lengths to help improve the chance of using ROV surveys in stock assessments (Pacific Fishery Management Council 2020). These recommendations are similar to the ones we recommend for MPA monitoring. Finally, as video technology has improved, so too have our abilities to identify and enumerate species. This improvement is positive, but one that makes it more difficult to evaluate changes in species richness and community composition in MPAs using time series where the cameras have changed.

One of the most valuable uses of the California MPA network is to help differentiate changes to coastal ecosystems that are caused by the environment from those caused by human activities. The information generated by MPA monitoring in all depth ranges will be increasingly useful as more years of data are collected. Mid-depth rock surveys conducted at MPAs on a regular basis will help identify the magnitude of changes in abundances of California marine fishes and invertebrates caused by climate change, point source pollutants, and fisheries. An example of this is a recent study by Meyer-Gutbrod et al. (2020), suggesting that there has been a long-term change in rockfish distribution due to changing oxygen levels. This finding would not have been possible without the long-term submersible surveys conducted in a variety of water depths.

Karpov et al. (2010, 2012) identified some of the statistical issues related to ROV surveys and developed approaches for analyzing ROV data. They equalized sampling effort by breaking their 500 m-long ROV transects into 50 m^2 subsets and randomly selecting an equal number of "subsamples" for each MPA, Reference site, and depth bin. CDFW has been working with the Science and Statistical Committee of the Pacific Fishery Management Council to determine if this approach can be utilized effectively. Our research team has not been involved in those discussions; rather than selecting subsets of transects, we opted to analyze fish density by habitat types and depth bin. We note, however, that most researchers tend to analyze entire transects because of the trade-off between transect lengths needed to significant quantities of target species and the number of replicates that are required to detect population change within and outside of an MPA (Svard et al. 2019).

We used 500-meter long ROV transect lines as a sample unit in our analyses. Perkins et al. (2021) conducted an analysis of the sampling power of this length of transects from ROV surveys conducted in California from 2014–2016 to detect differences in abundance of Brown Rockfish (*S. auriculatus*). Their work indicated that in places with low abundances of a species, such as Año Nuevo and Montara SMRs, the mean statistical power to detect a simulated change in abundance never exceeded 40% at Año Nuevo, and never exceeded 25% at Montara, regardless of the level of sampling effort tested. This is one reason why we think that the design of ROV surveys should be revisited for MPA monitoring, and why we recommend a different approach.

We suggest that a departure from the approach of surveying many MPAs at the statewide level as the state can afford in any one year and focus on a few focal MPAs. Our statistical analyses have shown that it will be better to have more (and more accurate) data from a few MPAs than trying to survey as many MPAs as possible. We suggest that surveys should be stratified, with more and more frequent surveys occurring in Southern California and Central California than Northern California. We recommend more intensive and frequent surveys that are more carefully conducted at specific times of the year. This may increase the expense of MPA monitoring. One solution is to greatly increase the budget for deepwater surveys, buy or rent another ROV or two, and increase the technical staff needed to operate ROVs. Another solution is to include the use of other tools and strategically distribute the sampling responsibility over broader geographic regions. A third solution is to identify MPAs that are most important ecologically and focus on surveying a larger proportion (e.g., depths and habitats) of those areas.

A primary need is for the development of a long-term, well-designed, consistent sampling program for mid-depth MPA habitats. The statistical tests we used to evaluate differences among MPAs and Reference sites would have provided more conclusive results if the original sampling had been designed with those tests in mind, and if enough samples had been collected to reduce the variability of mean values. Development of this type of sampling plan, however, will require a commitment to fund long-term monitoring. CDFW initiated ROV surveys for MPA monitoring as MPAs in California were being created in response to the MLPA (Karpov 2006). After that initial investment in monitoring MPAs with ROVs, CDFW has relied on MARE to collect and analyze video from ROV transects. Each year, MARE has provided CDFW with summaries of habitats, fishes, and invertebrates observed on transects. We presume CDFW has been evaluating that information, but were unaware of any results until Nick Perkins, a post-doctoral scholar was hired by OPC to review the statistical power of the ROV transects. As stated earlier, his work showed a low statistical power from transects (Perkins et al. 2021). That document, combined with our analyses, suggests that the state needs to invest some more funding in an MPA monitoring analytical team to provide leadership for ensuring that future surveys are designed to maximize the statistical likelihood of detecting reserve effects in California MPAs. An analytical team could be funded and led by CDFW, OPC, or from outside (e.g., university) sources, but is important to collect and analyze information in a rigorous way that is designed for MPA evaluation. This group might help CDFW as they work towards using ROVs for stock assessments as well. This recommended work is outside the scope and funding of the research effort presented here, but we would be glad to pursue this discussion with OPC and CDFW.

C) Spatial management tools such as MPAs are part of a suite of tools used for managing nearshore environments. Fishery management regulations have become more conservative since the passage of the federal Sustainable Fisheries Act in 1996 and the California Marine Life Management Act of 1999. Due to overfishing in the 1980s and 1990s, the Pacific Fishery Management Council and CDFW enacted very stringent management actions in 2000 as part of mandatory stock rebuilding plans. Management actions resulted in catch reductions, gear restrictions, and implementation of depth-based coast-wide fishing closures, known as Rockfish Conservation Areas, as managers took strong measures to avoid directed and incidental catch of the rebuilding species. These closed areas were essentially depth-based, de facto no-take MPAs for demersal species along the entire California MPA planning area in deep-water. Spatial and quota restrictions have only recently been relaxed as many groundfish populations have successfully recovered. During that 20-year period of increased fishery restrictions, we witnessed 4-5 years of higher-than-normal recruitment of a variety of species, due to some favorable environmental periods in the last 20 years, resulting in an increased abundance of many fished species in California waters. These population increases have been a fishery management success, but made it more difficult to detect differences between MPAs and Reference sites. We note, however, that the Rockfish Conservation Areas, which were essentially MPAs, have been shown to effectively increase populations of rockfishes in California (Marks et al. 2015), and create expectations that the same will happen in shallower MPAs.

D) It is possible that MPAs have not provided the level of resource protection that would lead to differences inside MPAs relative to Reference sites. Potential reasons for this would include high rates of movement of fishes across MPA boundaries, high levels of poaching inside MPAs, or differences in habitat quality between MPAs and Reference sites, each potentially leading to no differences in fish mortality rates inside and outside MPAs. We evaluated habitat quality among MPA and Reference sites and saw no large discrepancy among habitat quality inside and outside MPAs. We did not have information with which to evaluate the other alternative hypotheses, except that the scientific literature on fish movements would suggest that California MPAs are large enough to encompass the typical movements of many species.

Management Recommendations Supported by Results:

- A comprehensive plan for sampling mid-depth rock habitats should be developed and be based on specific scientific objectives and appropriate sampling designs. Results of the monitoring should be evaluated on a regular basis to ensure objectives are being met.
- Quantifiable targets for MPA performance (e.g., a given percent change in fish abundance) should be elucidated so that appropriate sampling levels can be set.
- Future surveys should be designed to more carefully account for habitat and depth differences and be conducted at the same time of year in each management area.
- Reference sites should be evaluated and new or additional ones chosen for mid-depth MPAs to cover the range of depths and habitats used by key species and thus increase chances of detecting changes.
- The number of ROV survey sample units should be increased at MPA and Reference sites to improve the ability to enable detections of significant change of a) all fish combined and b) the most abundant fishes and invertebrate communities. Depending on funds available, this may require monitoring fewer MPAs.
- Surveying the same sites at regular intervals is essential for documenting changes in fish species over time. Funding levels will influence how regularly MPAs can be surveyed. We suggest monitoring a few MPAs within each region as often as possible, while monitoring other MPAs less frequently. Invertebrate communities appear to be changing on a regional, rather

than MPA basis. Sampling invertebrates in 1-2 MPAs per region on an annual basis with more MPAs every 5 years may be sufficient to evaluate changes.

- Surveys should be stratified by habitat types and depths. Deeper habitats and SMCAs have been under-sampled and deserve more attention, as they are de facto MPAs for many species. More surveys should occur in habitats deeper than 50 m to encompass the full range of depths inhabited by target species.
- Both shallow and deep stereo-video landers have proven useful for evaluating species and communities inside and outside MPAs. They could be used to complement ROV surveys.
- It is critical to utilize stereo video on all tools (ROV, HOV, BRUVs, Landers) to enable a more accurate estimate of fish lengths and thus fish biomass. Stereo cameras need to be calibrated to ensure accuracy of data collected.
- As video technology continues to improve, scientists will need to determine how much the technological improvements affect apparent changes in MPAs when using historical data.
- Fishing pressure and/or fishery removals inside Reference sites and near MPAs are key variables that affect MPA performance and should be monitored along with environmental and biological variables.

Conclusions

In addition to conducting more intensive sampling in fewer MPAs, we believe that more ROV fish surveys should be placed in areas deeper than 50 m. The first reason for this recommendation is that there are teams of researchers who are surveying subtidal fishes in the 10–50 m water depths, using SCUBA, hook-and-line fishing gear, and underwater cameras. Those methods will provide similar information as ROVs, potentially at a lower cost. The second reason is that the fish and invertebrate communities in rocky habitats in the 50–130 m water depths, which are typically on the state's continental shelf, are not as well surveyed. A third reason is that by surveying primarily in shallower water we could miss changes in ontogenetic movement patterns caused by fishing (Frank et al. 2018) and miss the larger, more fecund individuals that may be present, which provide increased reproductive capacity inside MPAs. For example, ROV surveys suggest that the median size of Lingcod across our survey regions are 47 cm, 55 cm, and 45 cm in the North, Central and South regions, respectively. However, a recent study by Lam et al. (2021) surveyed shallow (<60 m) and deep (60–170 m) rocky reef habitats with hook and line surveys and found that median lengths of Lingcod were approximately 67 cm, 63 cm, and 61 cm in the North Central, and South regions, respectively. Despite the fact that hook and line surveys are known to target the larger fish in a population, these differences suggest that the ROV surveys are underestimating the overall size/age structure of fish populations by missing individuals located in deeper waters. Surveying the deeper habitats will be important for evaluation of MPAs, and also for evaluation of the effects of climate change on California's marine communities into the future.

Although our work did not show dramatic MPA effects across all of the organisms sampled or all of the tools used, we note that this does not constitute a failure of MPAs to achieve the many goals set out by the MLPA. For example, we are only beginning to understand the potential for MPAs to provide resilience to climate change including extreme events. Continued monitoring following the marine heatwave of 2014–2016 will allow California researchers to understand the patterns and time scales of recovery, which will contribute important information on MPA resilience. Similarly, the benefits of protecting biodiversity may be hard to measure from studies using methods that survey only a subset of organisms or habitats. A newly published scientific paper by Mumby et al. (2021) raises concerns that certain types of conservation outcomes are sufficiently complex or subtle that there is a high probability of studies falsely concluding that conservation is inconsequential. Their conclusion is that resource managers should be aware of the difficulty of clearly detecting statistical change and consider additional types of evidence, commission further research, or invoke the precautionary principle. Identifying funding for a sustainable long-term monitoring program will better inform questions about conservation of biodiversity and the effects of climate change.

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Figures

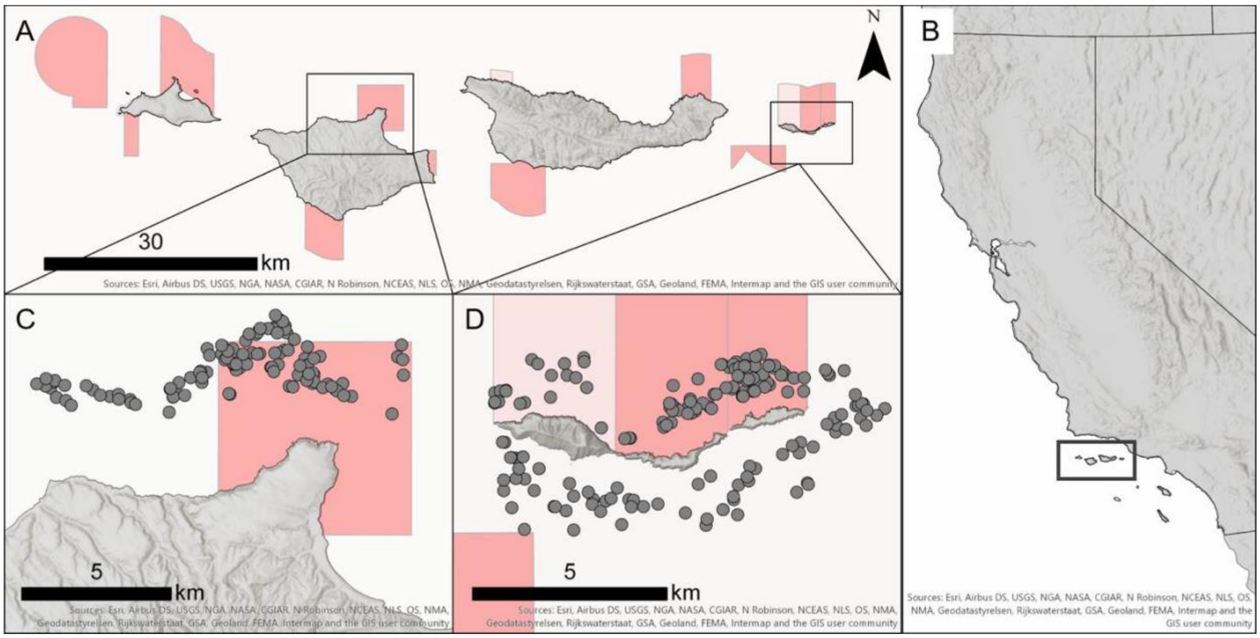


Figure 1. Maps showing locations of the two focal MPAs in the Santa Barbara Channel, Northern Channel Islands. Panel A shows the locations of Carrington Point and Anacapa Island, focal MPAs within the Northern Channel Islands. Panel B shows the location of the Northern Channel Islands along the California coast. Panels C and D show the locations of BRUV surveys over 2019 and 2020, at Carrington Point and Anacapa Island, respectively.

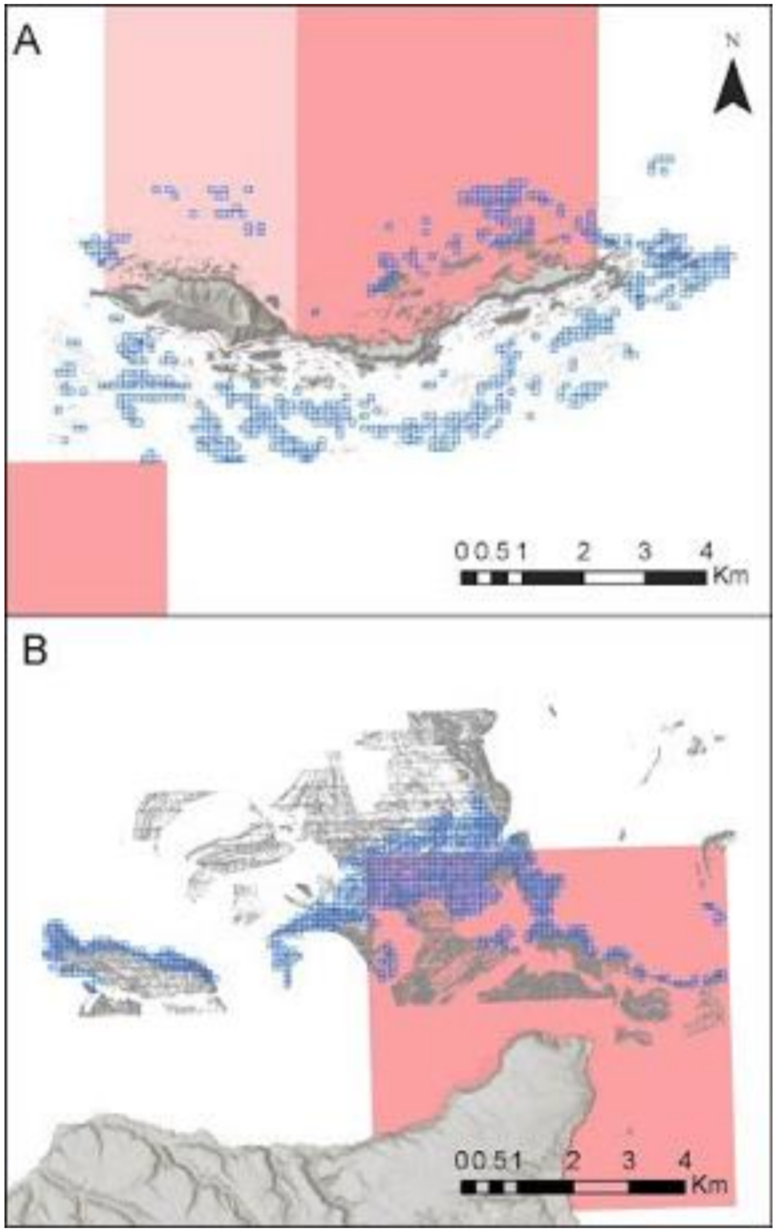


Figure 2. Maps showing the 100m X 100m sampling grid cells used for haphazard selection of daily BRUV deployment locations at Anacapa Island SMR/SMCA (A) and Carrington Point SMR (B). Blue grid cells represent areas that met the minimal requirements for hard bottom, were in the proper depth zone (30-100m for Anacapa Island and 30-70m for Carrington Pt.), and thus were eligible to be sampled. The grey shading represents hard bottom habitat (mapped by the California Seafloor Mapping Program) used to qualify eligible sampling cells.

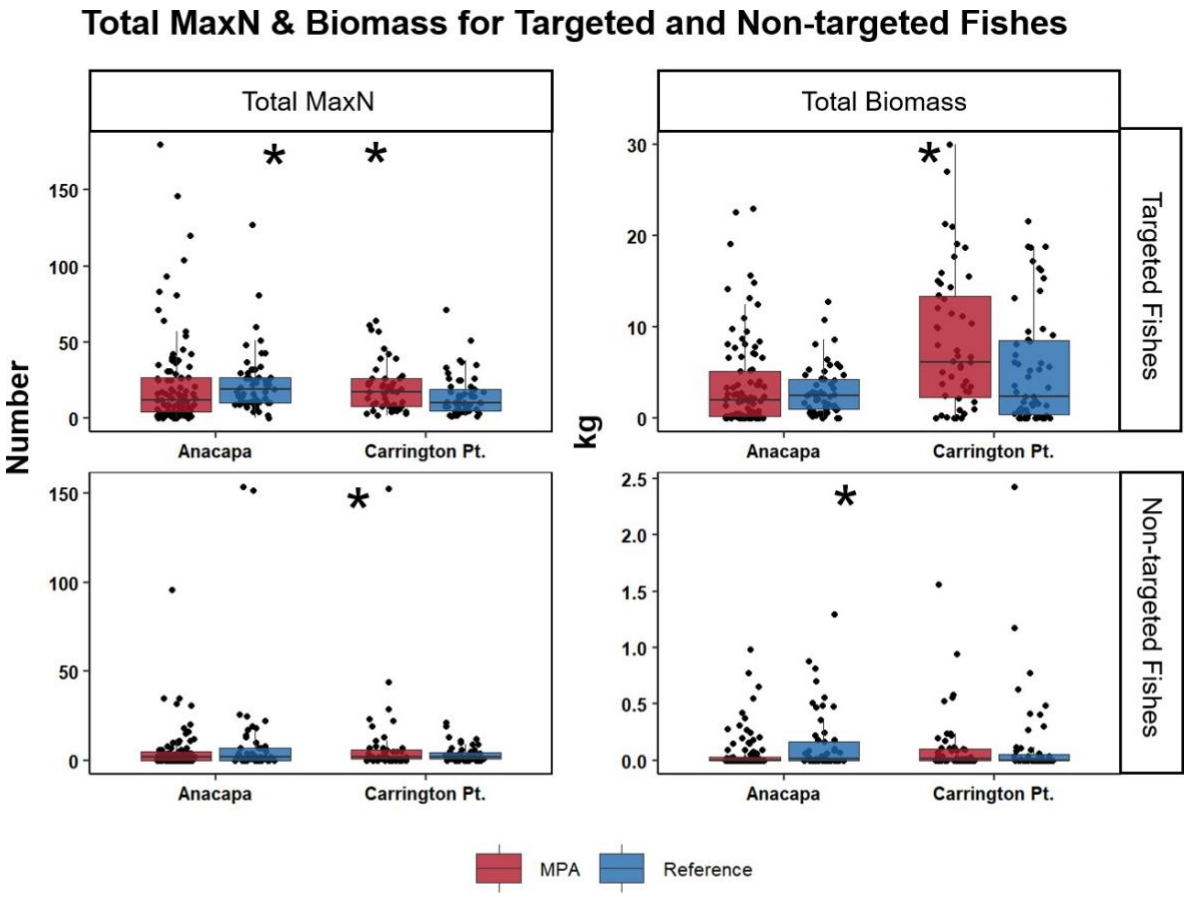
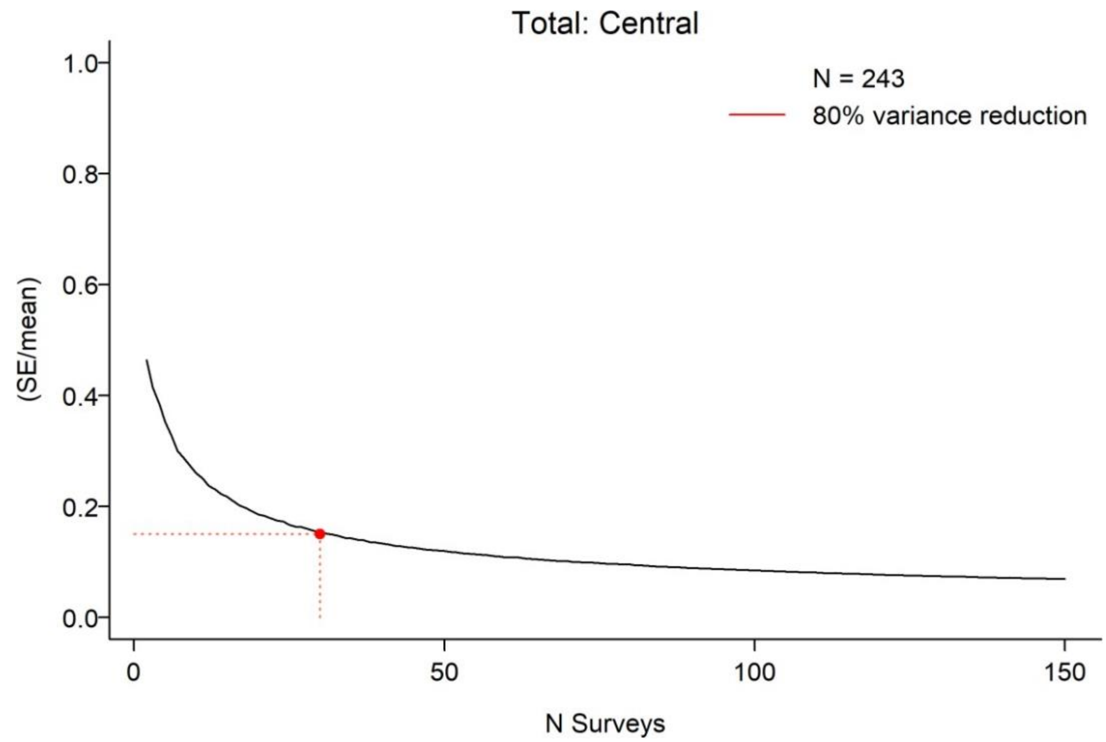


Figure 3. Summed MaxN and Total Biomass (kg) for each BRUV survey inside and outside the Anacapa and Carrington Pt. MPAs. Targeted and non-targeted species were separated. Upper and lower portions of the boxplot represent 1st and 3rd quartiles of the data and the points represent the observed values. * represents a significance level of ≤ 0.05.

A.



B.

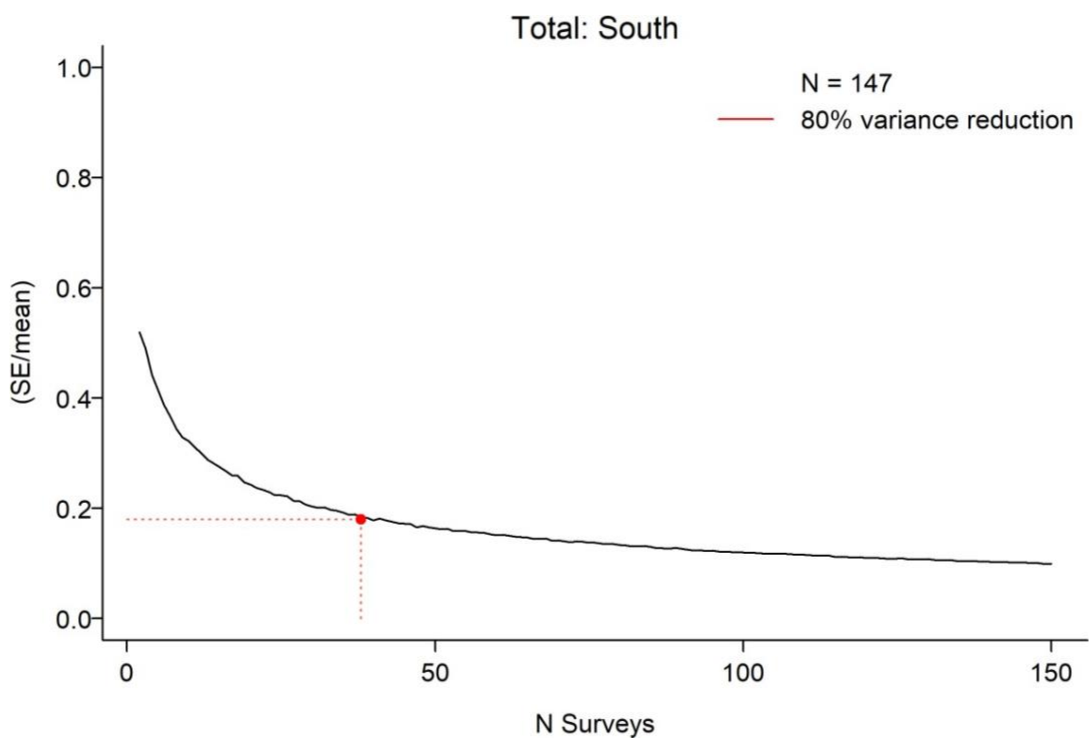


Figure 4. Precision (SE/mean) as a function of number of surveys for the BOSS in Central (A) and Southern California (B). Red dotted line represents 80% reduction in variance. Actual sample size=243 (A) and 147 (B).

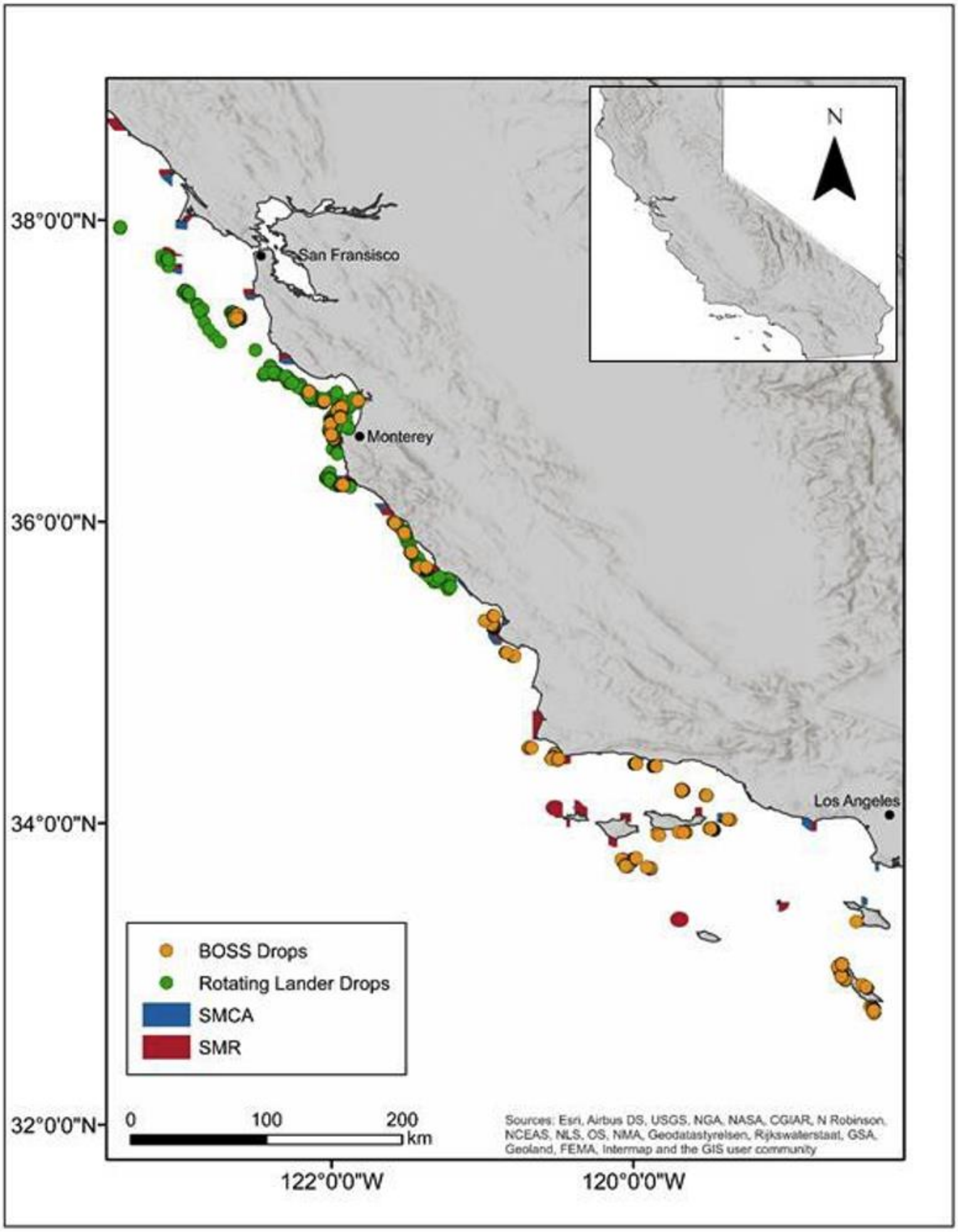


Figure 5. Map showing the location of Rotating Lander (green) and BOSS (yellow) drops along the California Coast.

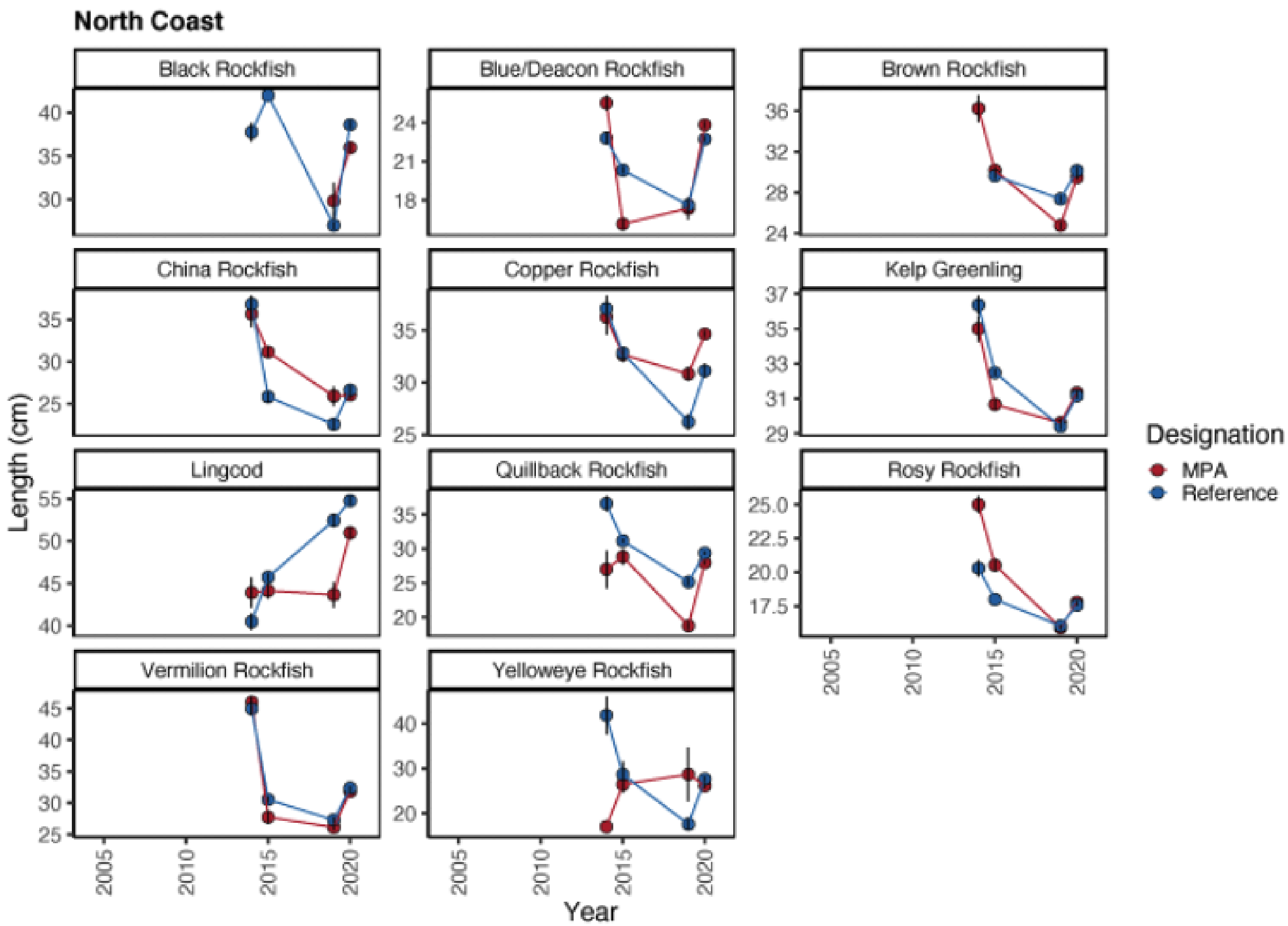


Figure 6. Differences in mean lengths of focal species from ROV surveys in the North Coast. Statistical differences for 2 of the 11 focal species (Kelp Greenling and Quillback Rockfish) between MPA and Reference sites and across years were found, however, there was no clear positive or negative trajectory through time.

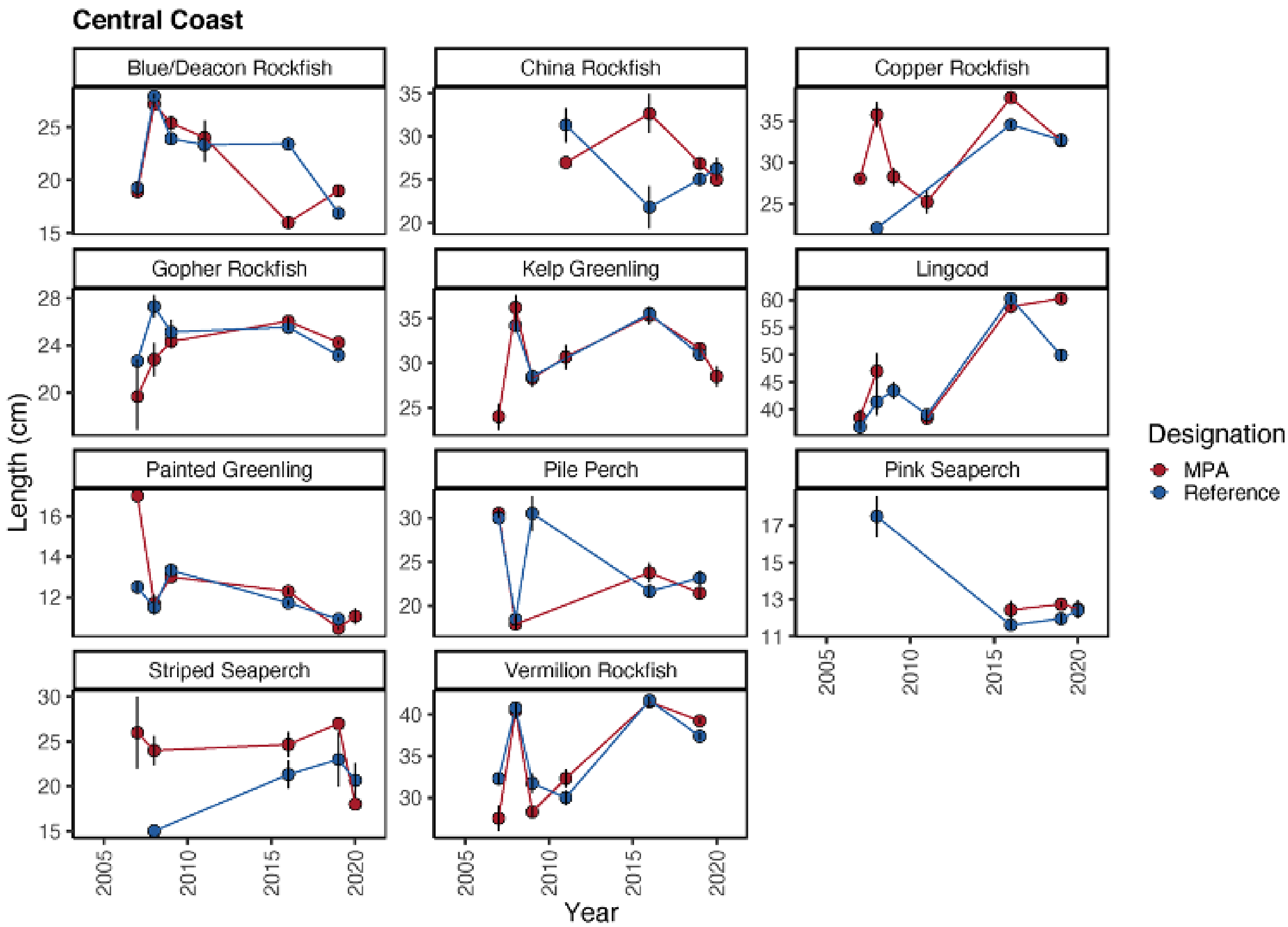


Figure 7. Differences in mean lengths of focal species from ROV and HOV surveys in the Central Coast. Statistical differences in body size among MPA and Reference sites across sampling years were apparent for 6 of 11 focal species (Blue/Deacon Rockfish, Gopher Rockfish, Lingcod, Painted Greenling, Pink Seaperch and Vermilion Rockfish) in the Central Coast.

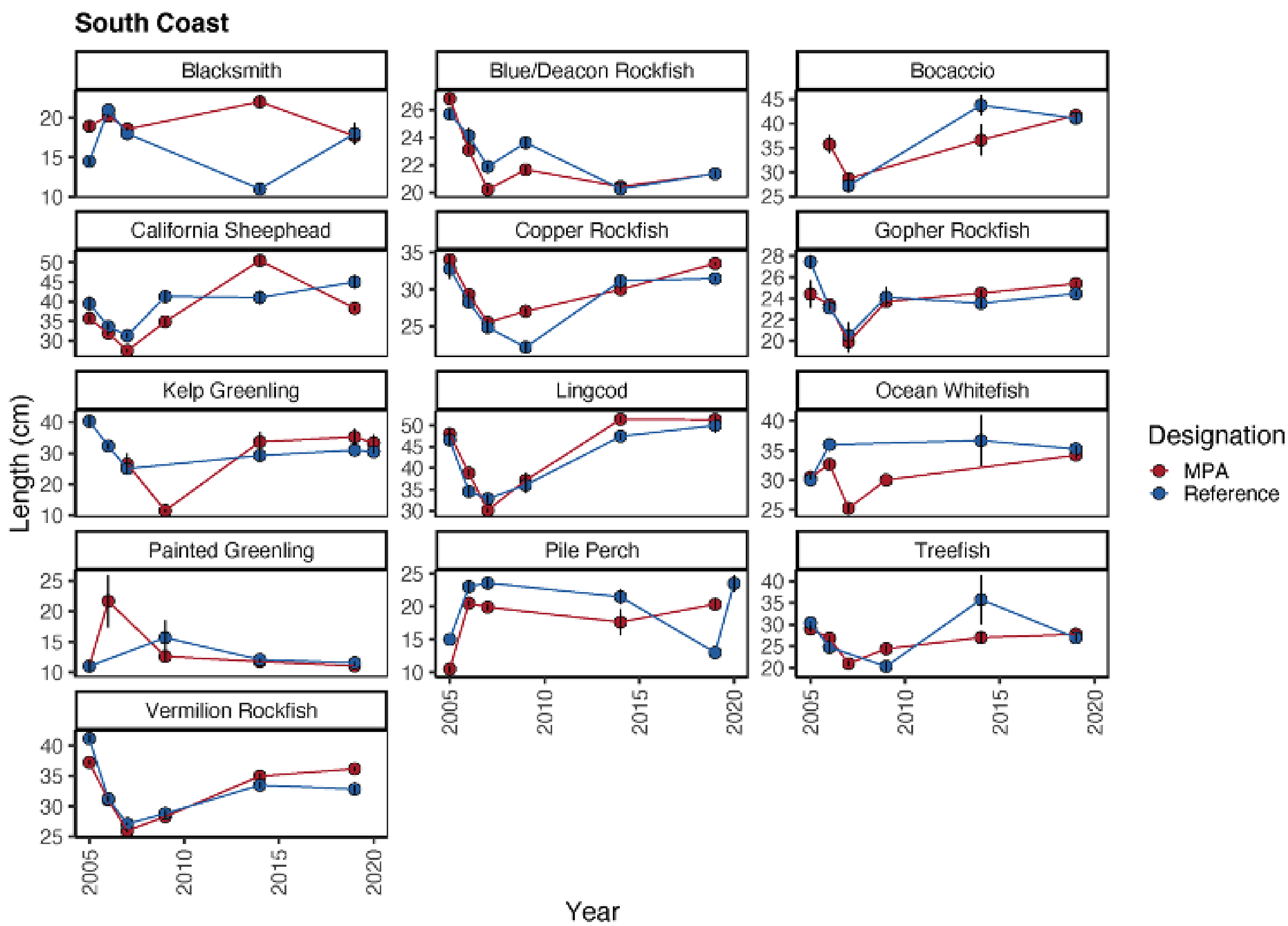


Figure 8. Differences in mean lengths of focal species from ROV and HOV surveys in the South Coast. In the South Coast, 7 of 13 species (Blacksmith, Blue/Deacon Rockfish, California Sheephead, Kelp Greenling and Vermilion Rockfish) showed statistically significant differences in mean lengths among MPAs and Reference sites across years.

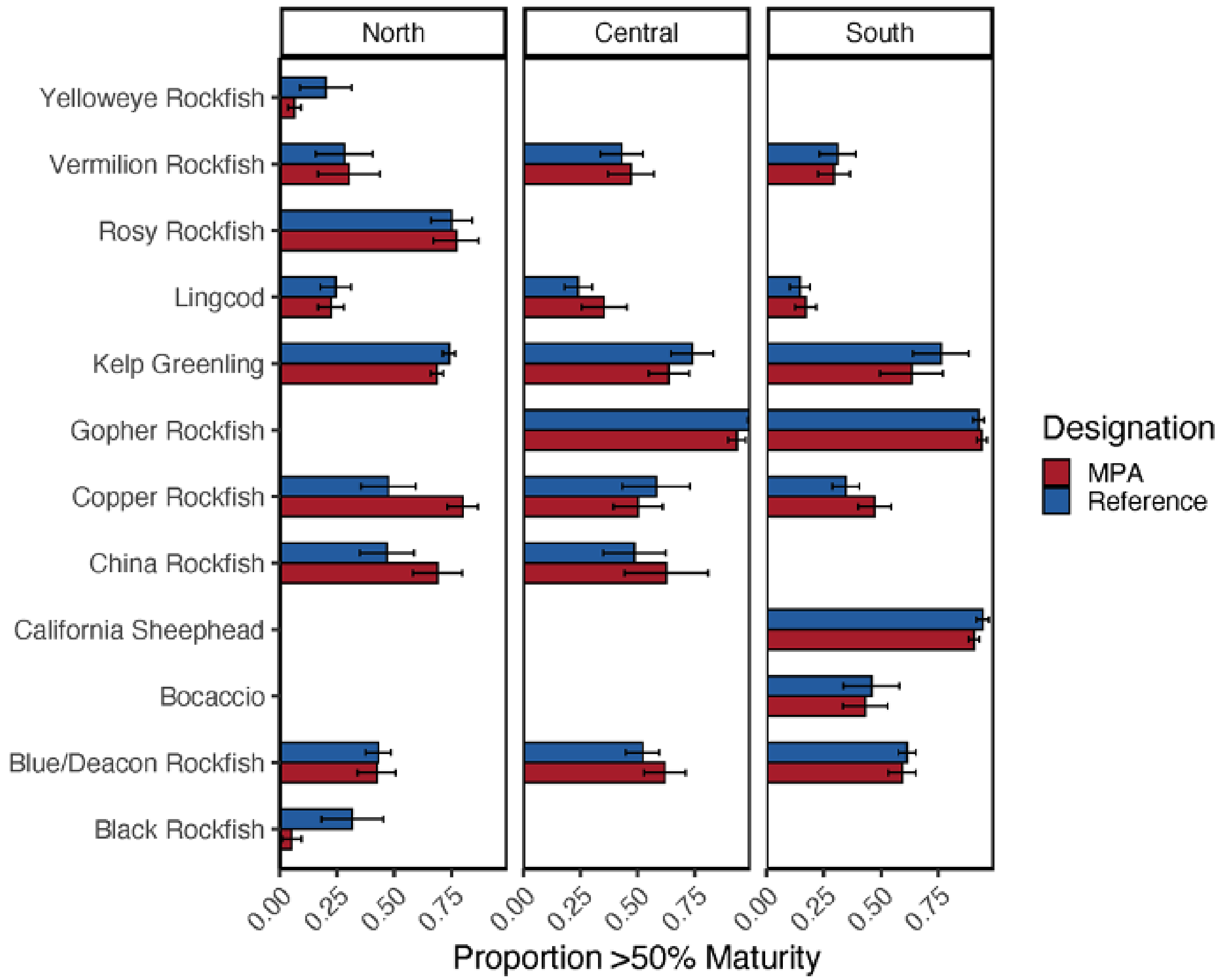


Figure 9. Assessing mean length at 50% maturity for species inside and outside MPAs, we found non-significant trends of increased proportion of individuals greater than 50% maturity for Copper Rockfish, China Rockfish, and Gopher Rockfish in the North Coast, Lingcod, China Rockfish, and Blue/Deacon Rockfish for the Central Coast, and Copper Rockfish in the South Coast.

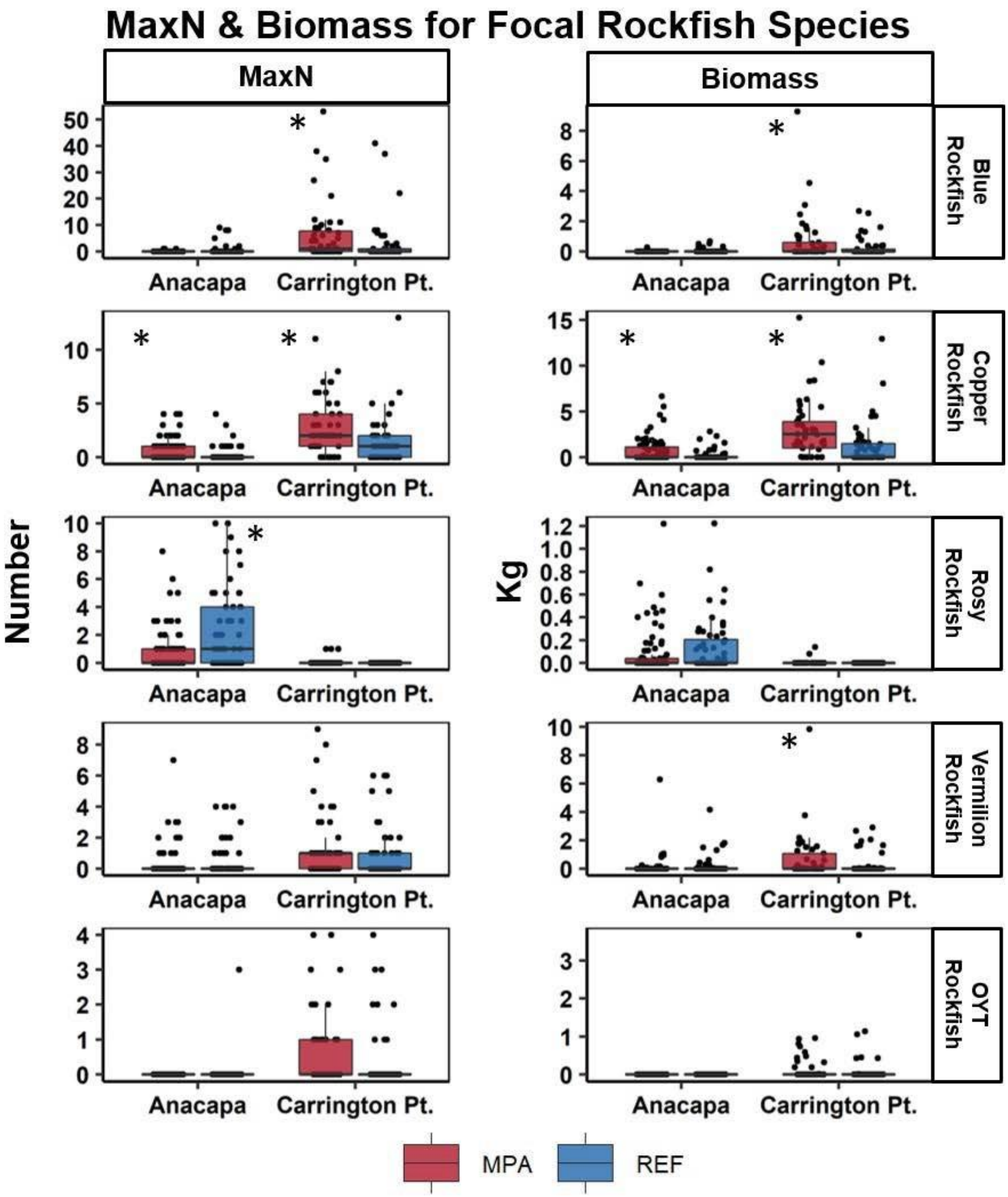


Figure 10. Mean MaxN and mean Biomass (kg) for select focal rockfish (genus Sebastes) species. Upper andlower portions of the boxplot represent 1st and 3rd quartiles of the data and the points represent the observed values. * represents a significant difference.

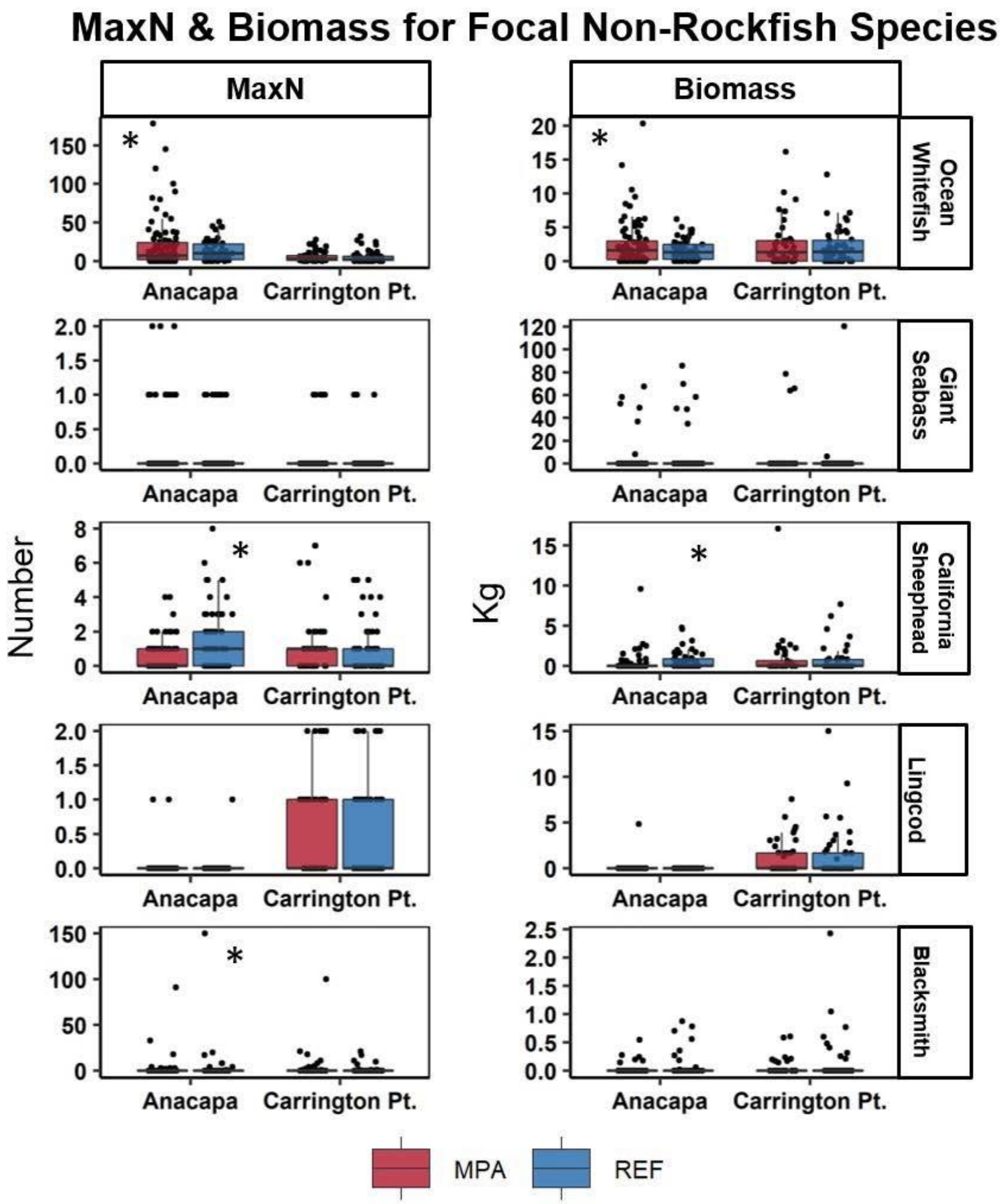


Figure 11. Non-rockfish focal species. Upper and lower portions of the boxplot represent 1st and 3rd quartiles of the data and the points represent the observed values. * represents a significant difference.

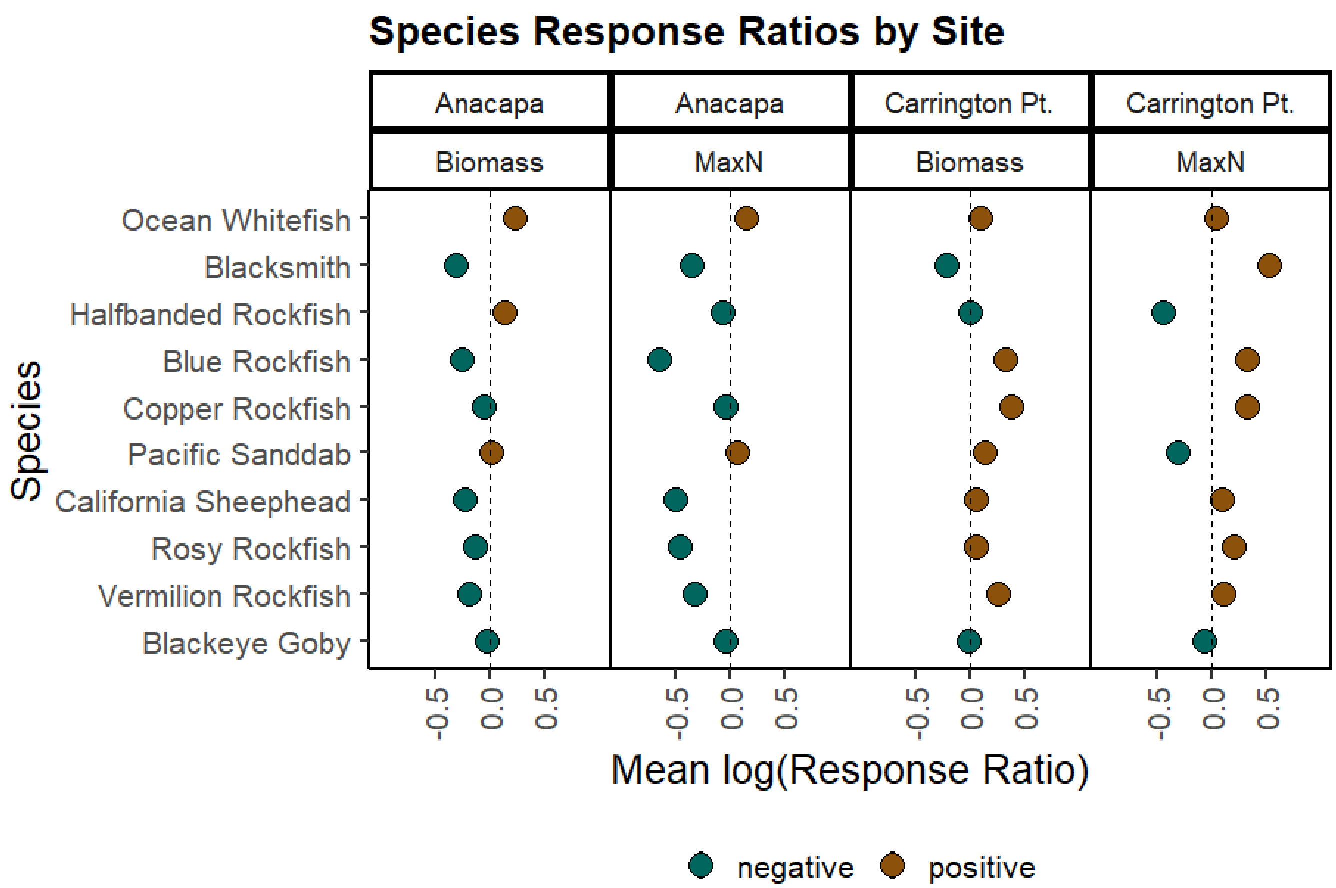


Figure 12. Log response ratios [Log (MPA/Ref)] for MaxN and biomass for selected focal species.

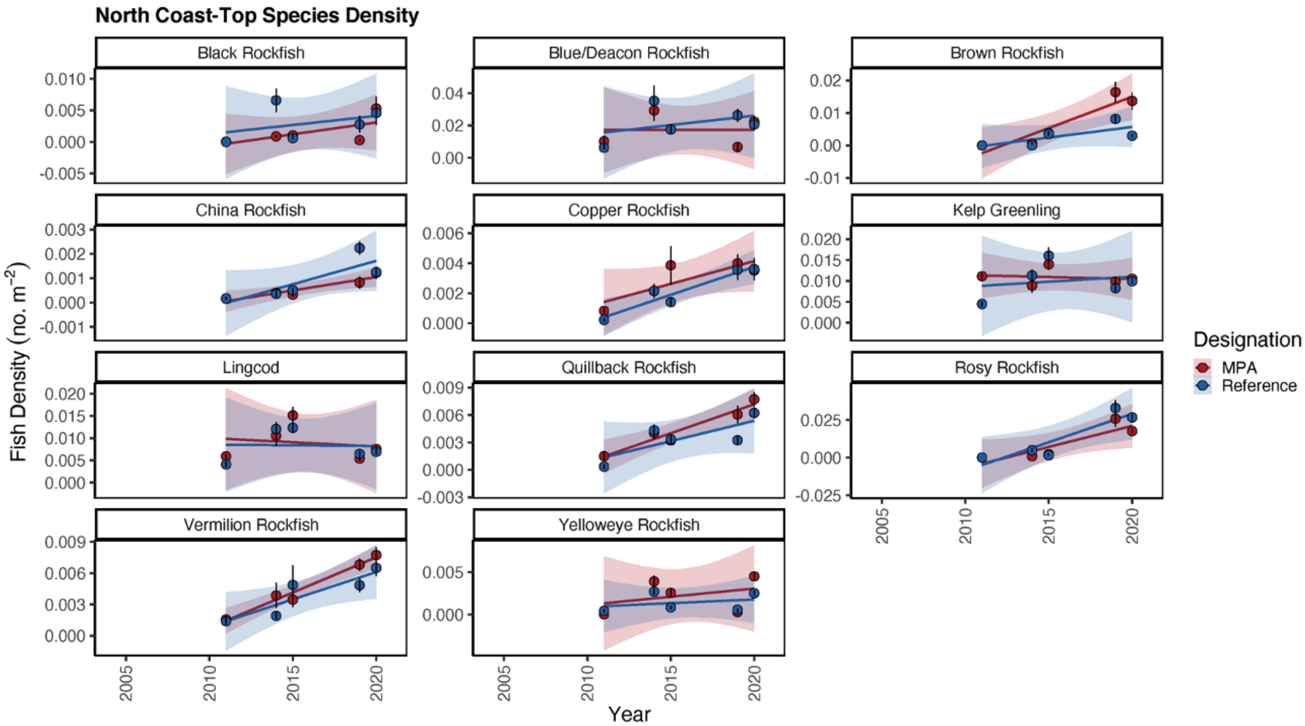


Figure 13. Densities of 11 focal species among MPA and Reference sites through time on the North Coast. For 4 of the 11 species, Brown Rockfish, Quillback Rockfish, Vermilion Rockfish, and Yelloweye Rockfish, there were higher densities inside the MPAs compared to Reference sites in the most recent sampling year (2020).

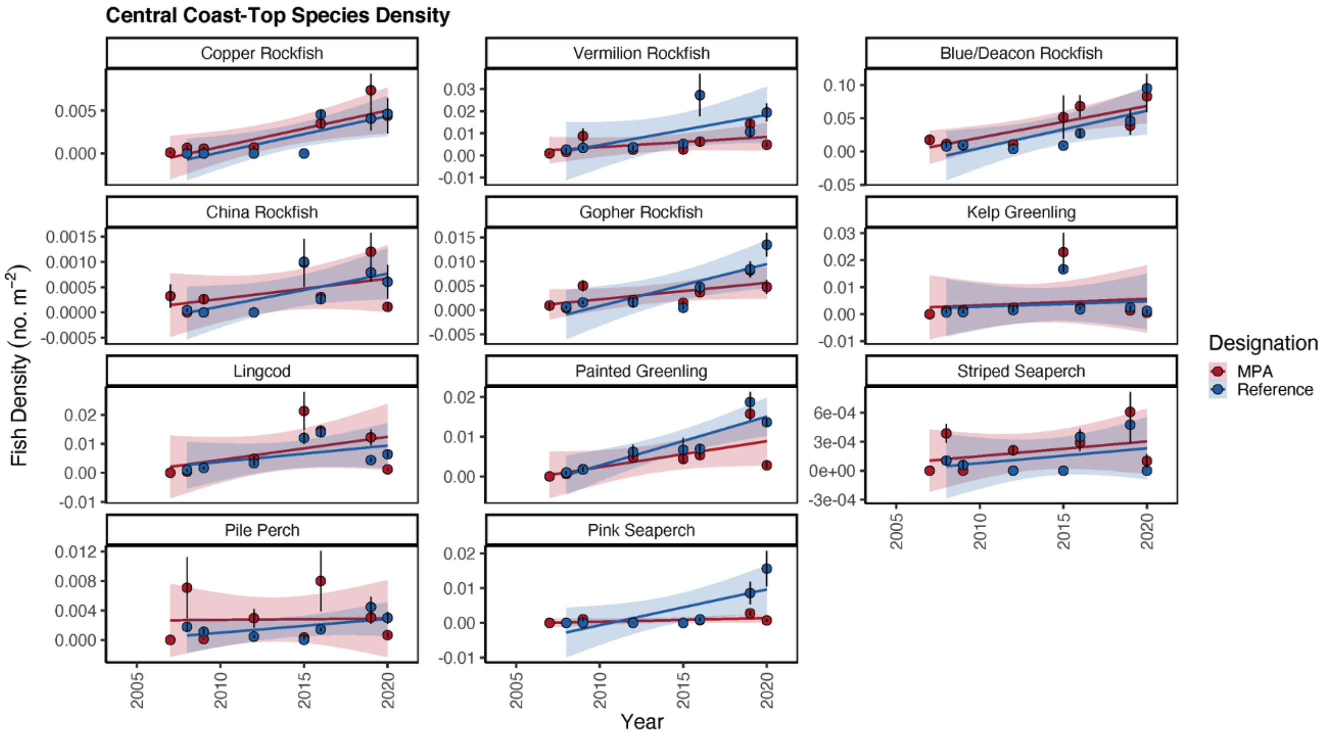


Figure 14. Densities of 11 focal species among MPA and Reference sites through time on the Central Coast. 9 of 11 species showed increasing densities through time however, there were no statistical differences among MPAs and Reference sites with the exception of higher densities in the Reference sites for Pink Seaperch.

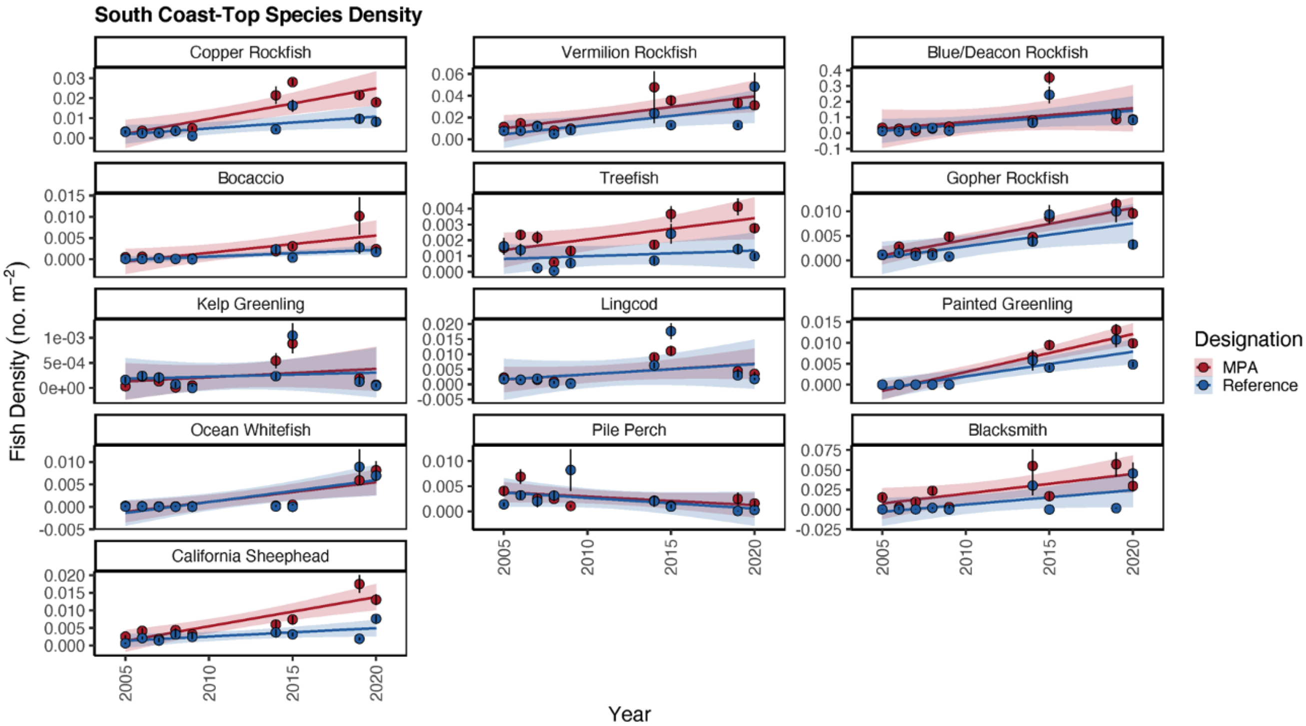


Figure 15. Densities of 13 focal species among MPA and Reference sites through time on the South Coast. For both Copper Rockfish and California Sheephead, the differences in densities between MPA and Reference sites increased through time, with statistically higher densities in the MPAs in 2020.

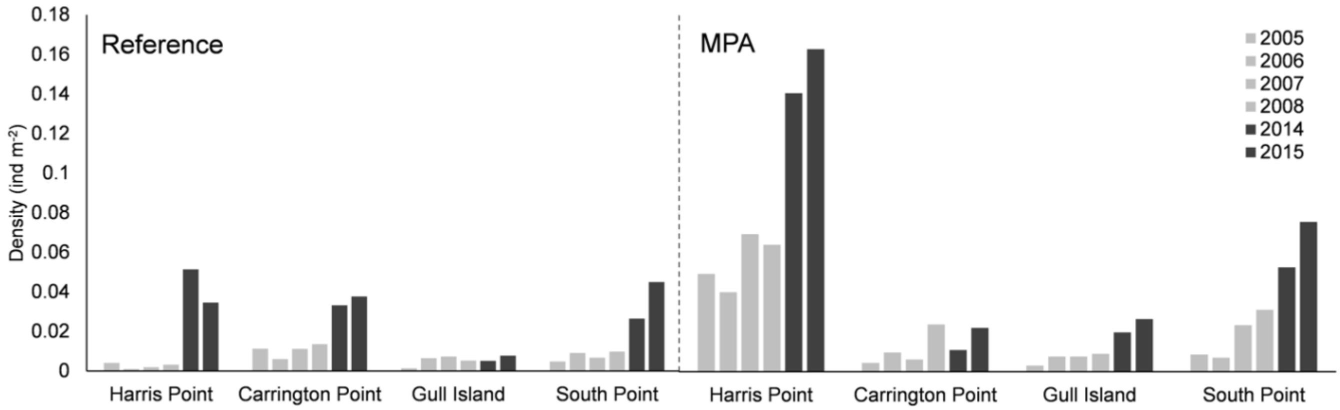


Figure 16. Density of California sea cucumber (*Apostichopus californicus*) observed in ROV surveys between 2005-2015. Densities were greater in MPAs than in associated Reference sites in selected Southern California locations.

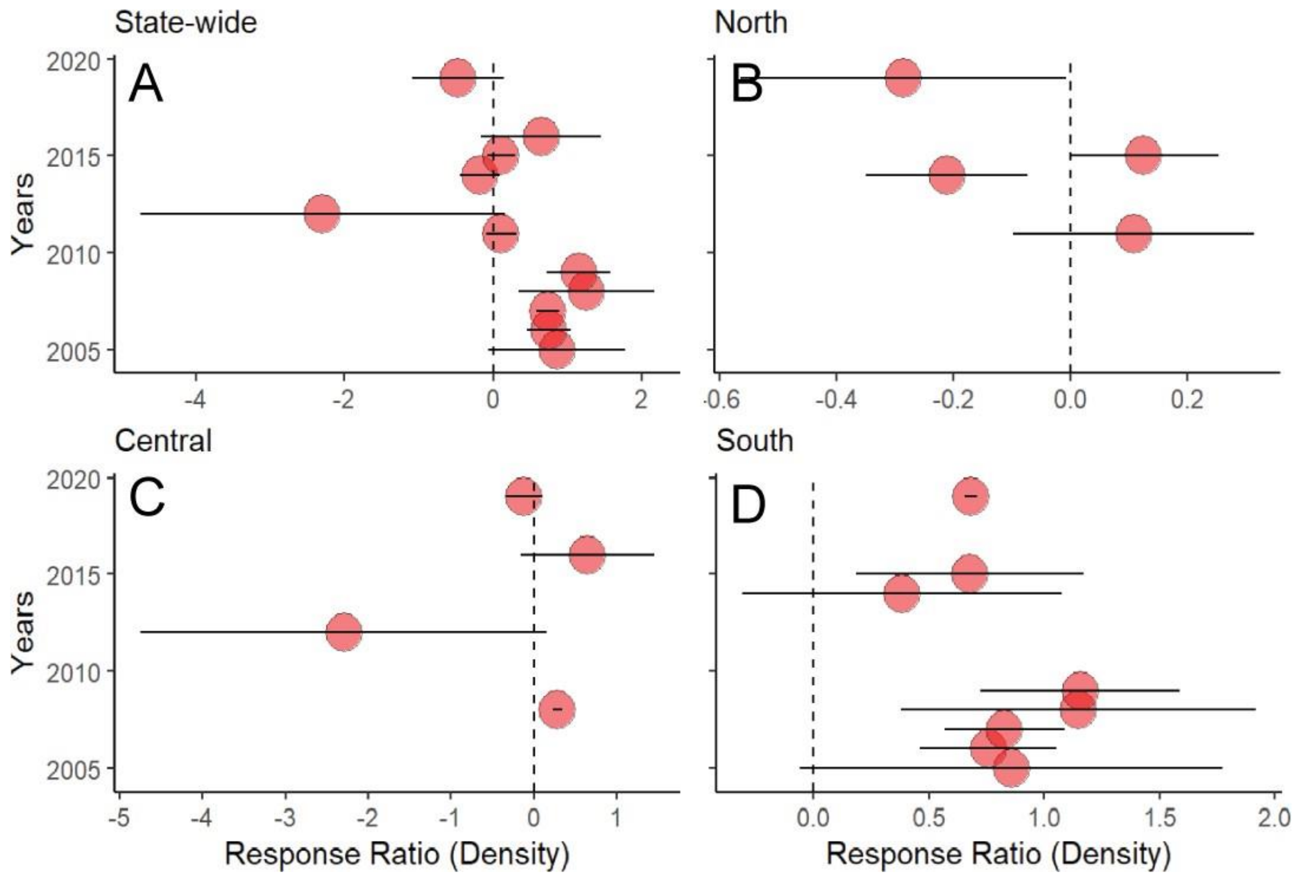


Figure 17. Density response ratios (Mean ± SE) for the California sea cucumber, *Apostichopus californicus*, from 2005–2019. Positive ratios indicate that populations were denser within MPAs compared to corresponding Reference sites. Responses varied by region and are plotted here statewide for MPAs (A State-wide, B) Northern, C) Central, and D) Southern California.

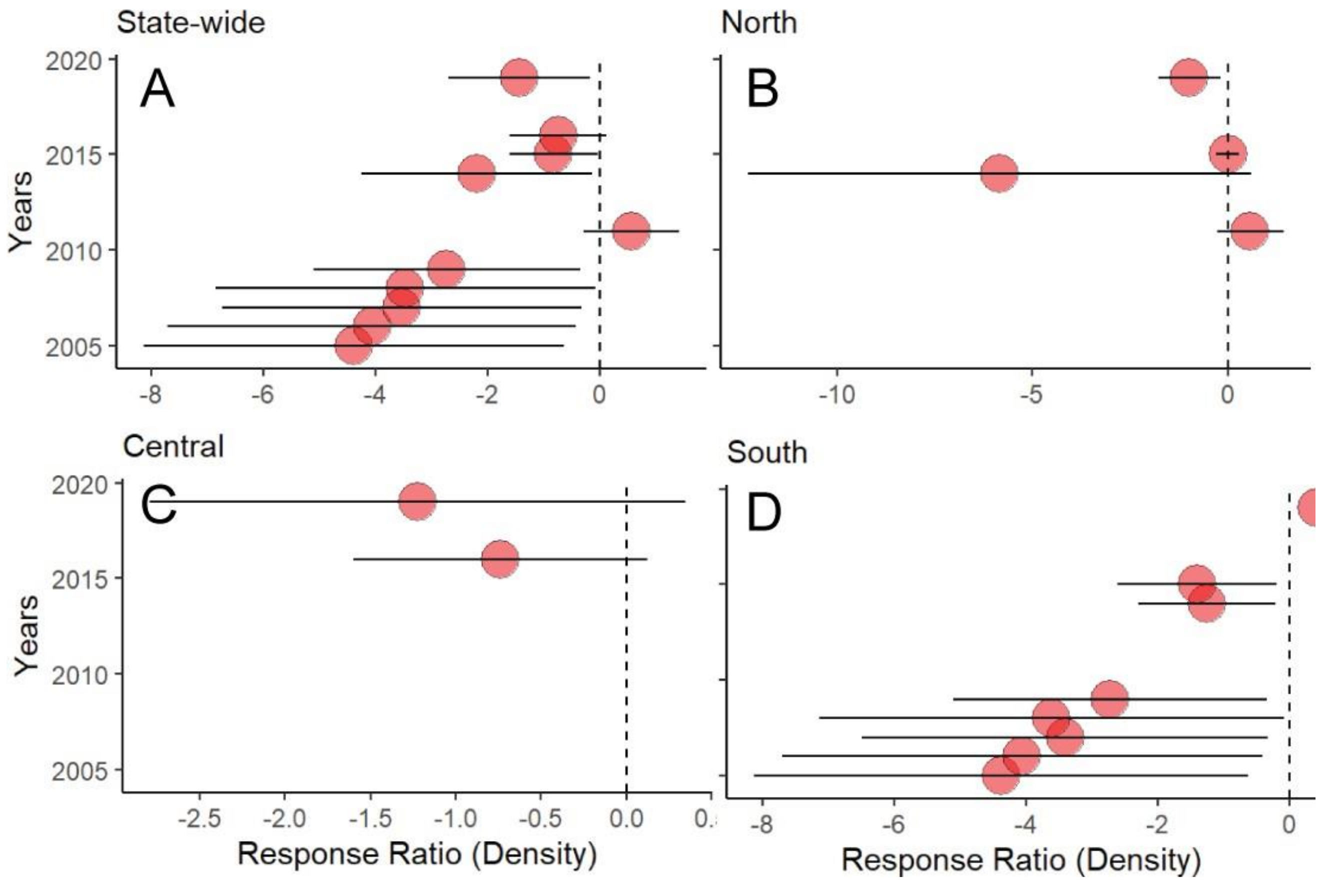


Figure 18. Response ratios (Mean ± SE) for the red sea urchin, *Mesocentrotus franciscanus*, from 2005–2019. Positive ratios indicate that populations were denser within MPAs compared to corresponding Reference sites. Responses varied by region and are plotted here for MPAs (A State-wide, B) Northern, C) Central, and D) Southern California.

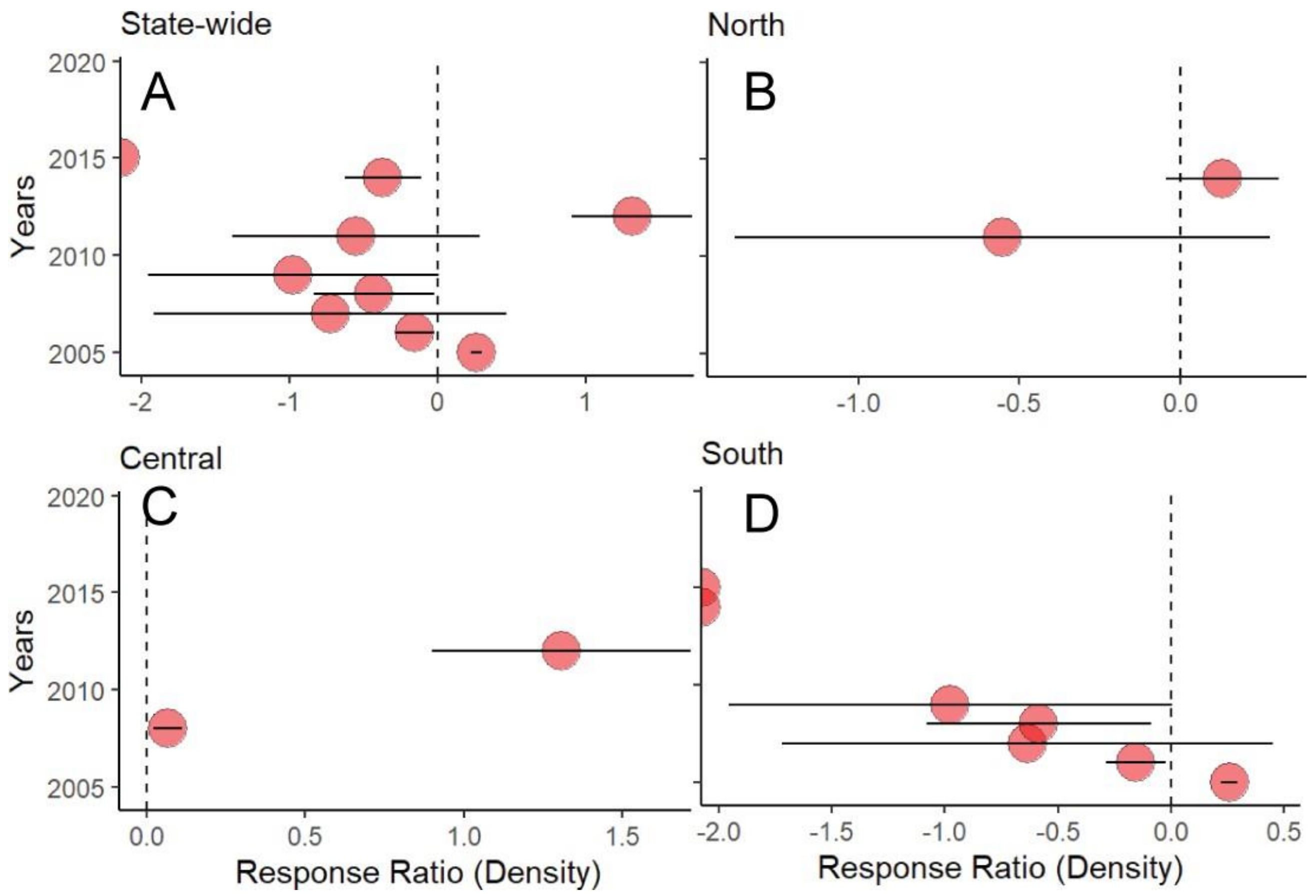


Figure 19. Response ratios (Mean ± SE) for the sunflower sea star, *Pycnopodia helianthoides*, from 2005–2019. Positive ratios indicate that populations were denser within MPAs compared to corresponding Reference sites. Responses varied by region and are plotted here statewide for MPAs (A State-wide, B) Northern, C) Central, and D) Southern California.

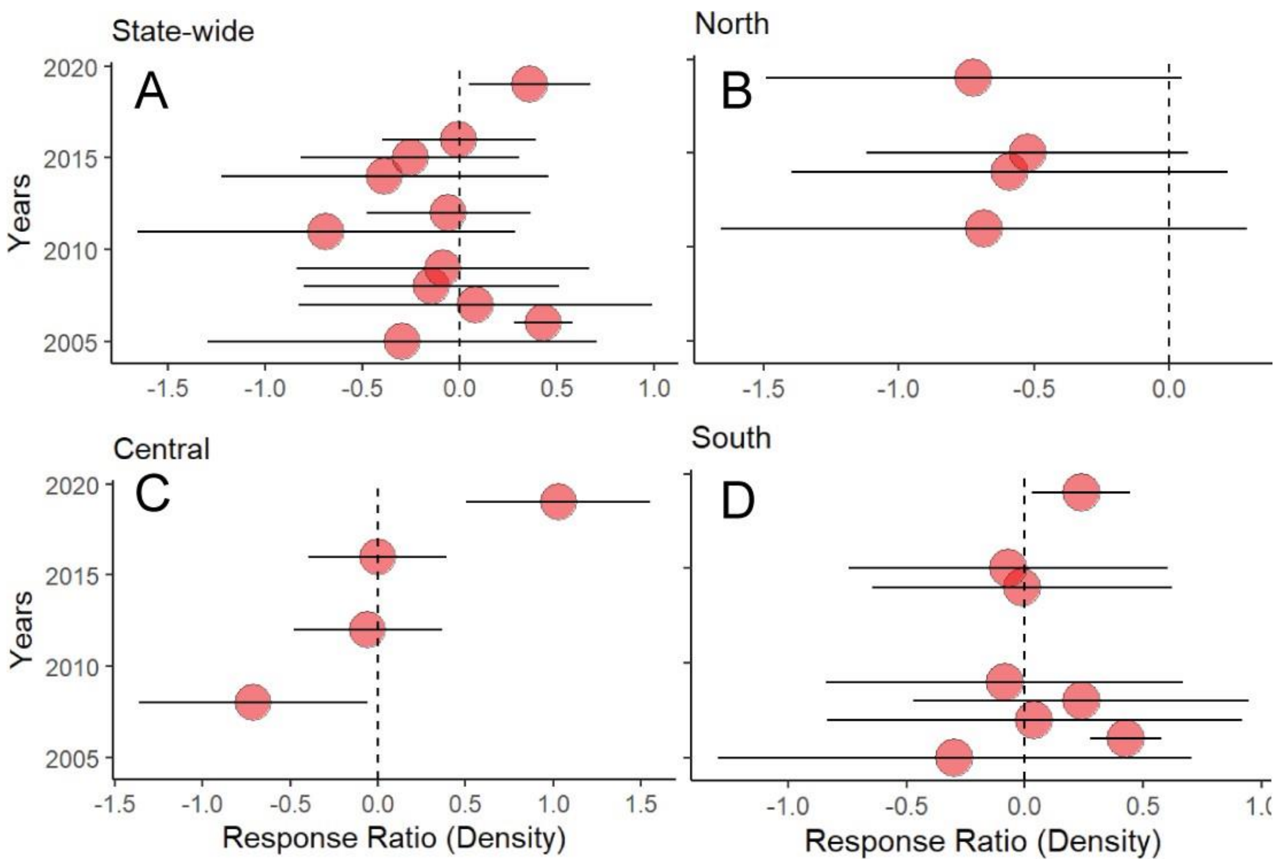


Figure 20. Response ratios (Mean ± SE) for the vermilion sea star, *Mediaster aequalis*, from 2005–2019. Positive ratios indicate that populations were denser within MPAs compared to corresponding Reference sites. Responses varied by region and are plotted here statewide for MPAs (A State-wide, B) Northern, C) Central, and D) Southern California.

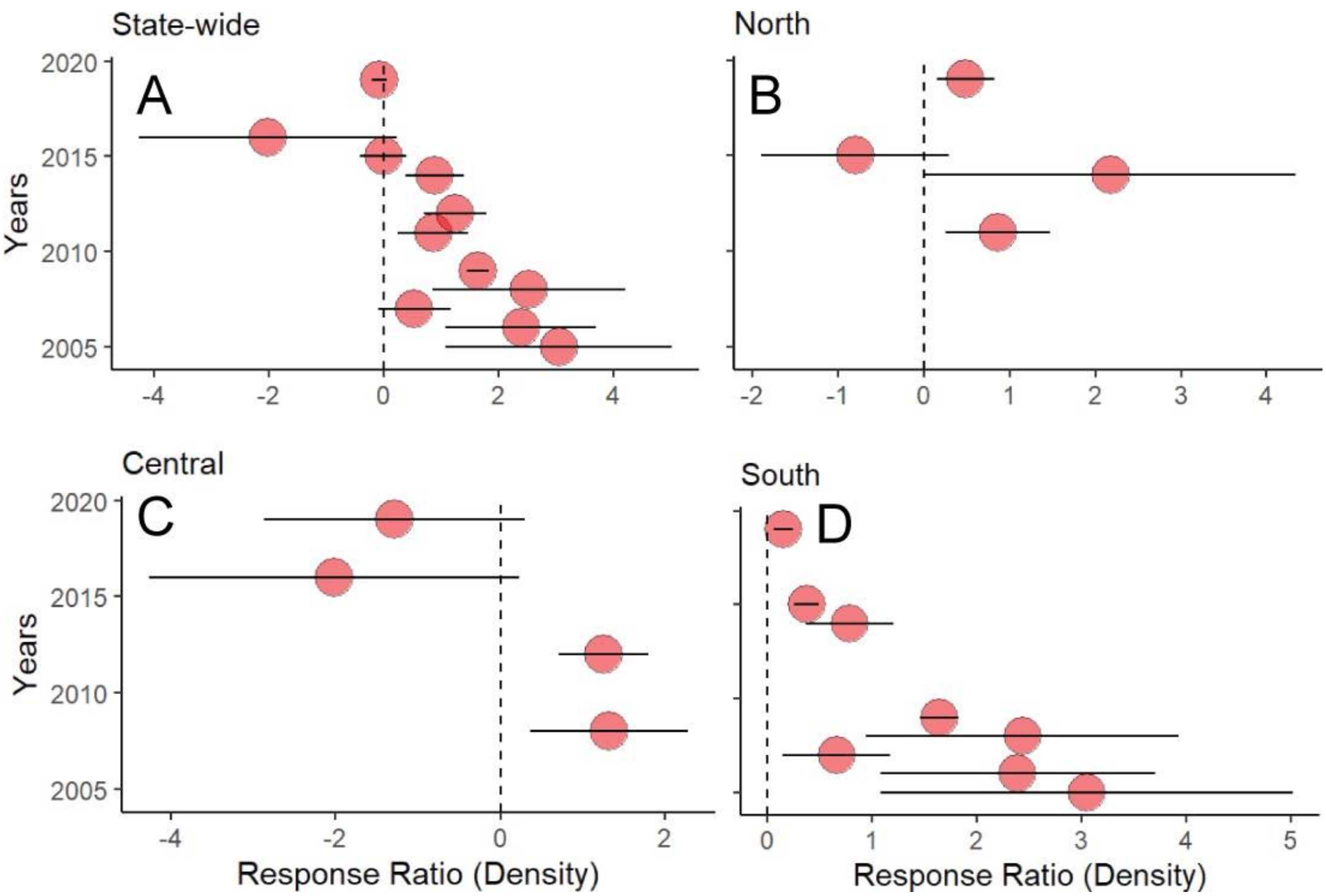


Figure 21. Response ratios (Mean ± SE) for the slender sea pen, *Stylatula elongata*, from 2005–2019. Positive ratios indicate that populations were denser within MPAs compared to corresponding Reference sites. Responses varied by region and are plotted here statewide for MPAs (A State-wide, B) Northern, C) Central, and D) Southern California.

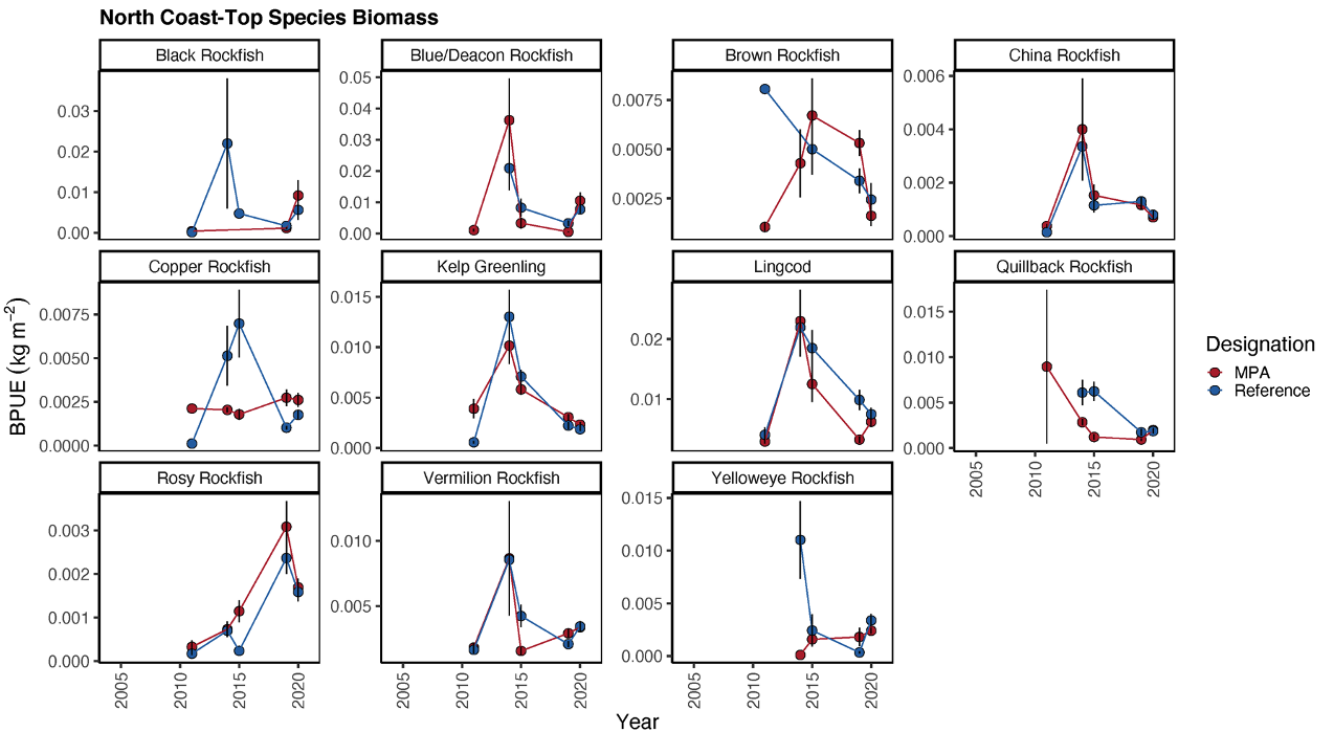


Figure 22. Differences in biomass between MPAs and Reference sites across ROV survey years were statistically significant for 3 of 11 focal species (Copper Rockfish, Kelp Greenling and Yelloweye Rockfish) along the North Coast.

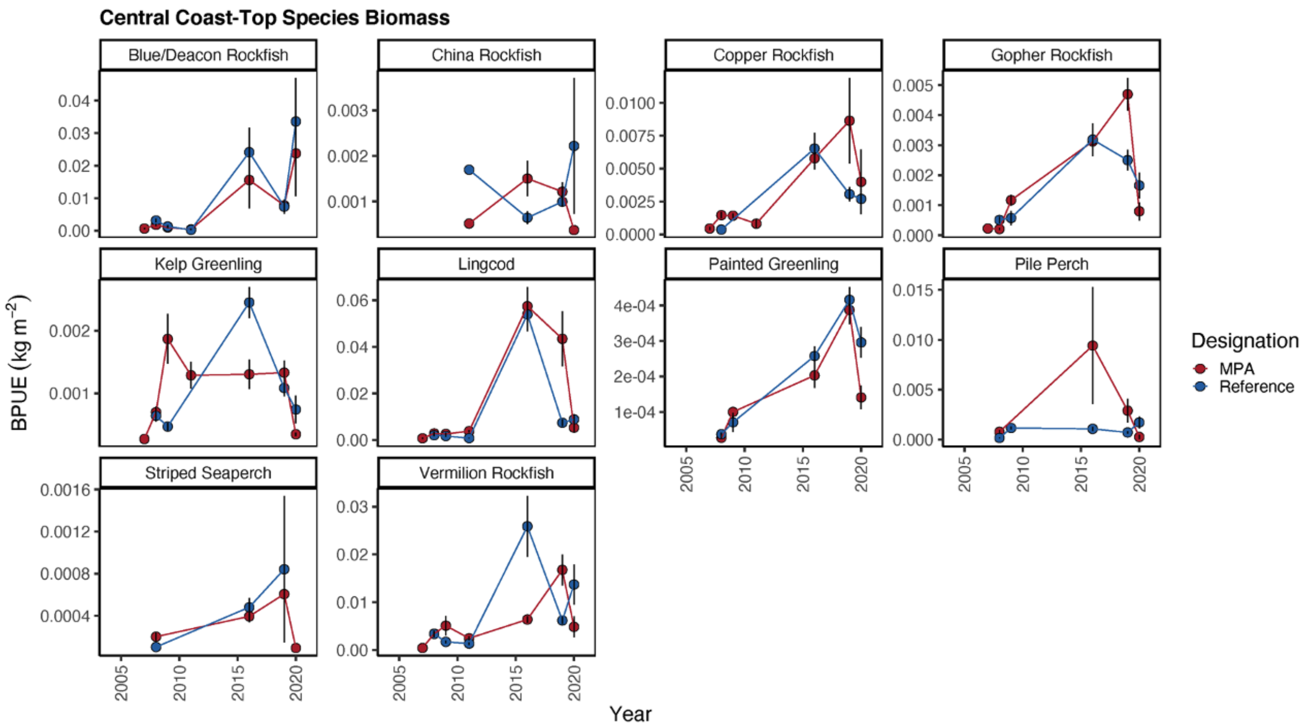


Figure 23. Along the Central Coast, total biomass varied across survey years for 5 of 11 focal species (Blue/Deacon Rockfish, Gopher Rockfish, Lingcod, Painted Greenling, and Vermilion Rockfish); however, there were no significant differences in biomass among MPAs and Reference sites from HOV and ROV surveys.

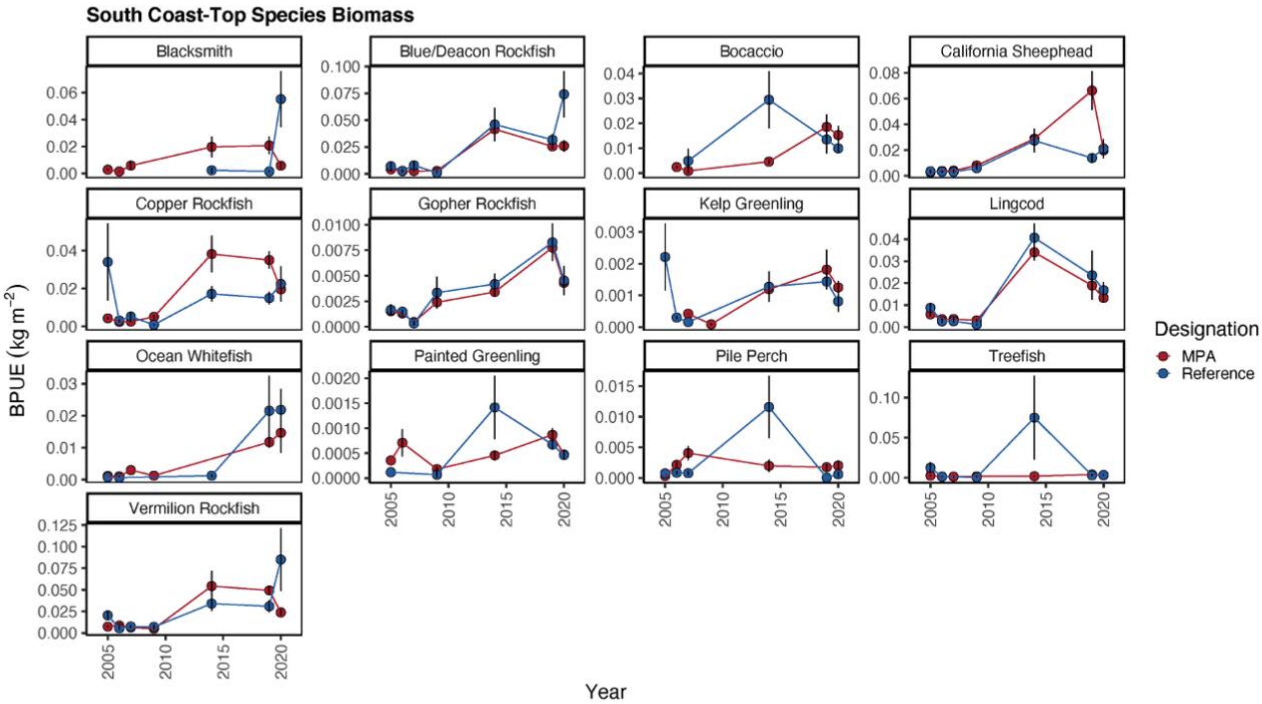


Figure 24. Along the South Coast, 6 out of 13 species (Blue/Deacon Rockfish, California Sheephead, Copper Rockfish, Gopher Rockfish, Lingcod, and Vermilion Rockfish) displayed varying biomass through time.

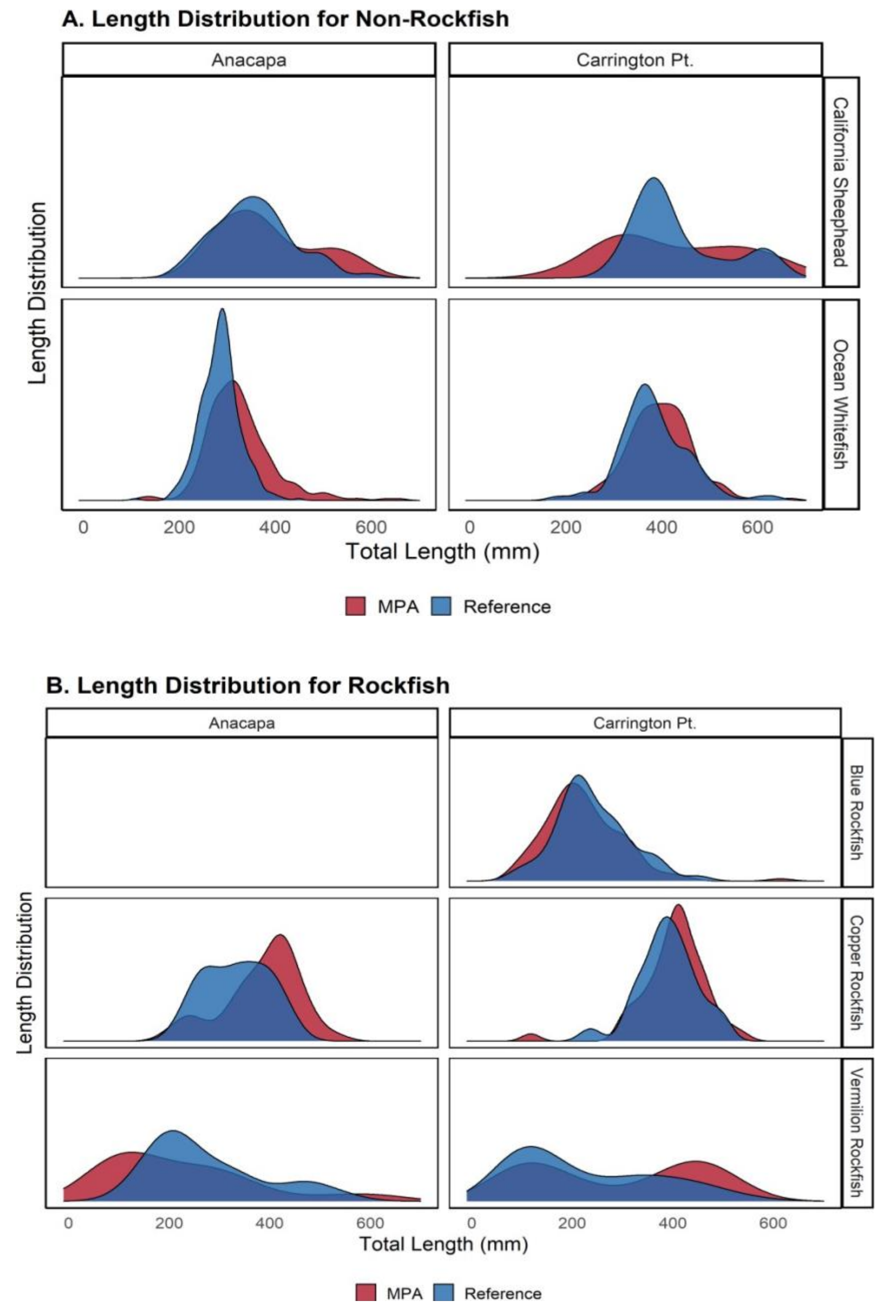


Figure 25. A) Length distributions for three species of Rockfish: Blue Rockfish, Copper Rockfish, and Vermilion Rockfish from the Anacapa and Carrington Pt. MPAs, based on BRUV surveys. B) Length distributions for California Sheephead and Ocean Whitefish. The blue and red distributions represent data from the Reference areas and MPAs, respectively.

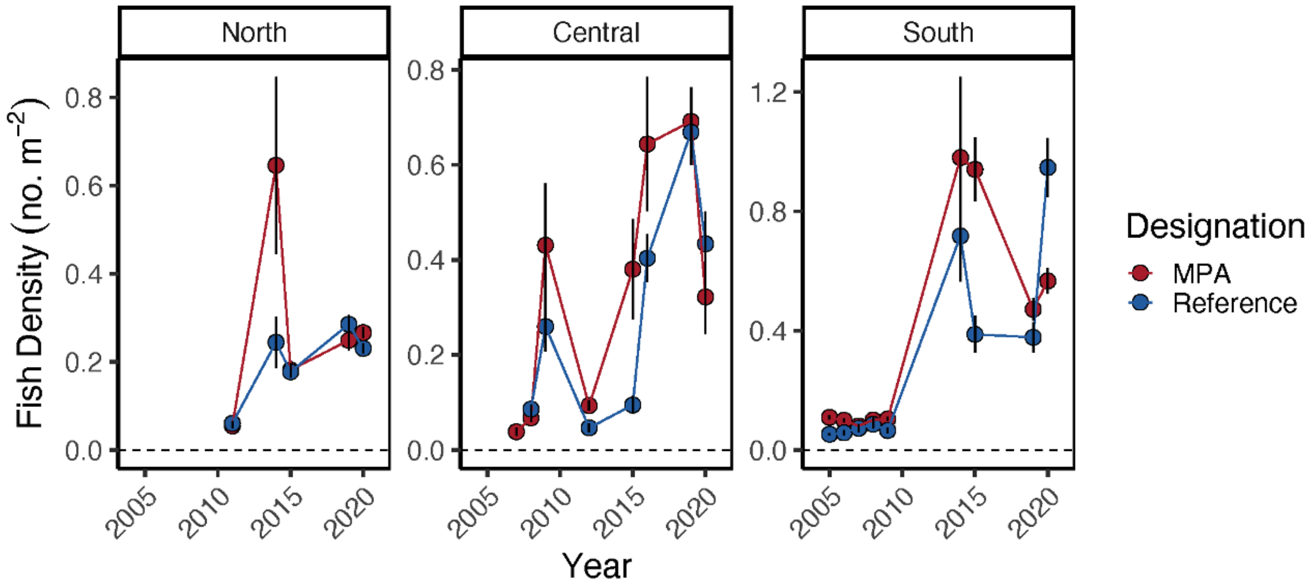


Figure 26. Trends in total density (no. m-^{2}) for all MPAs combine within a region for MPAs sampled for 3 or more years at both MPA and Reference sites.

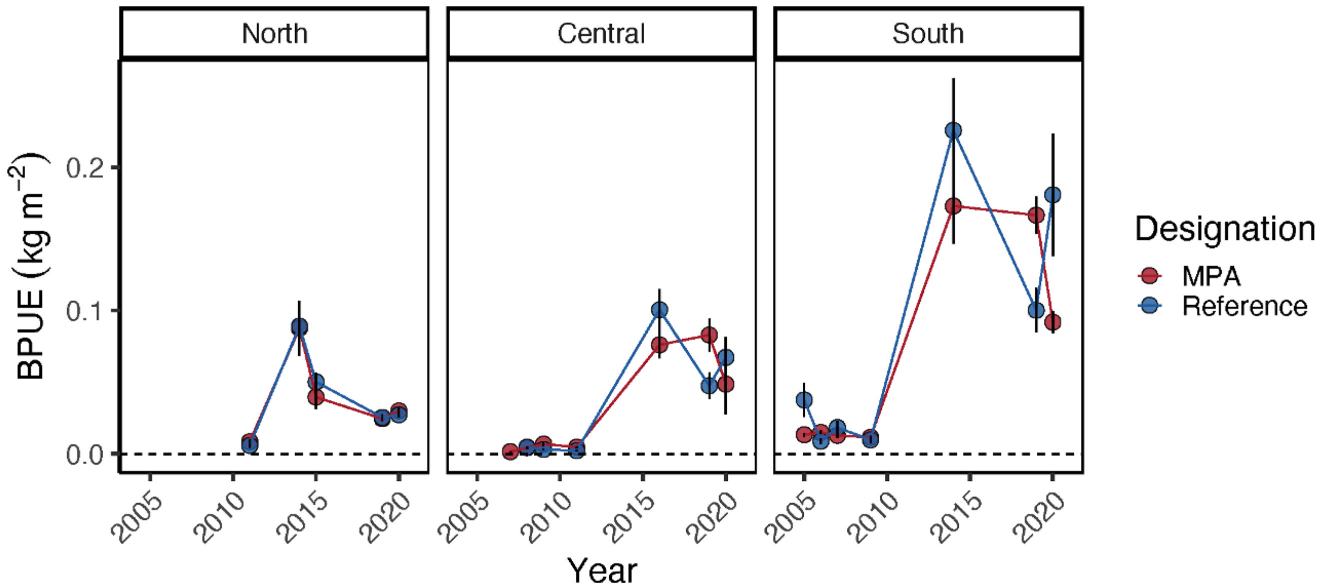


Figure 27. Trends in total biomass (kg m^{-2}) for all MPAs combined within a region and each individual MPA sampled for 3 or more years at both MPA and Reference sites.

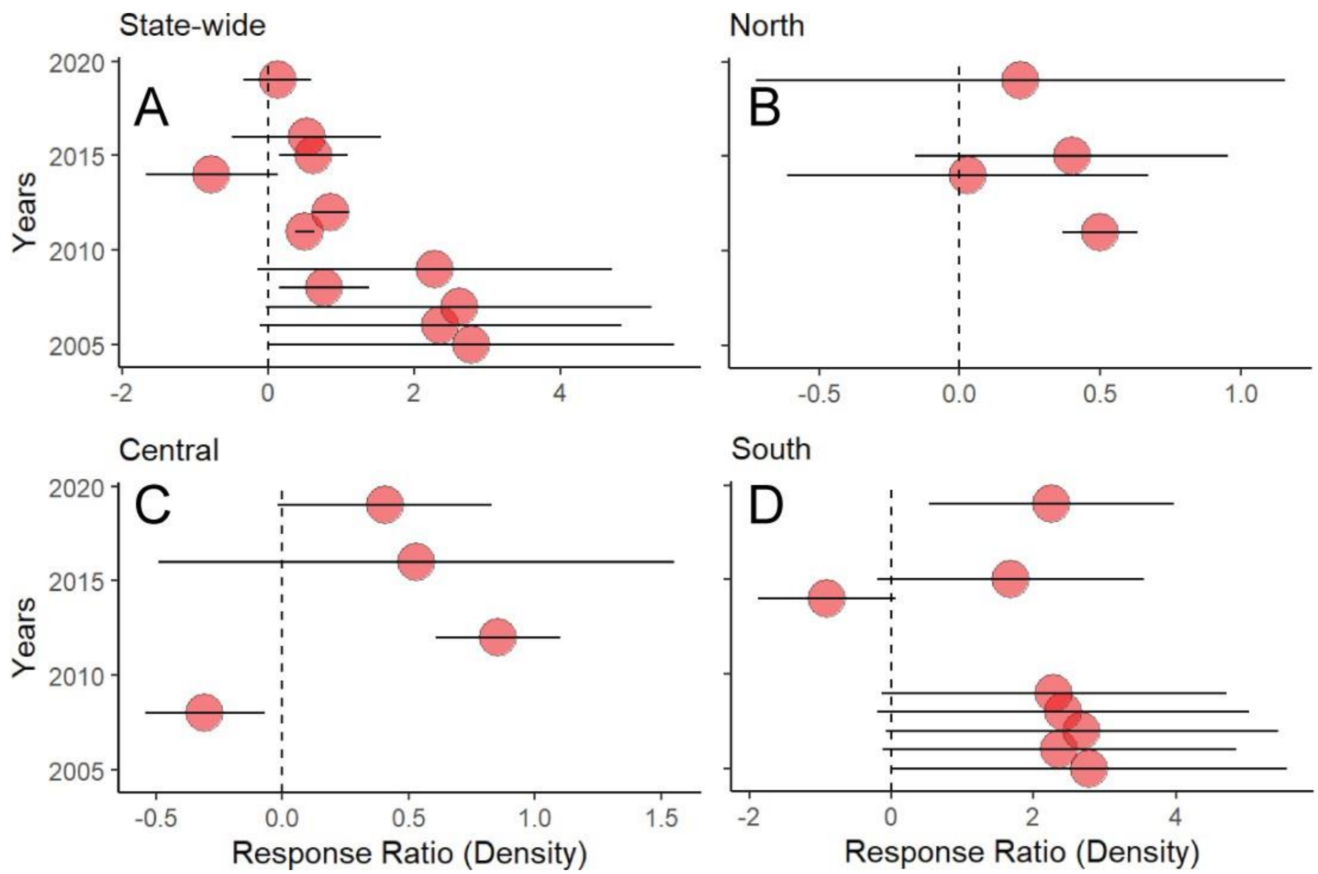


Figure 28. Response ratios (Mean ± SE) for corals over time from 2005–2019. Positive ratios indicate that populations were denser within MPAs compared to corresponding Reference sites. Responses varied by region and are plotted here for A) statewide, B) Northern, C) Central, and D) Southern California MPAs.

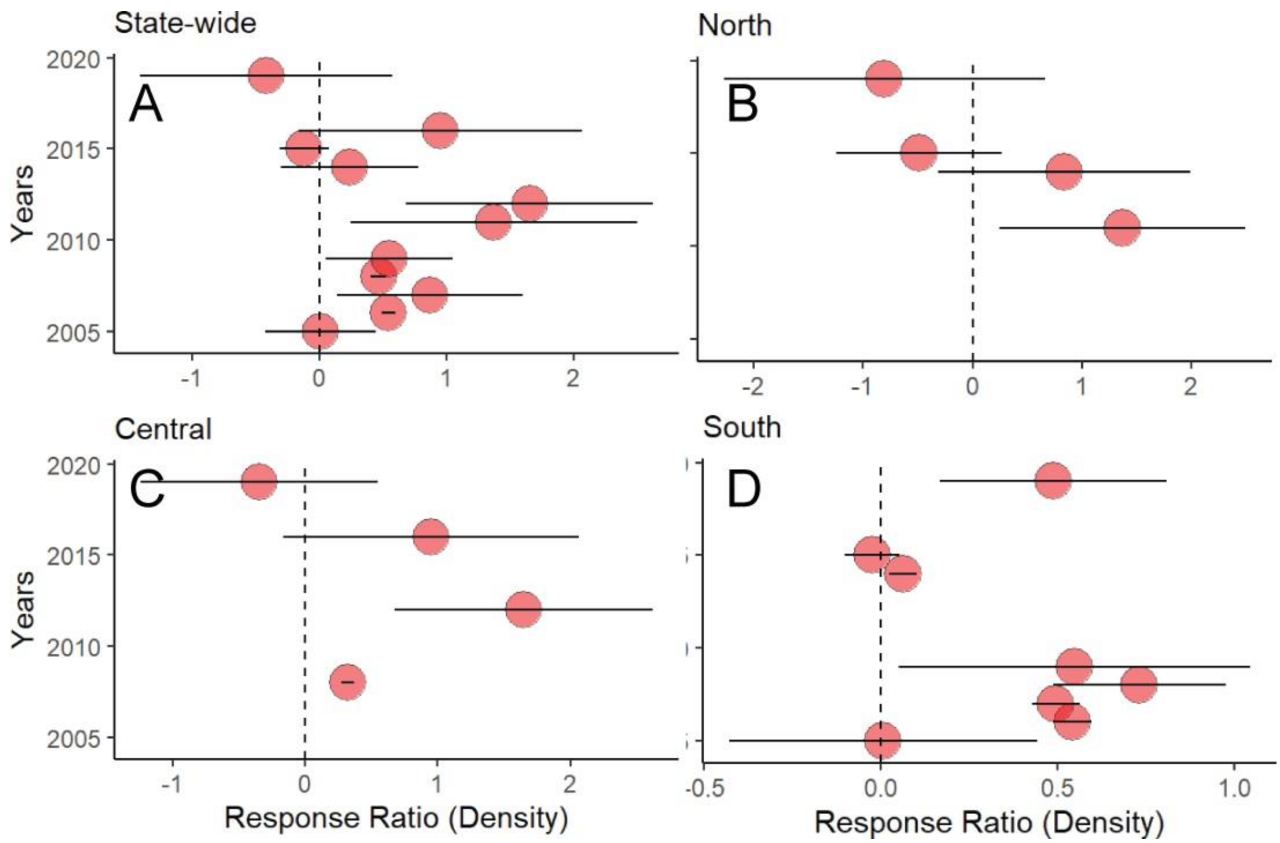


Figure 29. Response ratios (Mean ± SE) for sponges (Phylum Porifera) over time from 2005 to 2019. Positive ratios indicate that populations were denser within MPAs compared to corresponding Reference sites. Responsesvaried by region and are plotted here for A) statewide, B) Northern, C) Central, and D) Southern California MPAs.

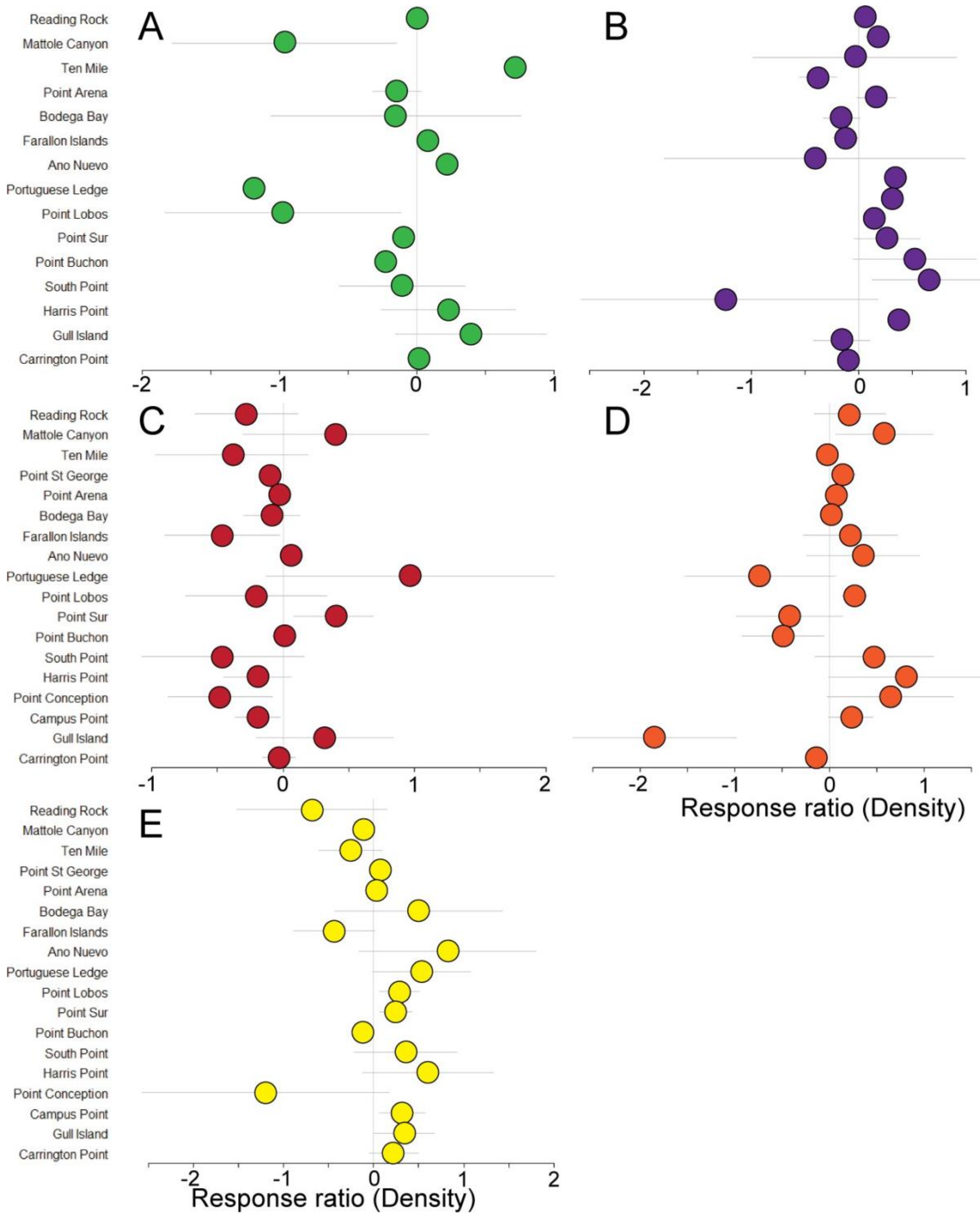


Figure 30. Response ratios (Mean ± SE) for densities of different functional groups of benthic invertebrates observed in ROV surveys of deepwater MPAs from 2005–2016. Feeding functional groups assessed were A) herbivores, B) scavengers, C) mobile predators, D) sessile predators, and E) suspension feeders.

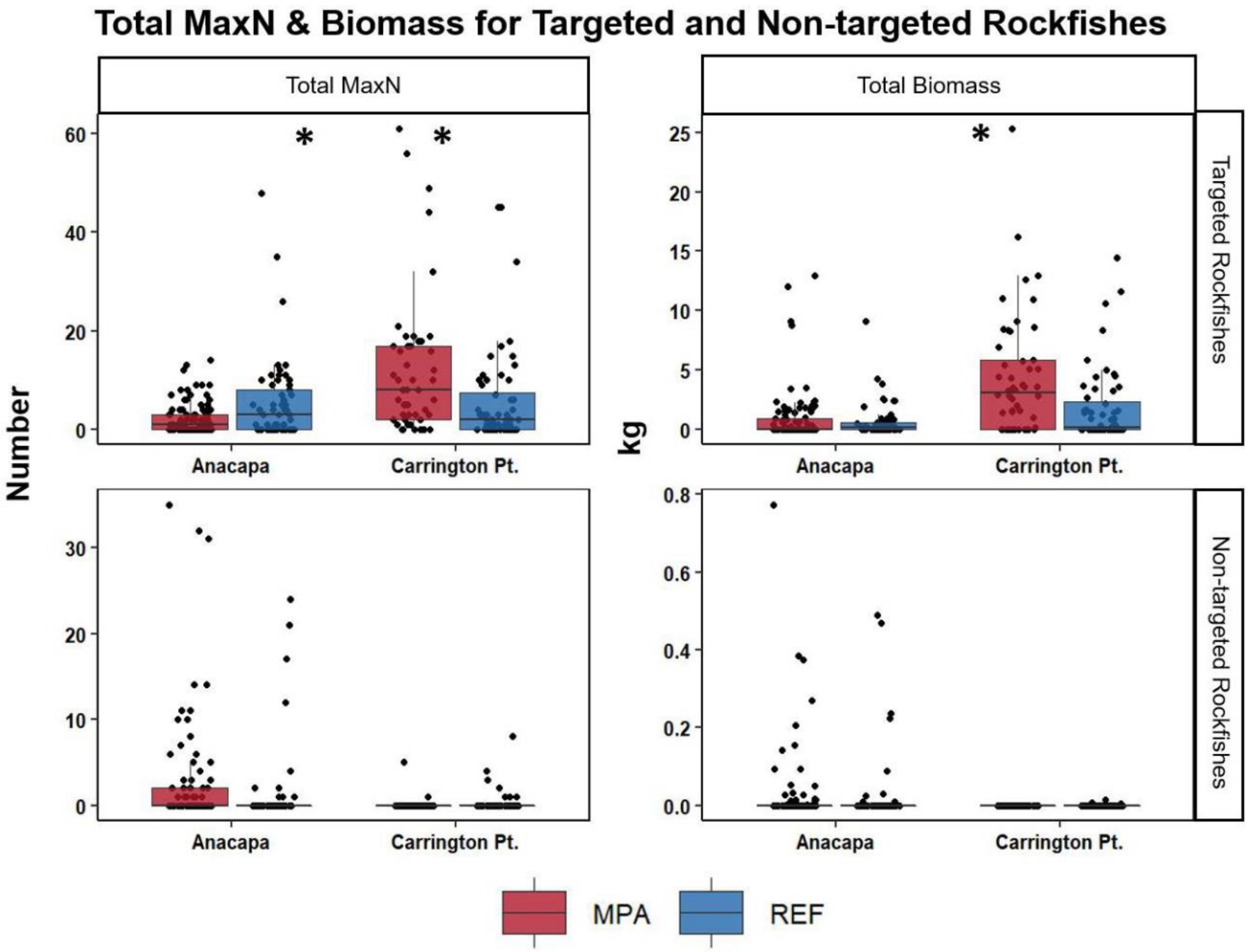


Figure 31. Summed MaxN and Total Biomass (kg) for targeted and non-targeted rockfishes (genus Sebastes). Upper and lower portions of the boxplot represent 1st and 3rd quartiles of the data and thepoints represent the observed values. * represents a significance level of ≤ 0.05.

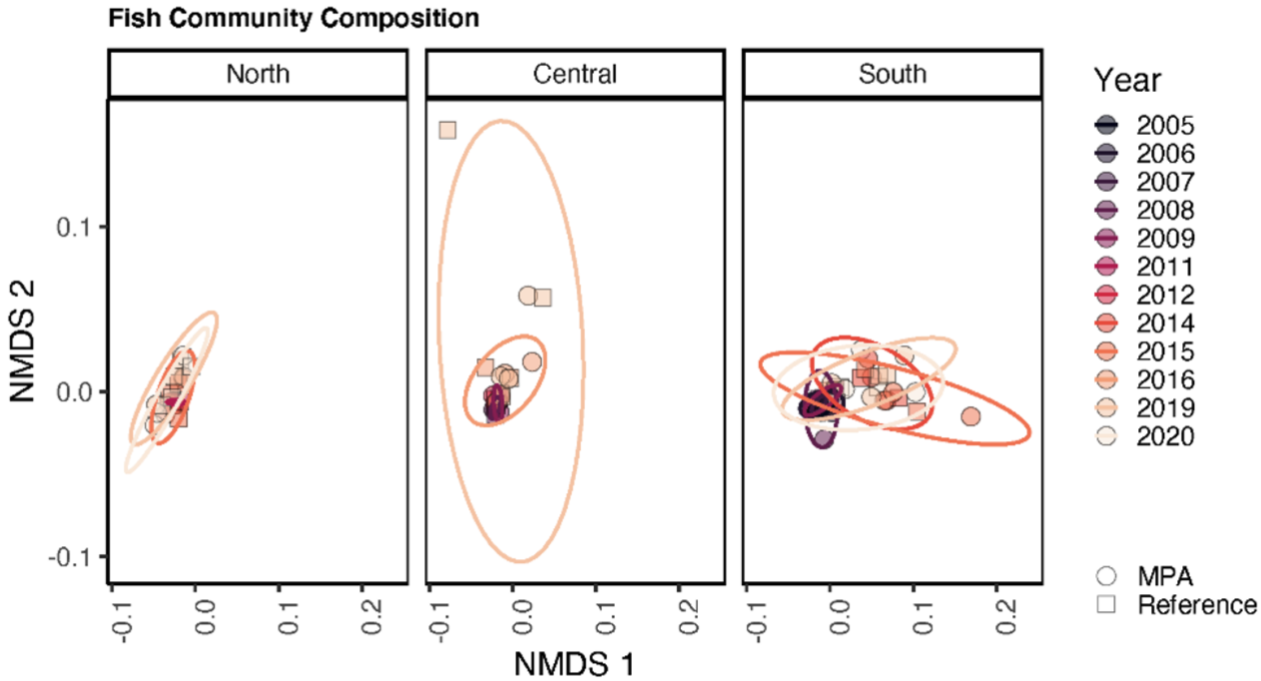


Figure 32. A three-way interactive permutational analysis of variance (PERMANOVA) and a non-metric multidimensional scaling ordination (NMDS) to determine if community composition differed across MPAs and Reference sites, across years, and among regions.

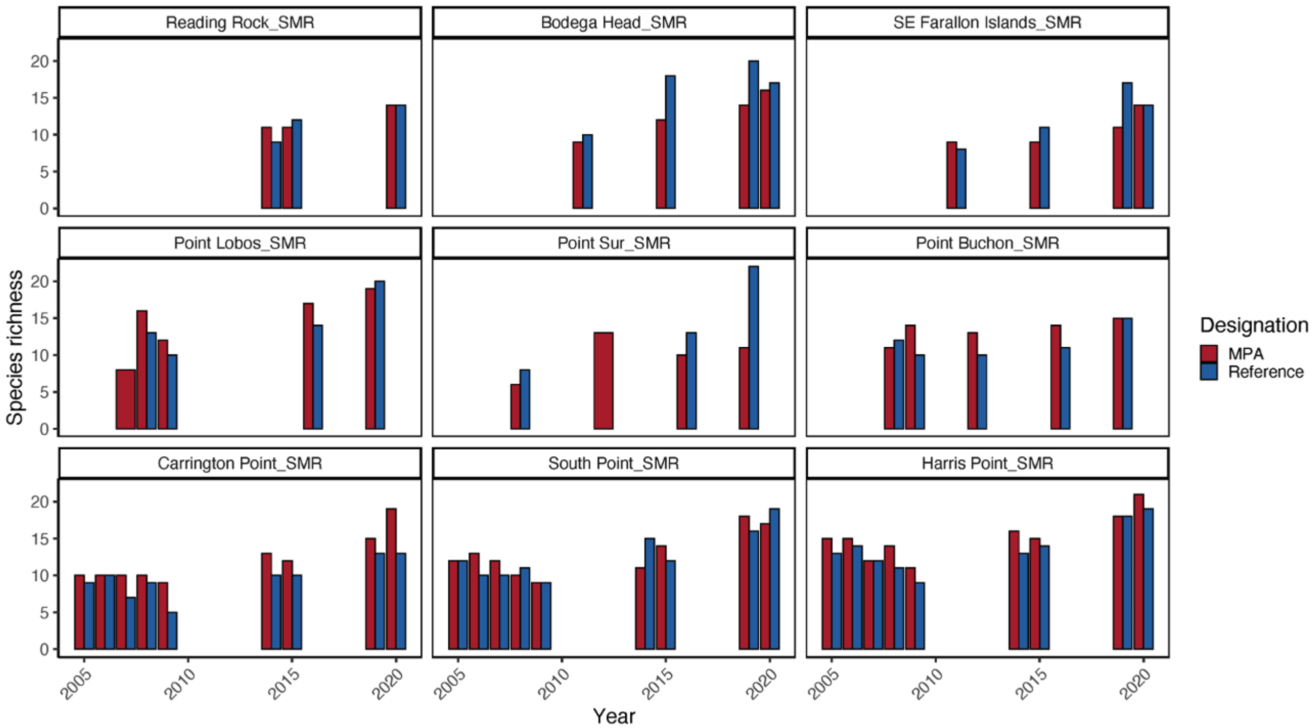


Figure 33. Species richness from ROV surveys across all MPAs ranged from an anomalously low 6 species at Point Sur SMR in 2008 to 21 species at Harris Point SMR in 2020. Overall, there was no difference in species richness through time for MPAs or associated Reference sites, with the exception of the Reference sites at both Bodega Head SMR and Point Sur SMR.

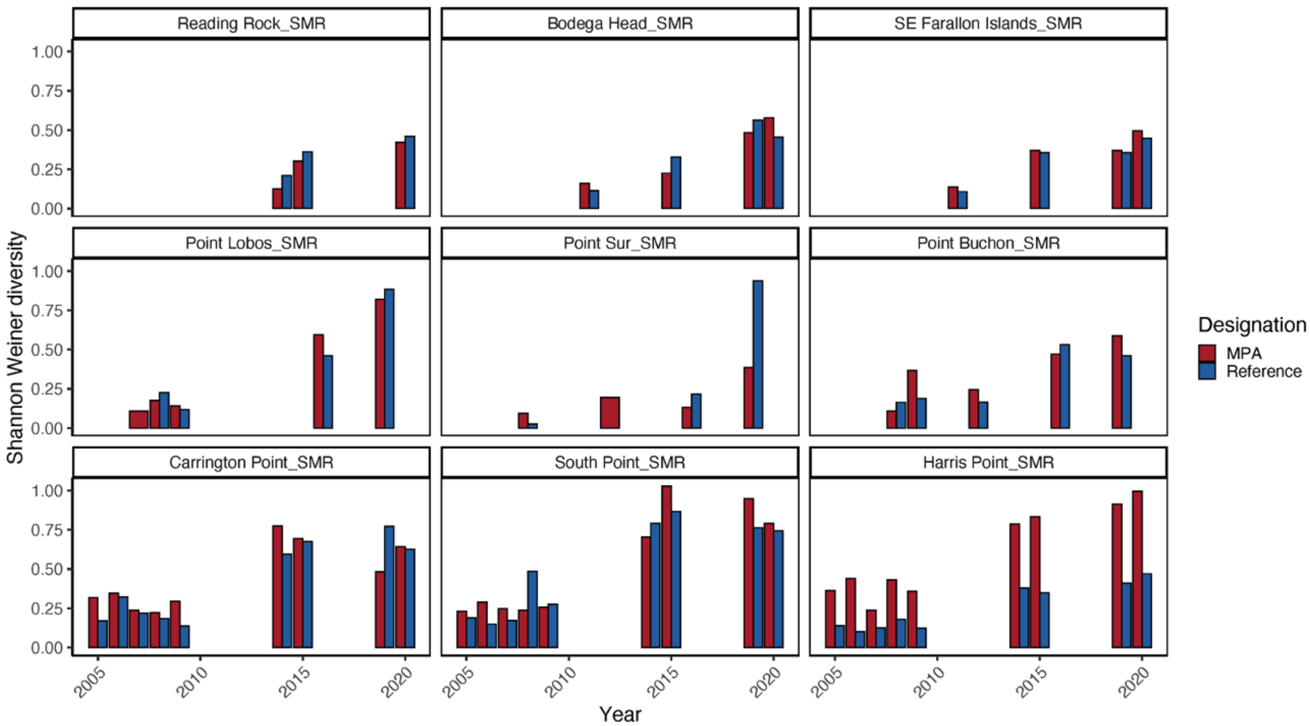


Figure 34. Shannon diversity index obtained from ROV fish surveys differed slightly from species richness and ranged from 0.093 at Point Sur in 2008 to 1.03 at South Point SMR in 2015. There were increases in diversity through time for all sites both inside the MPA and in associated References.

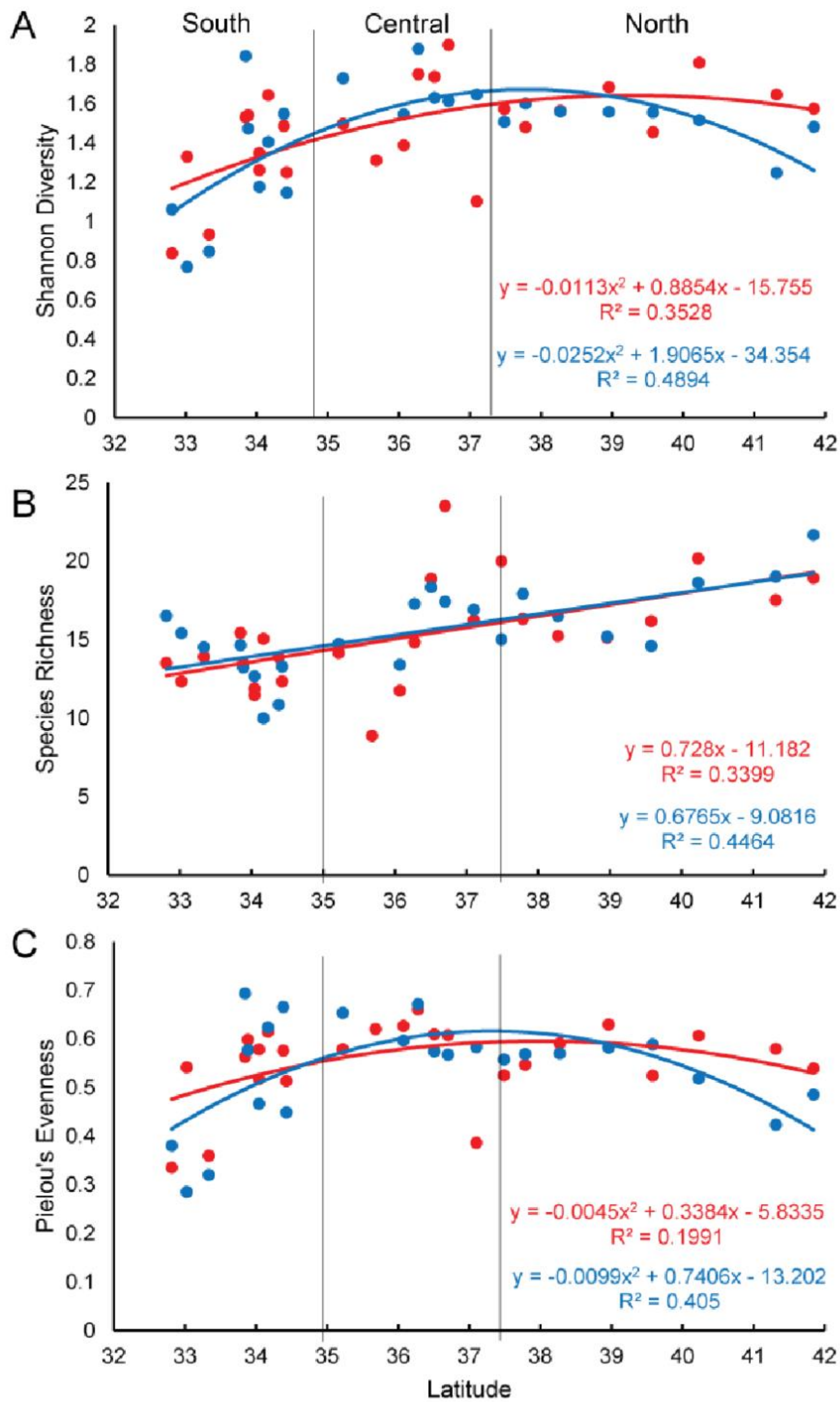


Figure 35. Species diversity (A), richness (B), and evenness (C) at different latitudes along the California coast for all years of ROV sampling at MPA locations (red) and Reference sites (blue). Trendlines were plotted for all MPAs across different latitudes (blue) and Reference sites (red).

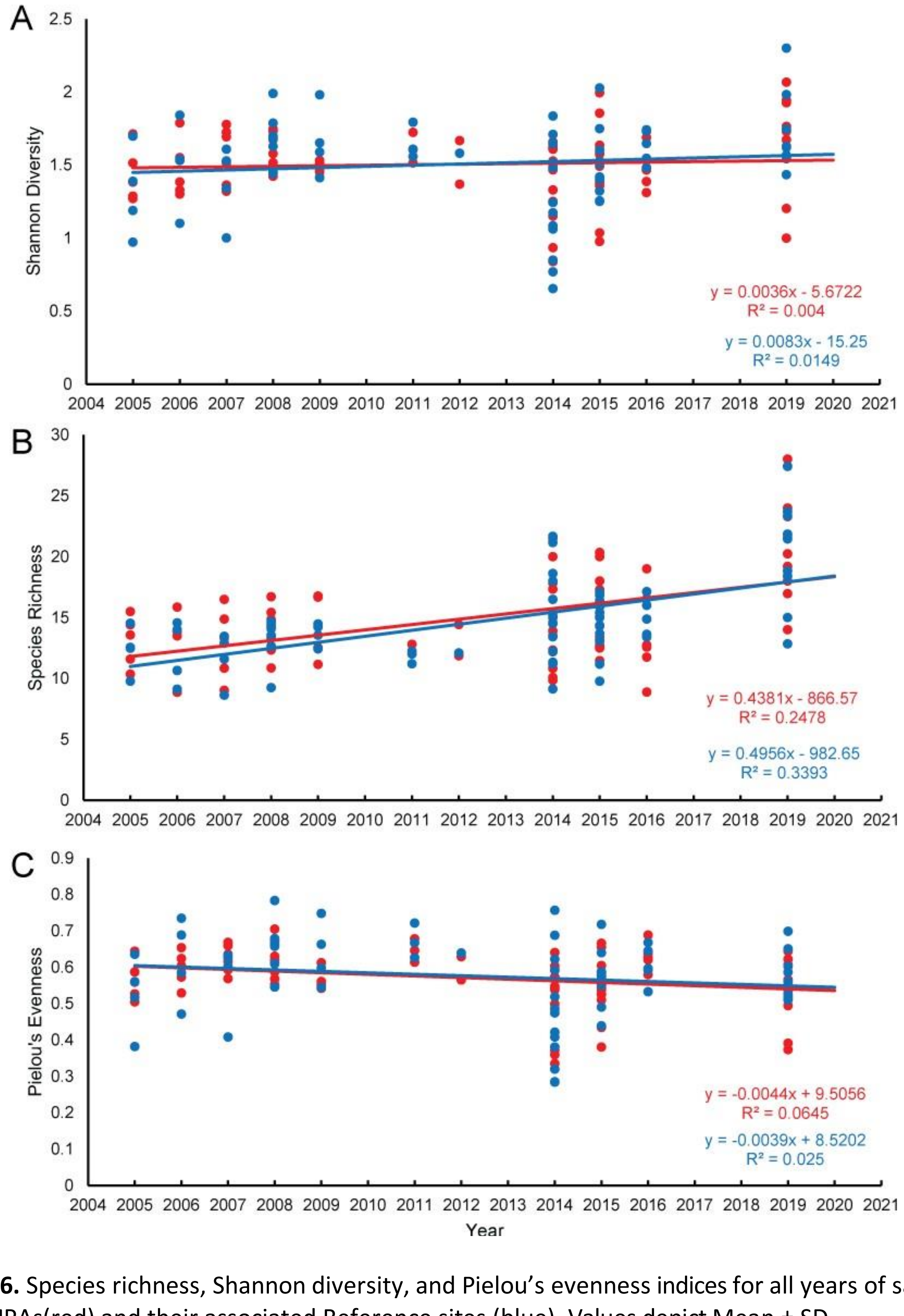


Figure 36. Species richness, Shannon diversity, and Pielou's evenness indices for all years of sampling for all MPAs(red) and their associated Reference sites (blue). Values depict Mean ± SD.

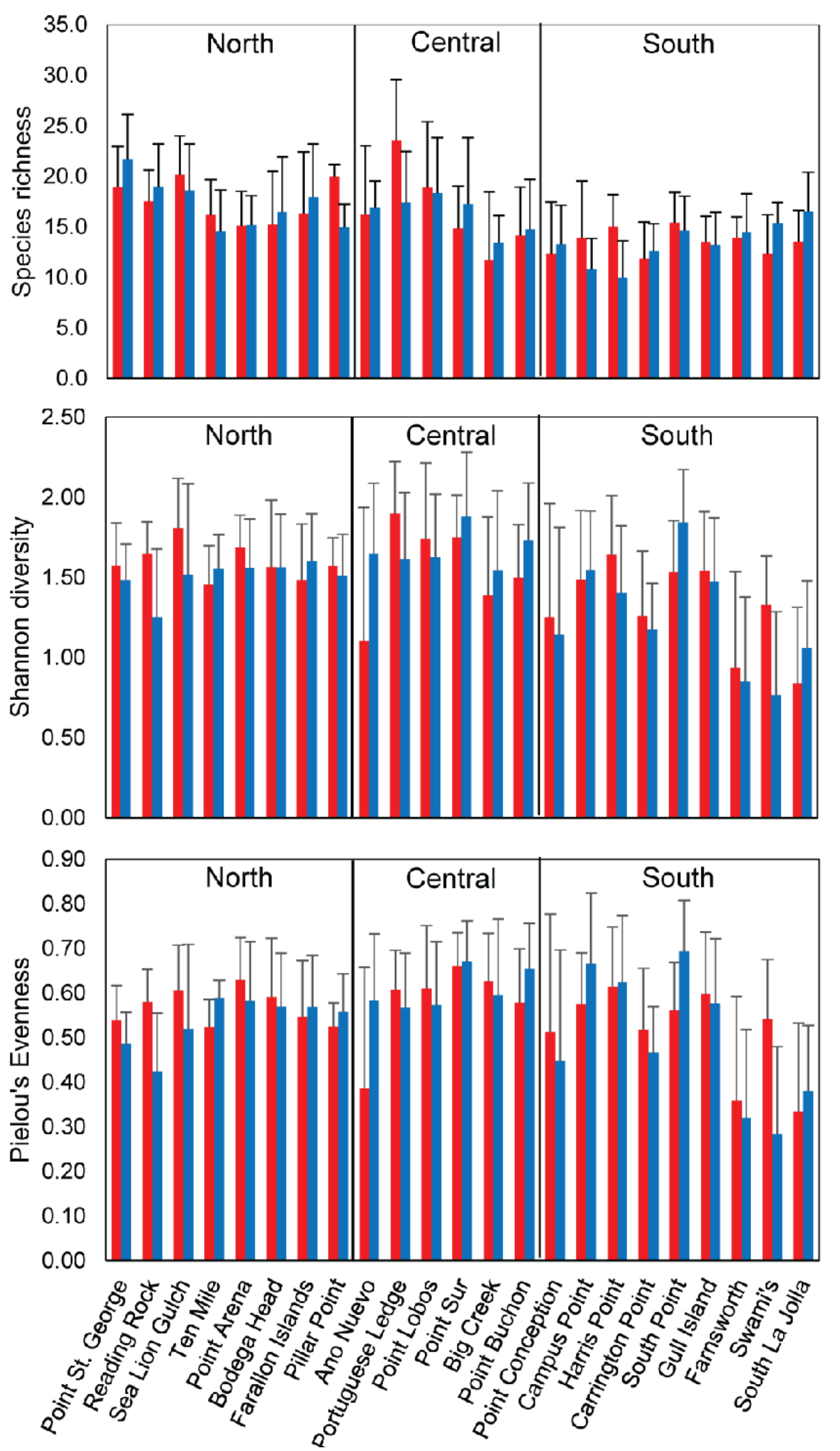


Figure 37. Species richness, Shannon diversity, and Pielou's evenness for all years of sampling at eachMPA locations (red) and their associated Reference sites (blue). Values depict Mean ± SD.

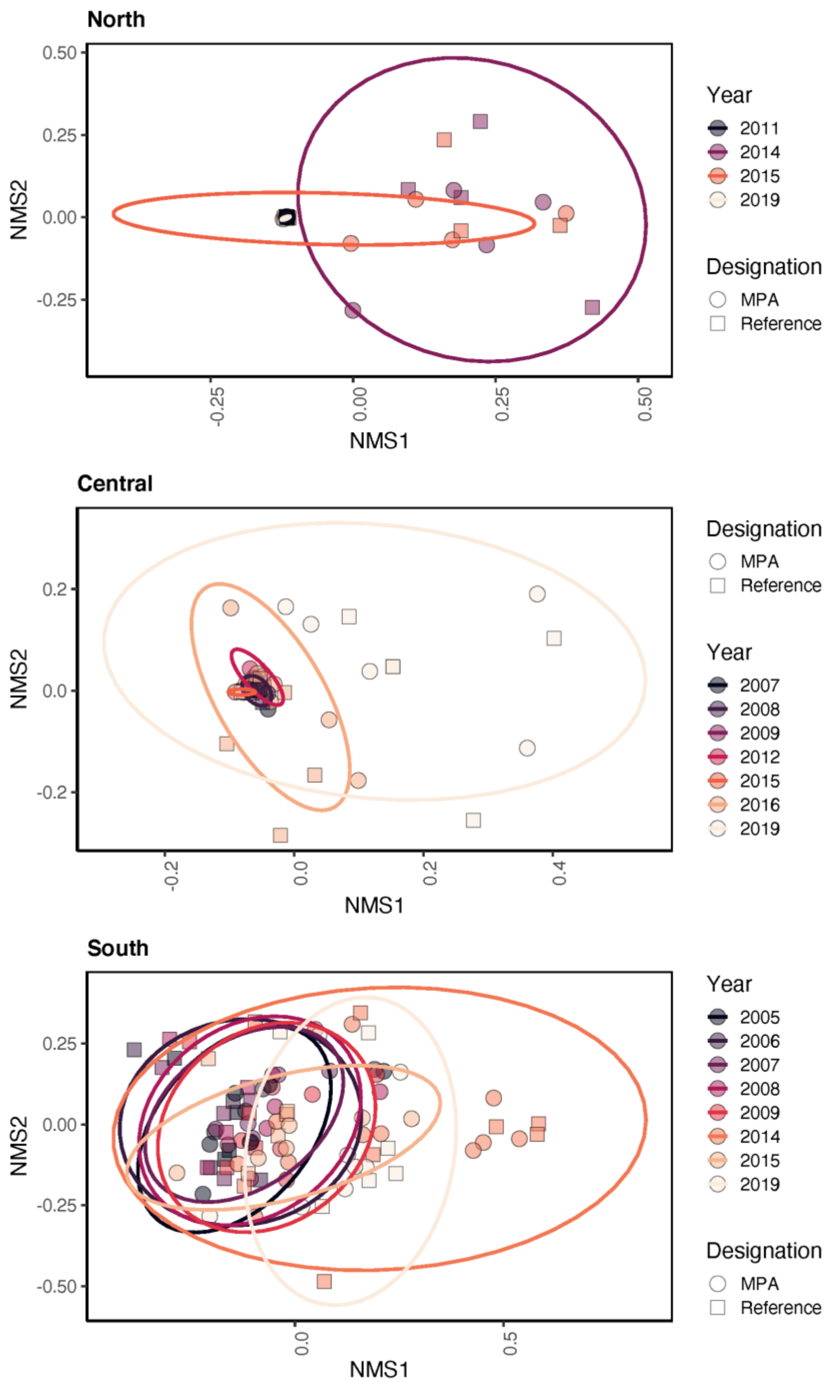


Figure 38. NMDS plot depicting fish and invertebrate community compositions in Northern, Central, andSouthern California by year for MPAs (circles) and associated Reference areas (squares). All three regions show shifts in community composition after the 2014–2016 marine heatwave. Ellipses represent 95% confidence intervals.

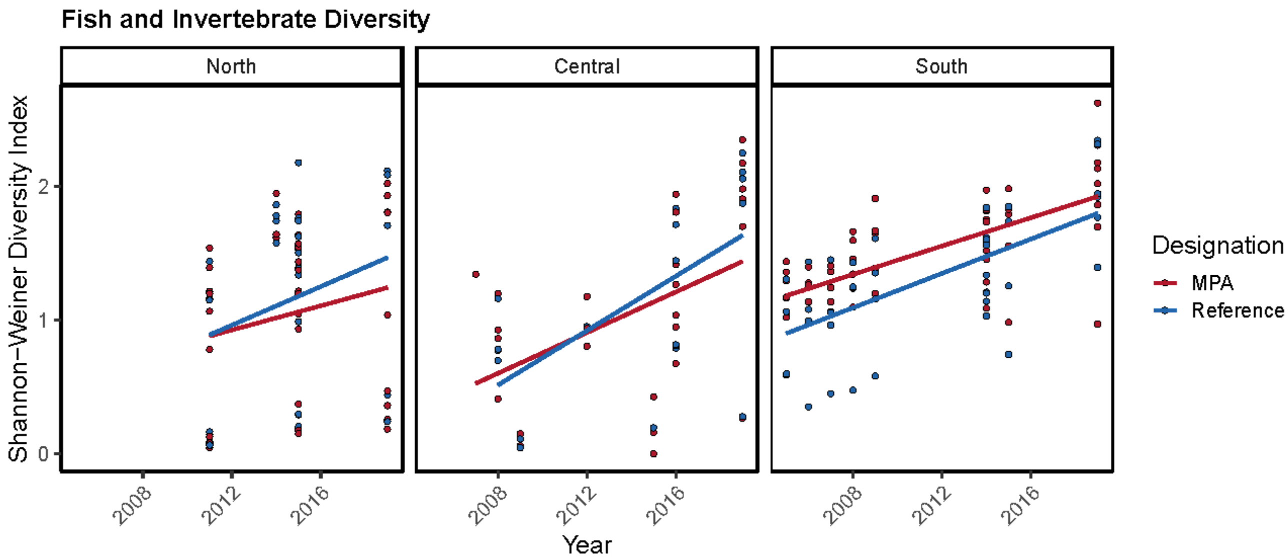


Figure 39. Shannon-Weiner diversity indices for fish and invertebrates in Northern, Central and Southern California, by year for MPAs (red) and associated Reference sites (blue). Across all regions fish and invertebrate diversity increased through time in both the MPAs and Reference sites.

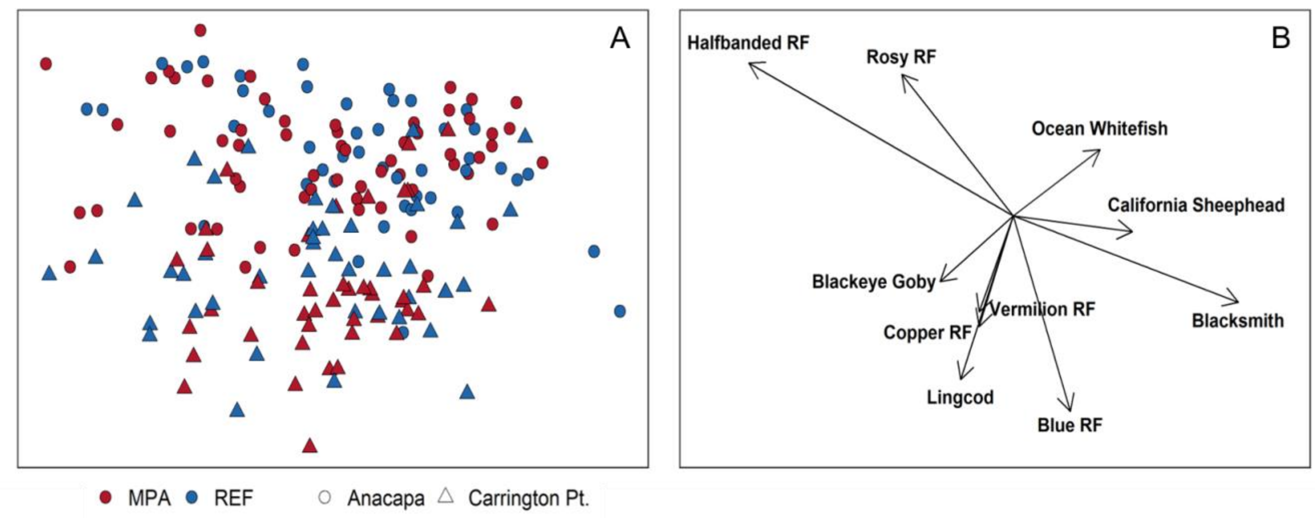


Figure 40. Non-metric multidimensional scaling (NMDS) plot showing the position of each survey in multidimensional space. Circles indicate BRUV surveys from Anacapa, while triangles represent surveys from Carrington Pt. Red symbols represent surveys within the MPA and blue represent surveys from the Reference area. B. Vector diagram showing the relative strength and direction for the top ten species that were responsible for 75% of the cumulative dissimilarity between Anacapa and Carrington Pt. 'RF'stands for rockfish.

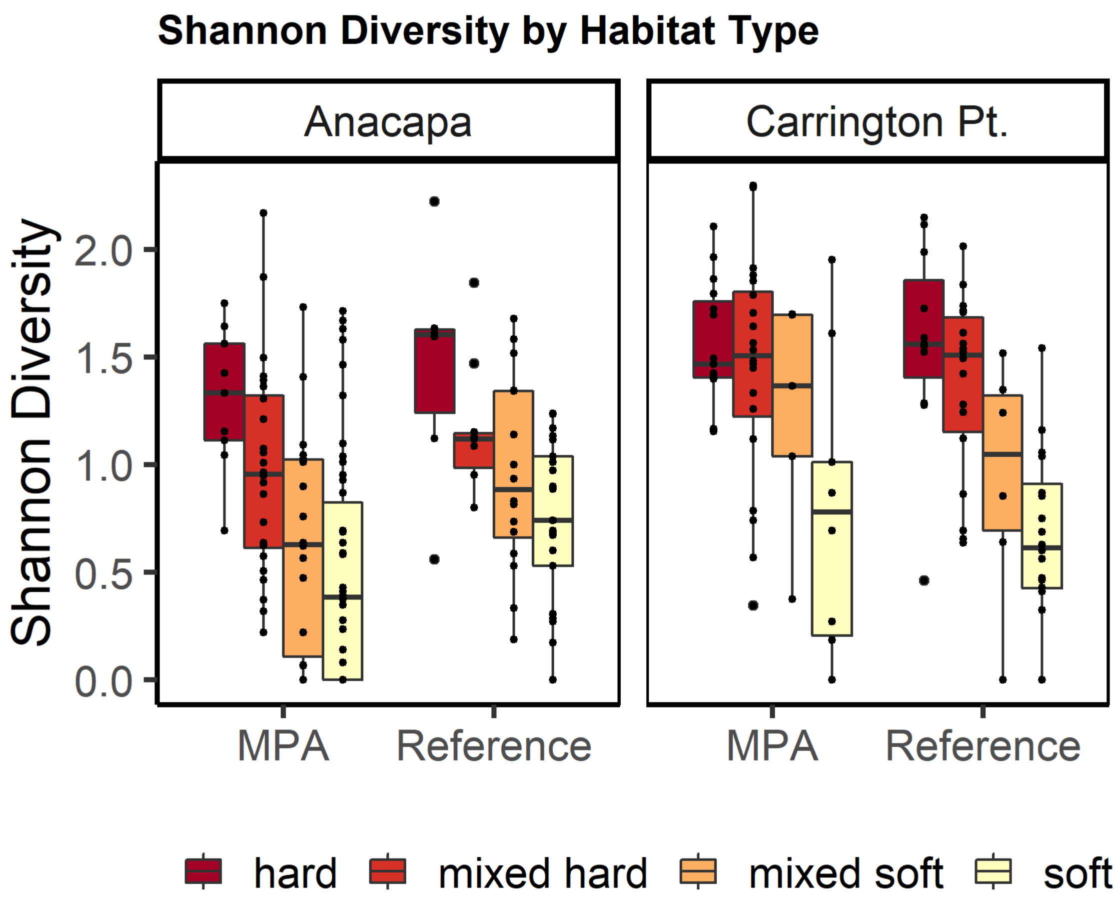


Figure 41. Shannon diversity indices grouped by habitat classification at fished and un-fished areas at Anacapa and Carrington Pt.

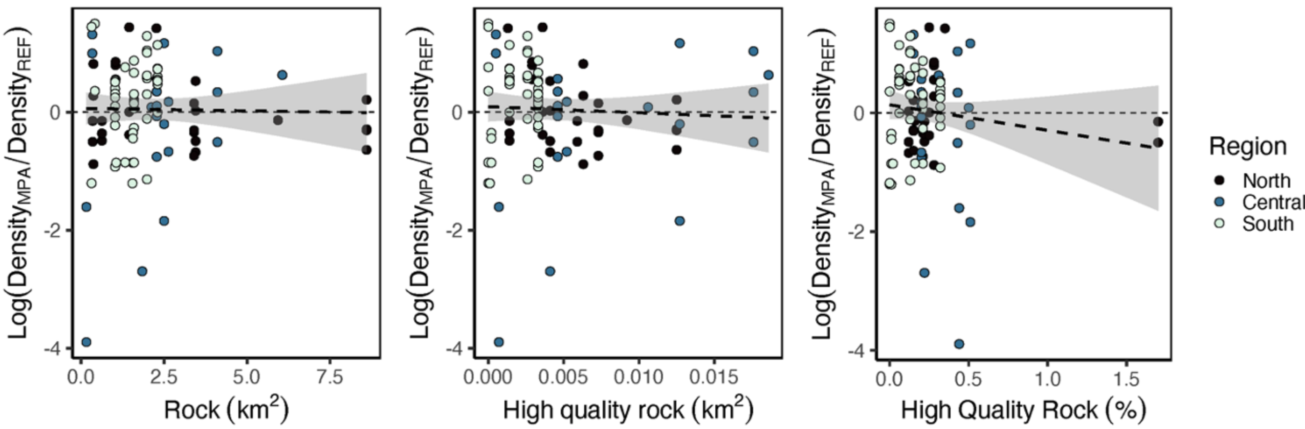


Figure 42. Total density response ratios across all years sampled and response ratios of focal species in relation to the amount of rocky habitat (km^2), high-quality rock habitat (km^2) and the percent of high-quality rock (%) inside each MPA.

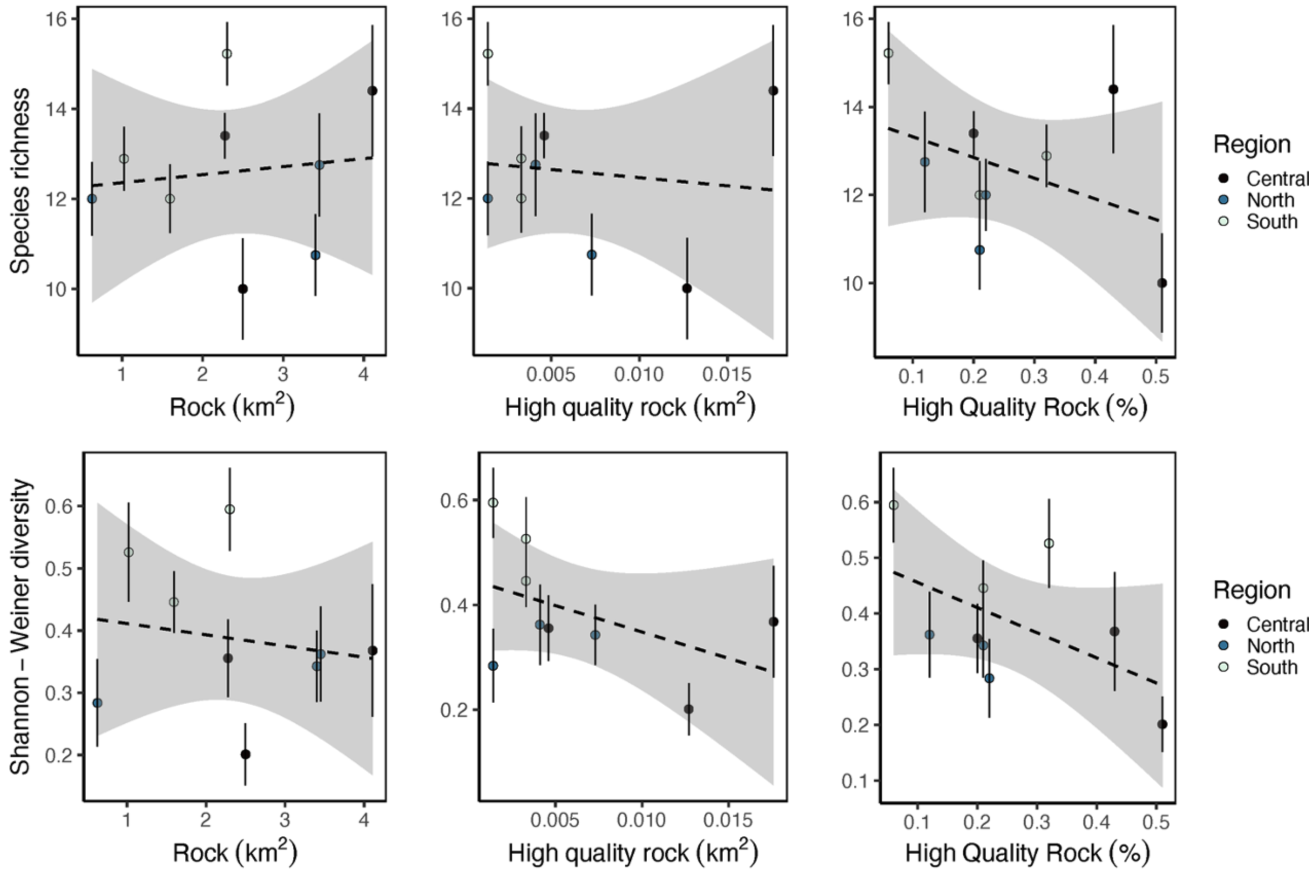


Figure 43. 9 sites spanning the entire coast of California (Reading Rock SMR, Bodega Head SMR, SE Farallon Islands SMR, Point Lobos SMR, Point Sur SMR, Point Buchon SMR, Carrington Point SMR, Harris Point SMR and South Point SMR), were examined for how species richness and Shannon-Weiner diversity related to the amount of rocky habitat (km^2), high-quality rock habitat (km^2) and the percent of high-quality rock (%) inside each MPA.

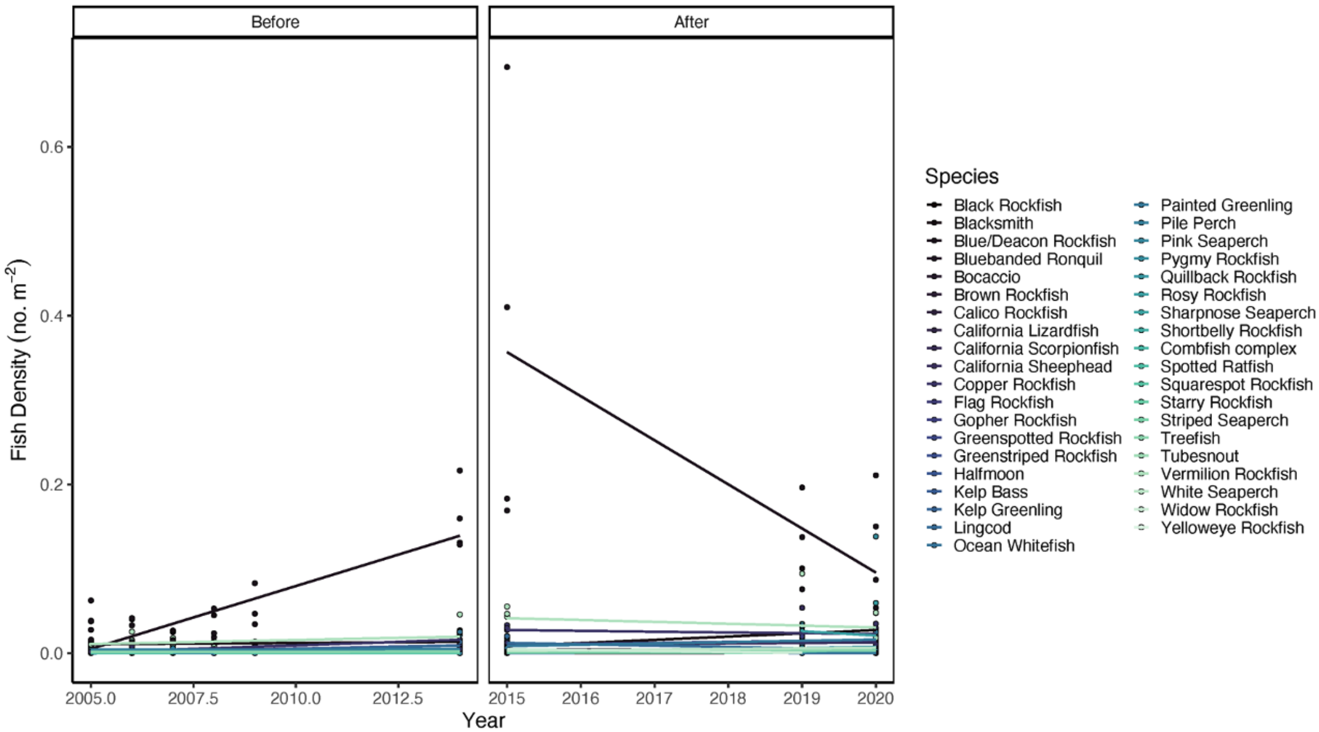


Figure 44a. Changes in slope of densities in MPAs before and after the marine heatwave (2014–2016) for all species observed in ROV surveys.

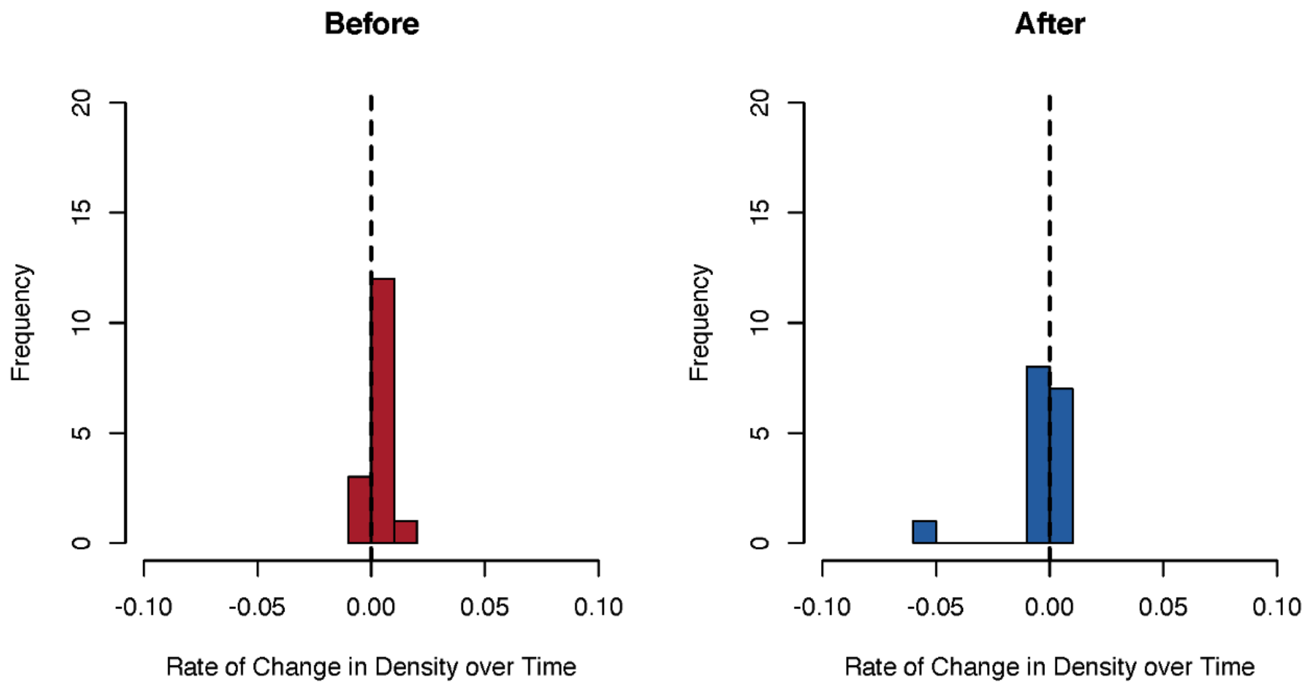


Figure 44b. Following the marine heatwave (2014–2016), only 7 of 16 species showed positive slopes in density, and 9 of the species that initially displayed increasing densities showed negative slopes following the heatwave.

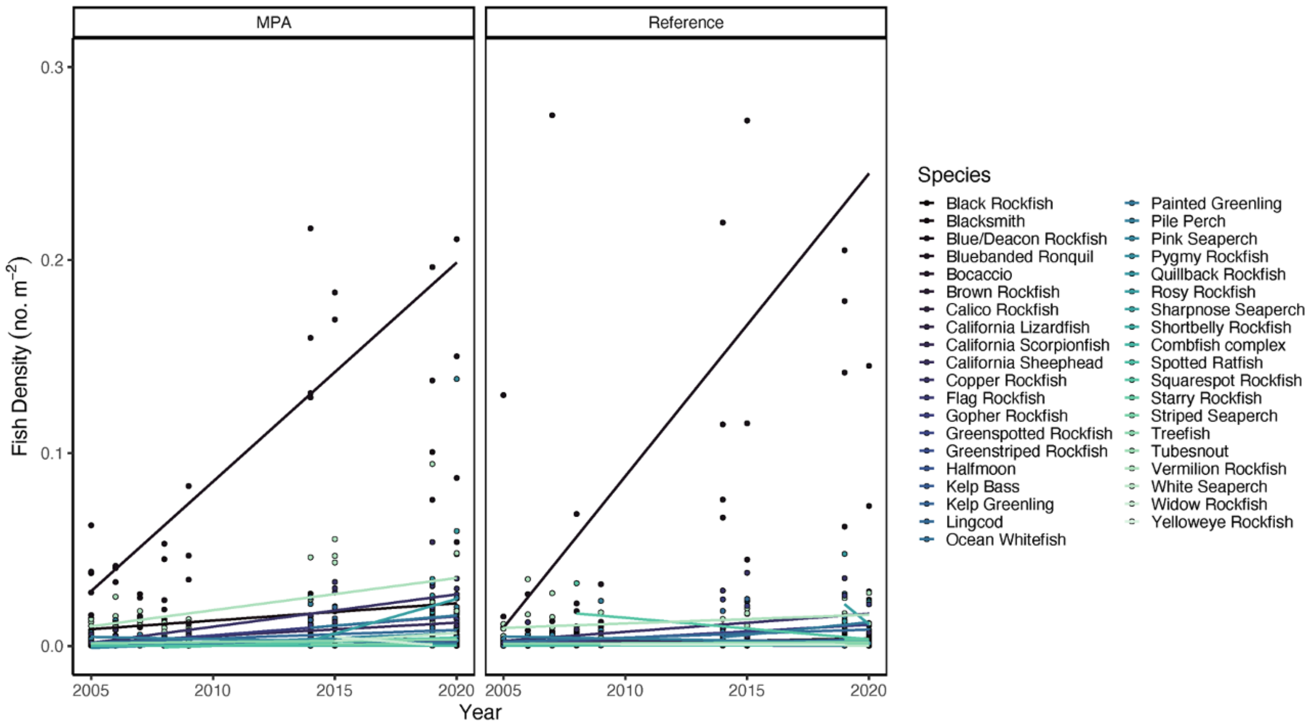


Figure 45a. Response rates, as defined by changes in fish density from ROV surveys, for individual species in the Channel Islands MPAs (South Point, Harris Point. Carrington Point and Gull Island SMRs) and associated Reference sites.

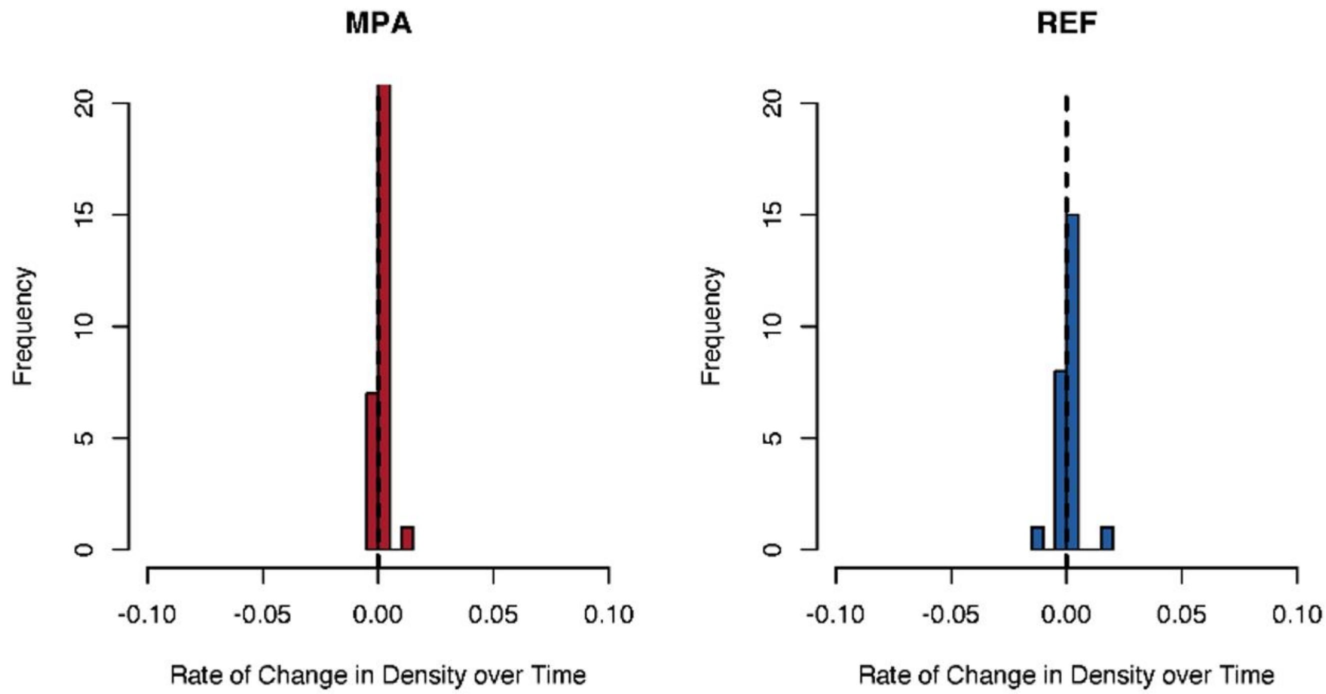


Figure 45b. Frequency histogram of changes in density over time among species in MPA and Reference sites.

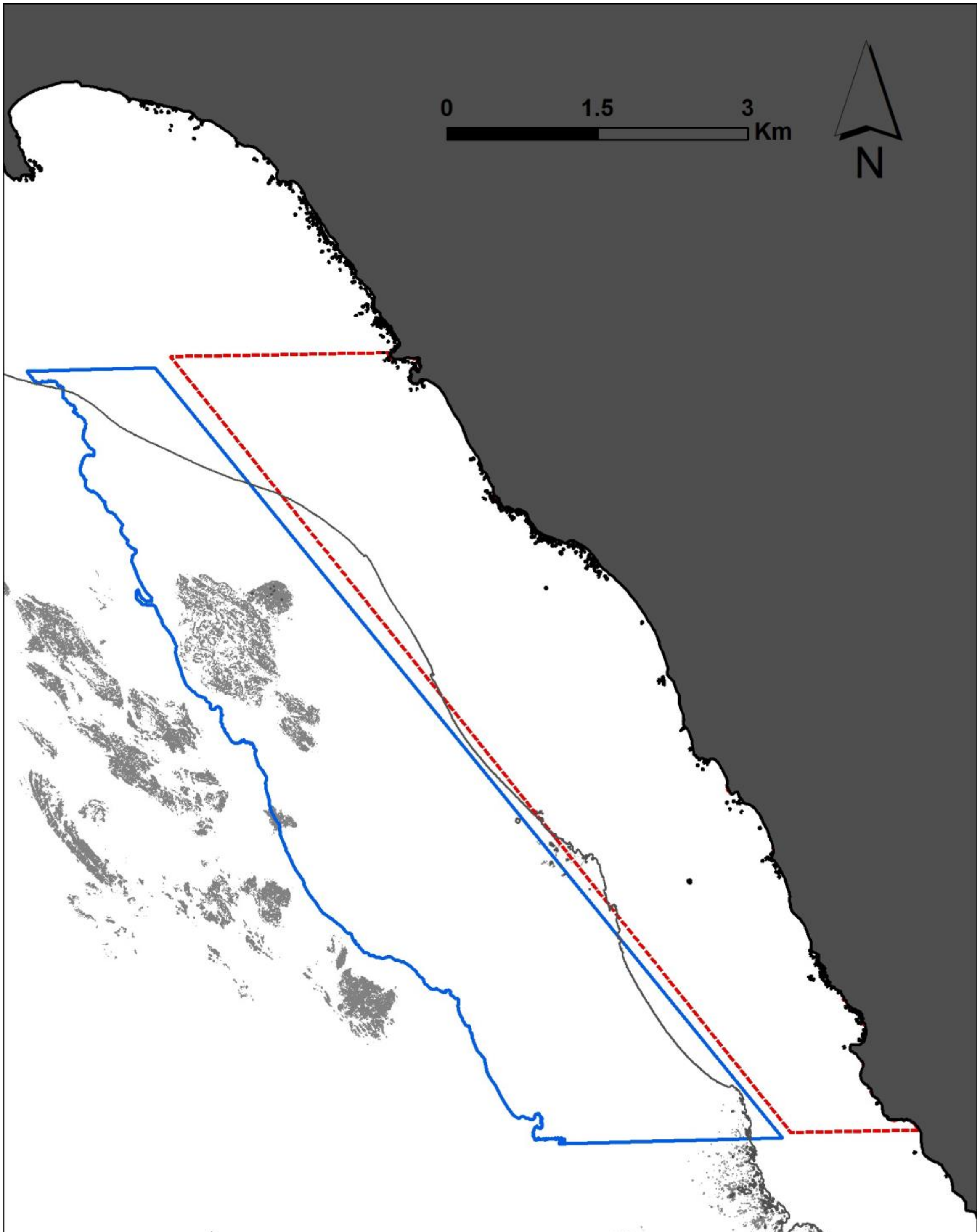


Figure 46. Map of the Cambria SMCA (red dotted line) and surrounding vicinity. Included is the area of rocky reef (dark grey) and high-quality habitat (black), as well as the 30–100m isobaths

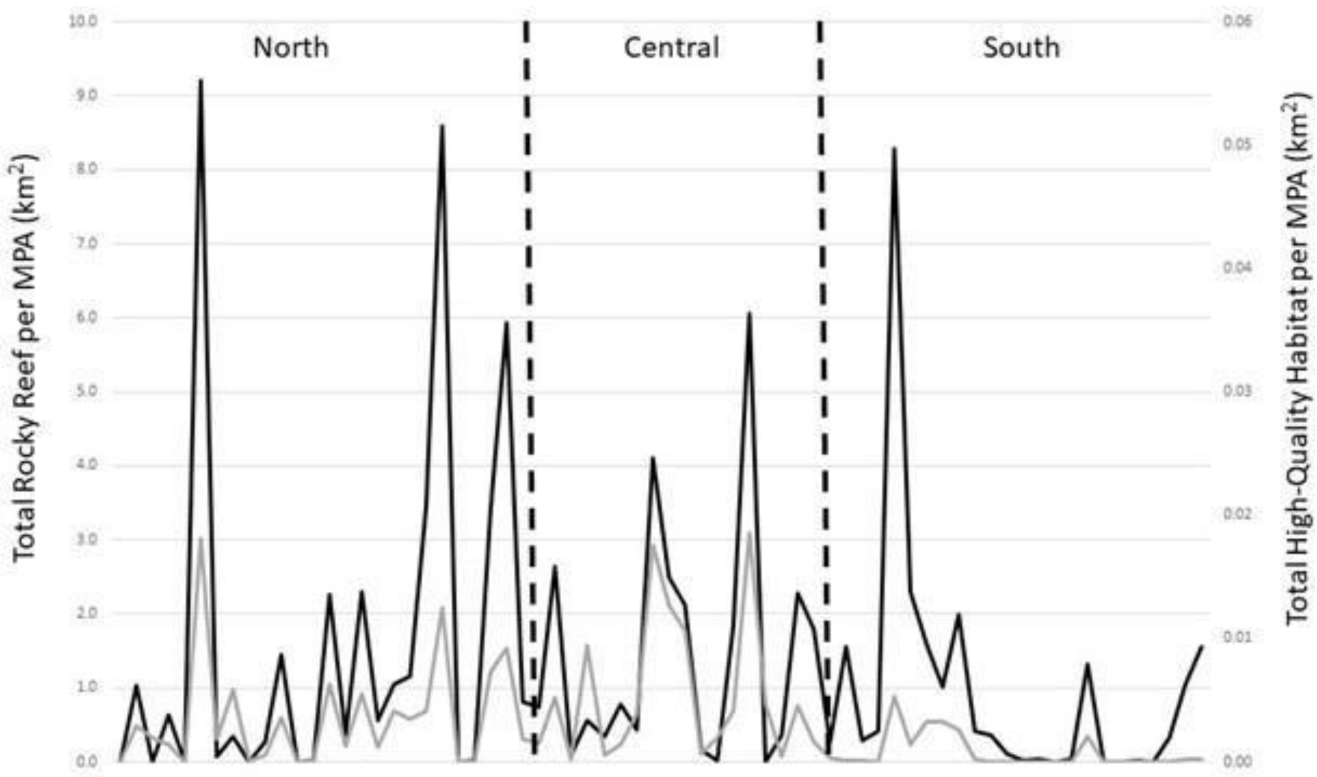


Figure 47. Latitudinal distribution of the total amount of rocky reef per MPA in km^2 (black line) and total amount of high-quality habitat per MPA in km^2 (grey).

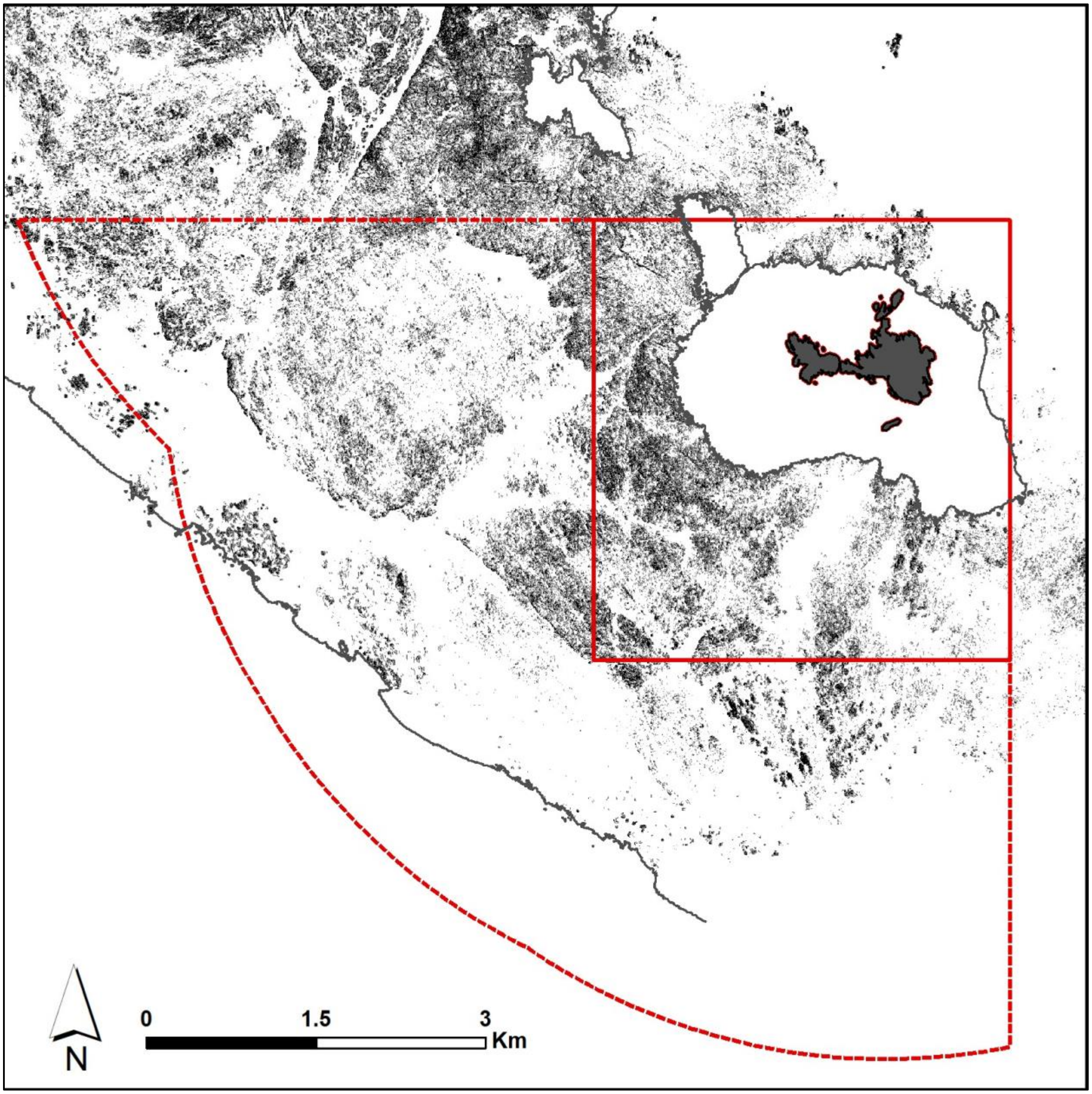


Figure 48. Map of the MPAs at Southeast Farallon Island, including the total rocky reef within the 30–100 m isobaths (grey), and high-quality habitat (black). The percentage of high-quality habitat is slightly higher in the SMR (red line) when compared to the SMCA (red dotted line).

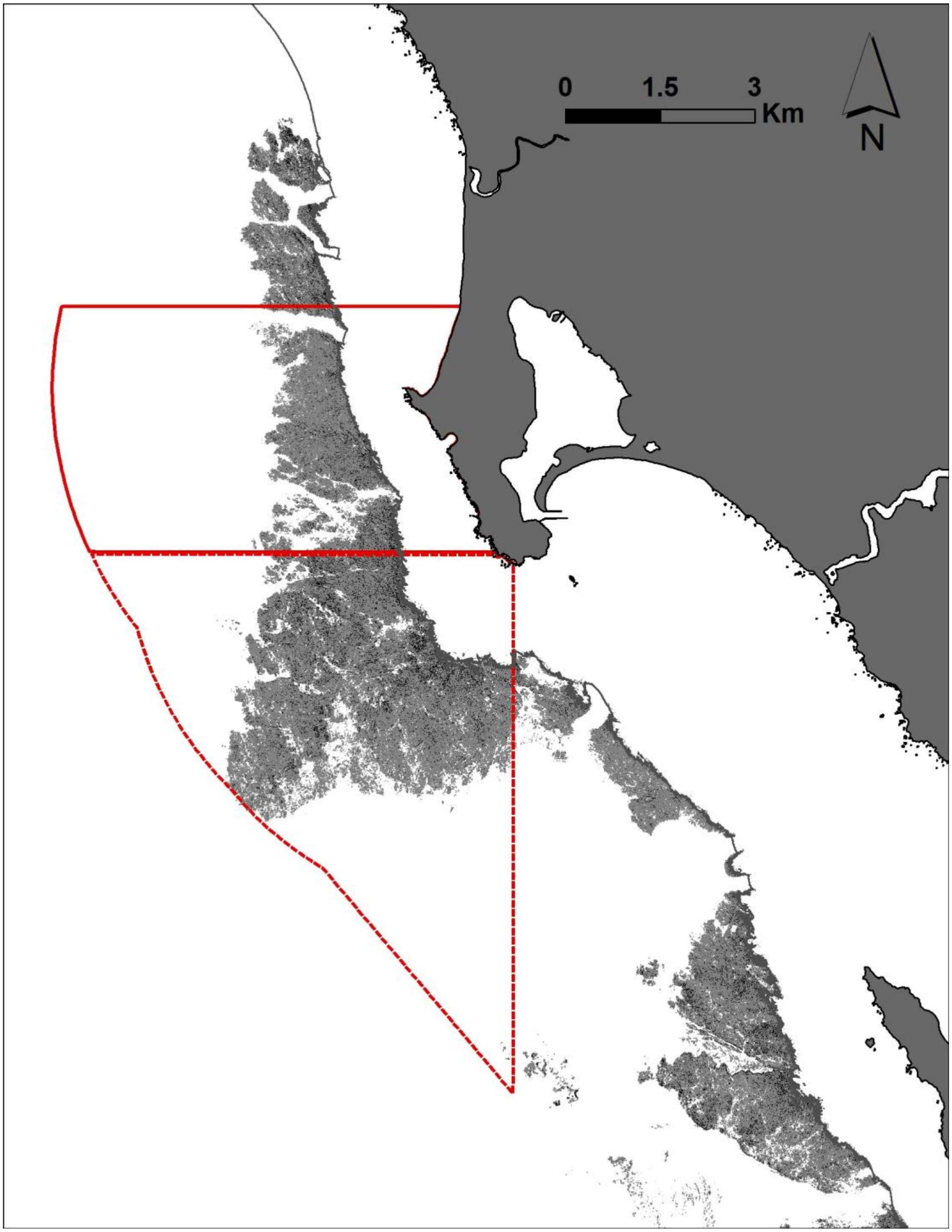


Figure 49. Map of the MPAs at Bodega Head, including the total rocky reef within the 30–100 m isobaths(grey), and high-quality habitat (black). The percentage of high-quality habitat is slightly higher in the SMCA (red dotted line) when compared to the SMR (red line).

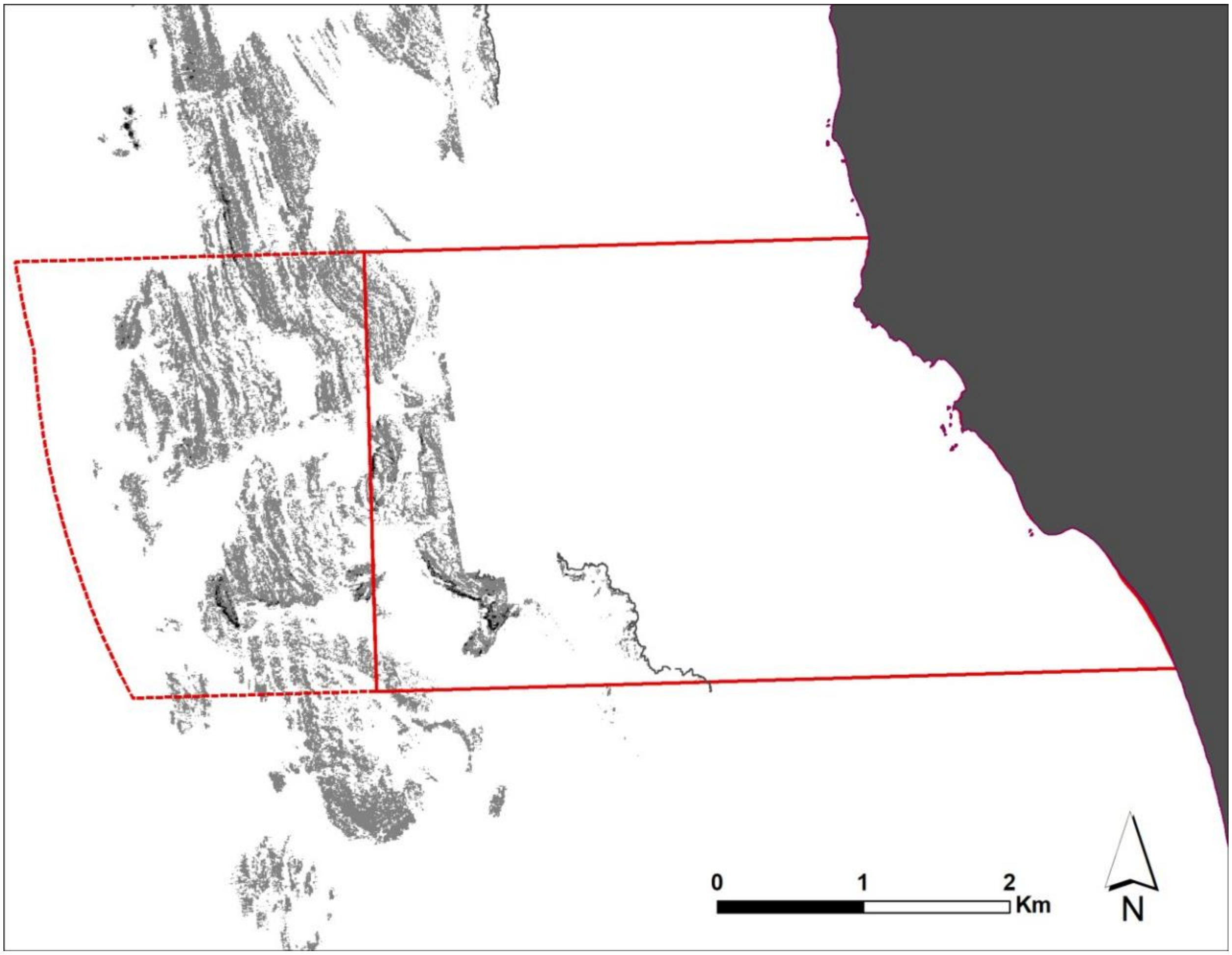


Figure 50. Map of the MPAs at South La Jolla, including the total rocky reef within the 30–100 m isobaths (grey), and high-quality habitat (black). The percentage of high-quality habitat (black) is nearly equivalent between the SMR (red line) and the SMCA (red dotted line).

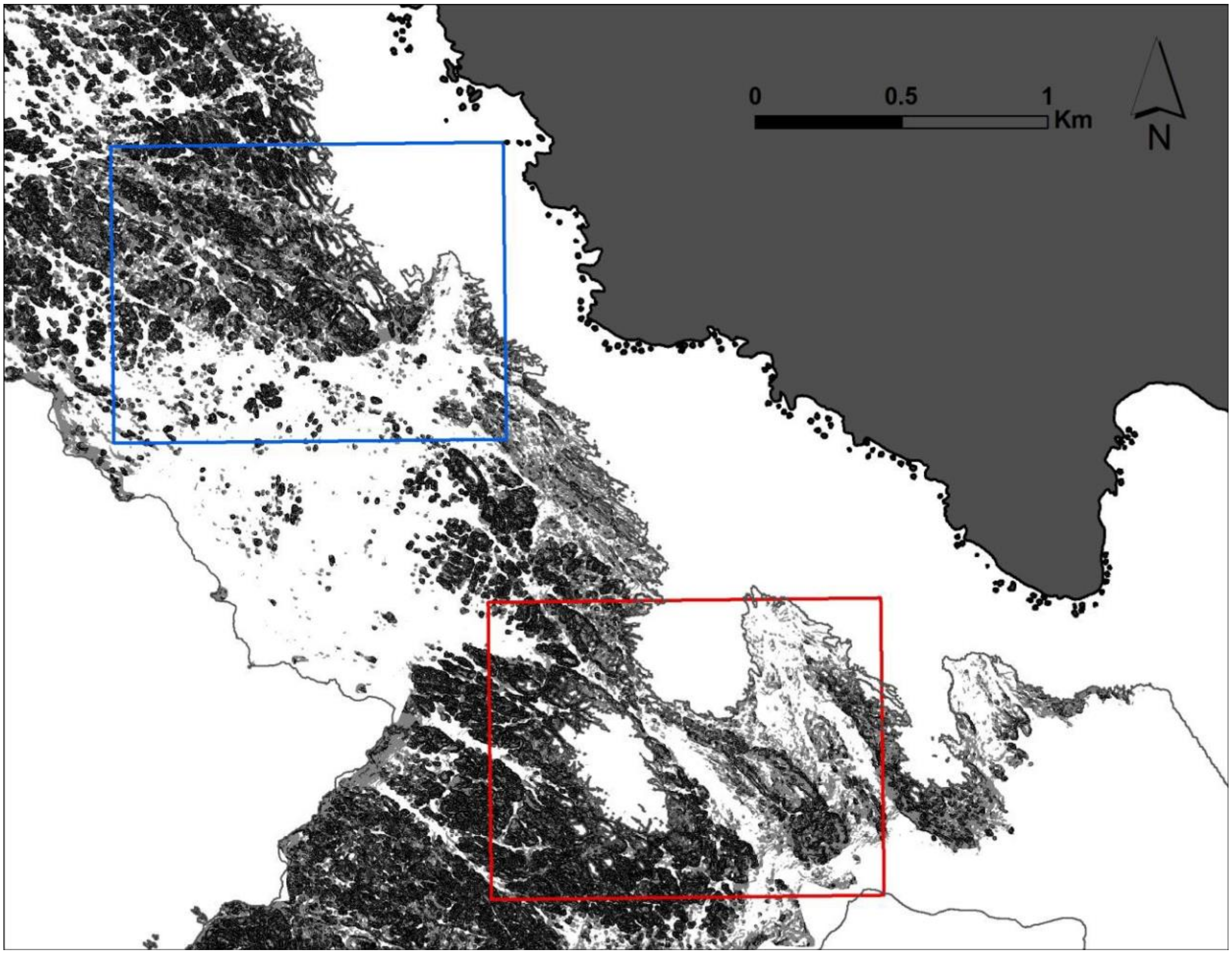


Figure 51. Map of the Carmel Pinnacles SMR, including the total rocky reef within the 30–100 m isobaths (grey), and high-quality habitat (black). Rocky reef and high-quality habitat are abundant in both the SMR (red line) and an adjacent unprotected Reference area of equivalent size (blue line) to the northwest.

Figure 52. Map of the Point Lobos SMR, including the total rocky reef within the 30–100 m isobaths (grey), and high-quality habitat (black). Rocky reef and high-relief habitat are more abundant in the MPA(red) than in an adjacent unprotected Reference area of equivalent size (blue line) to the immediate south.

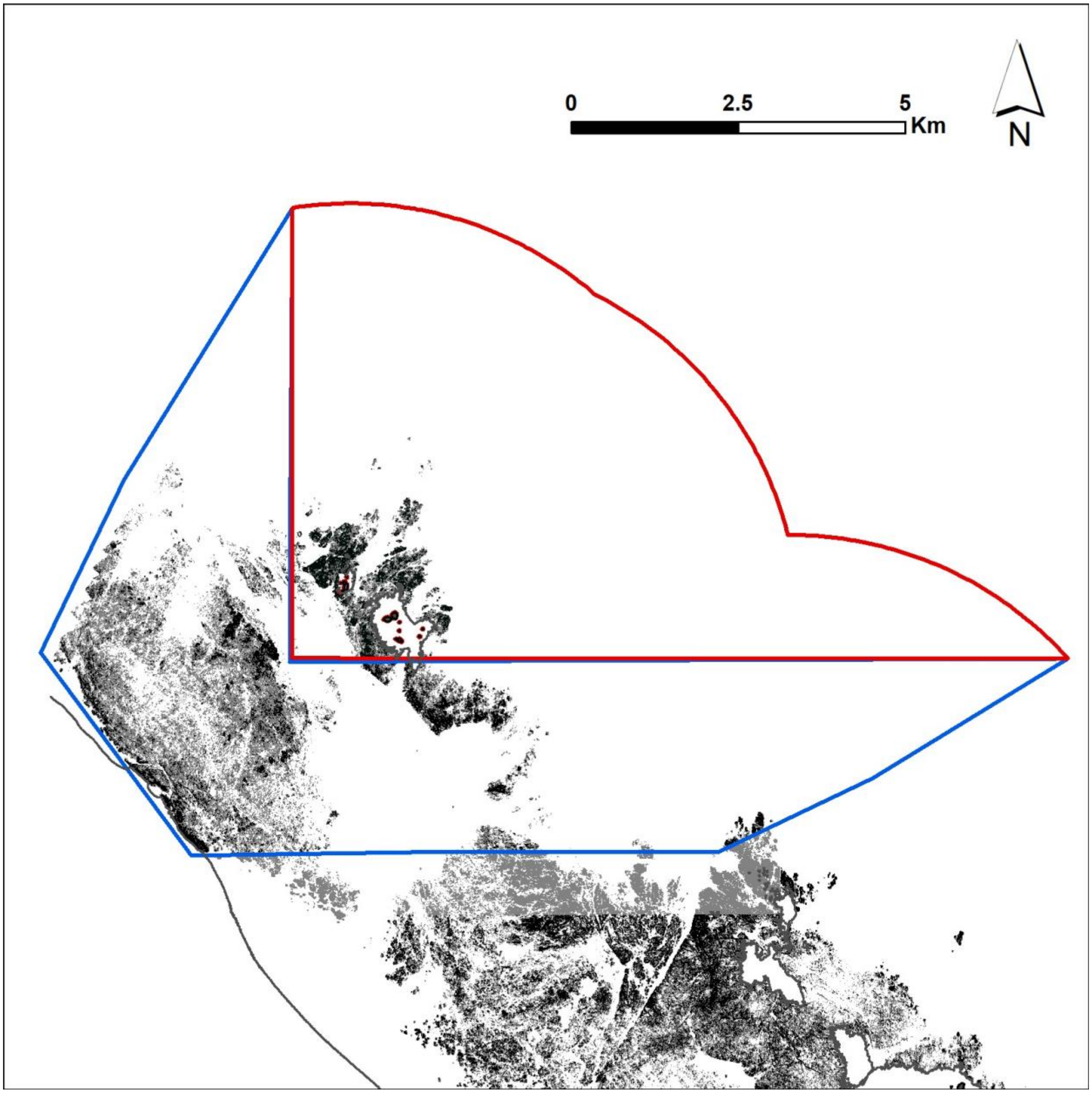


Figure 53. Map of the North Farallon Islands SMR, including the total rocky reef within the 30-100 m isobaths (grey), and high-quality habitat (black). Rocky reef and high-relief habitat are less abundant inthe MPA (red line) than in an adjacent unprotected Reference area of equivalent size (blue line) to the immediate west and south.

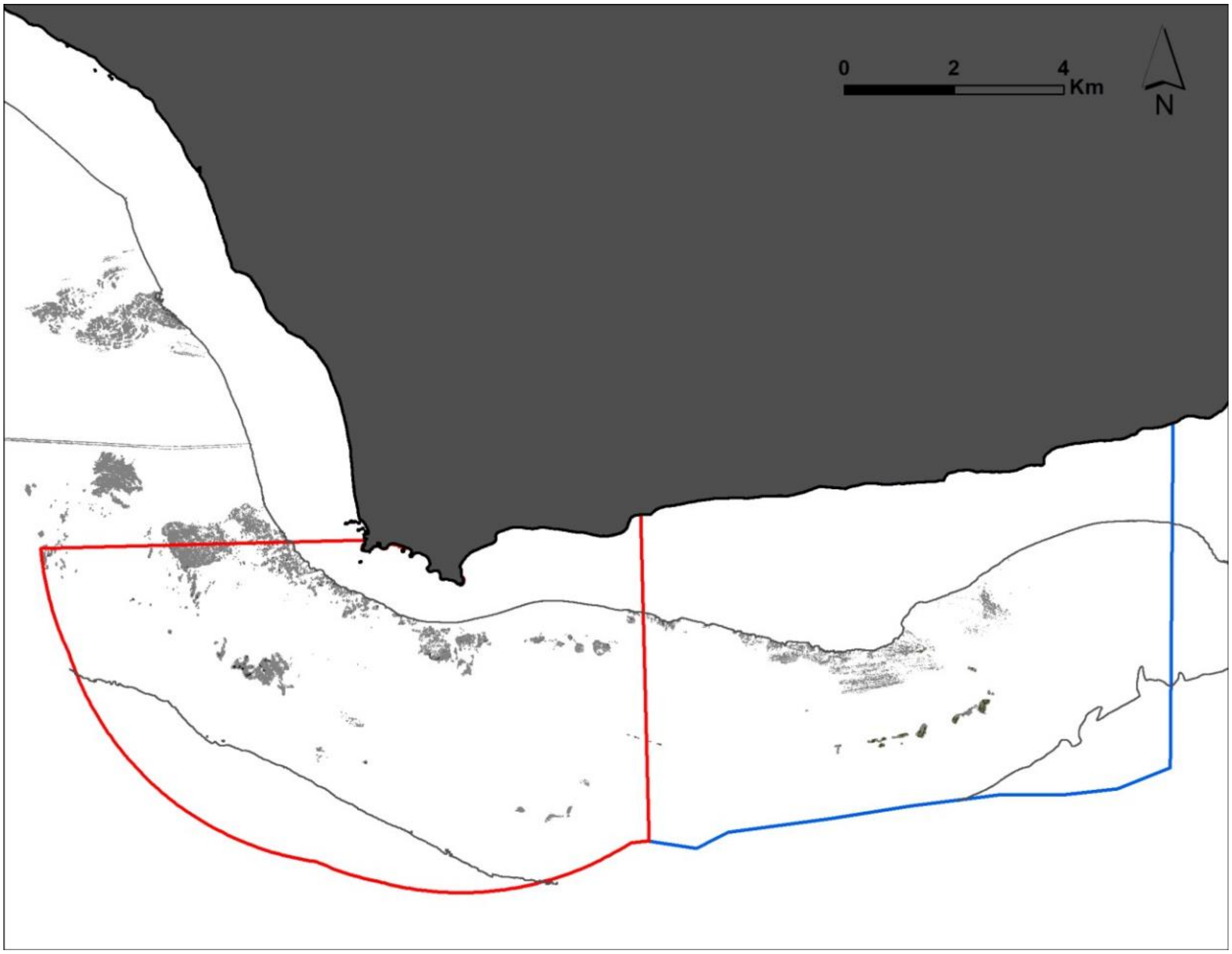


Figure 54. Map of the Point Conception SMR, including the total rocky reef within the 30–100 m isobaths (grey), and high-quality habitat (black). Rocky reef and high-relief habitat are equivalently low in the MPA (red) and an adjacent unprotected Reference area of equivalent size (blue line) to the immediate east.

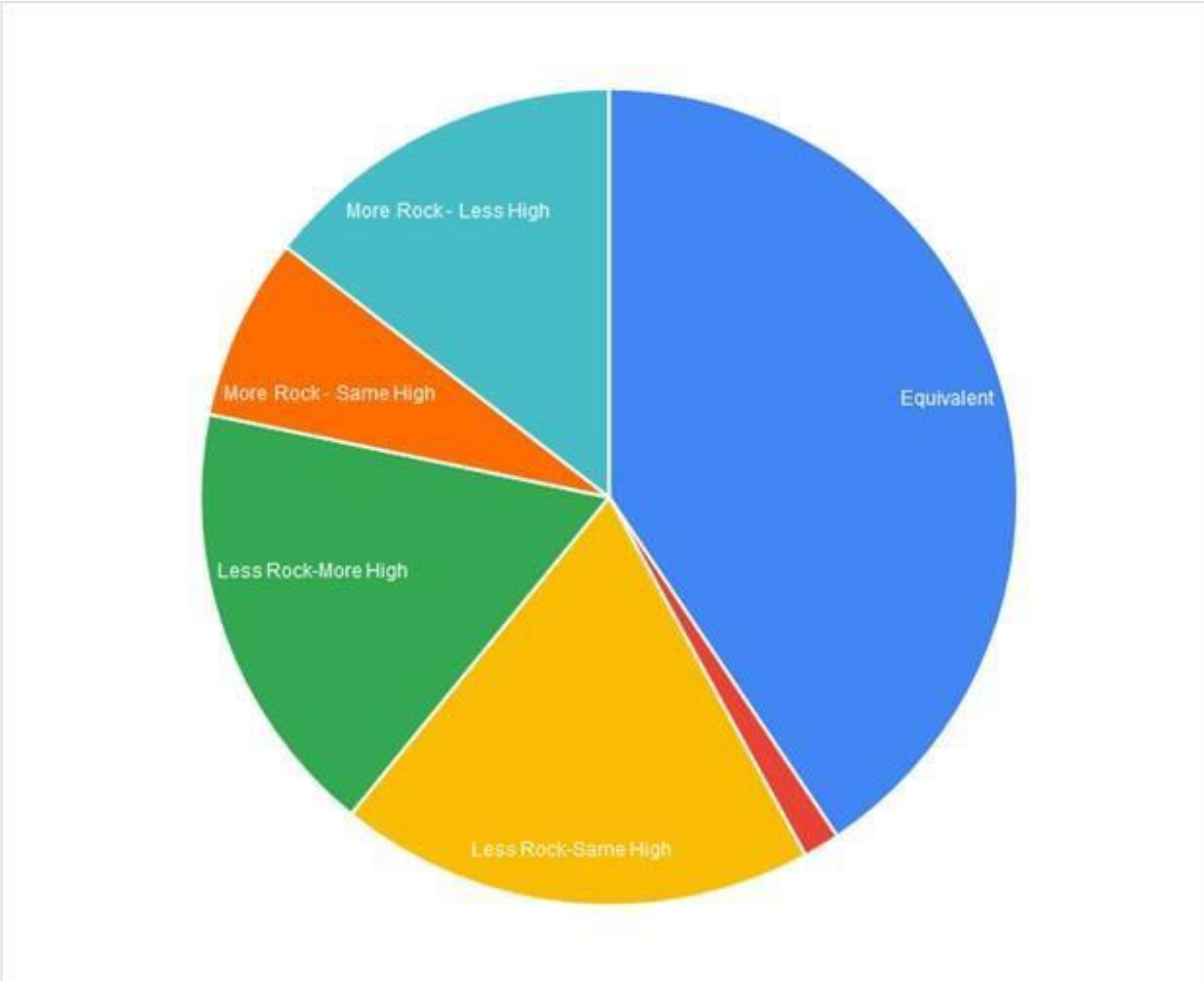


Figure 55. Pie chart depicting patterns in differences between MPAs and adjacent unprotected Reference sites with respect to Rocky Reef and high-quality Habitat. The patterns inside and out of MPAs differ in the majority of the sites included in the study.

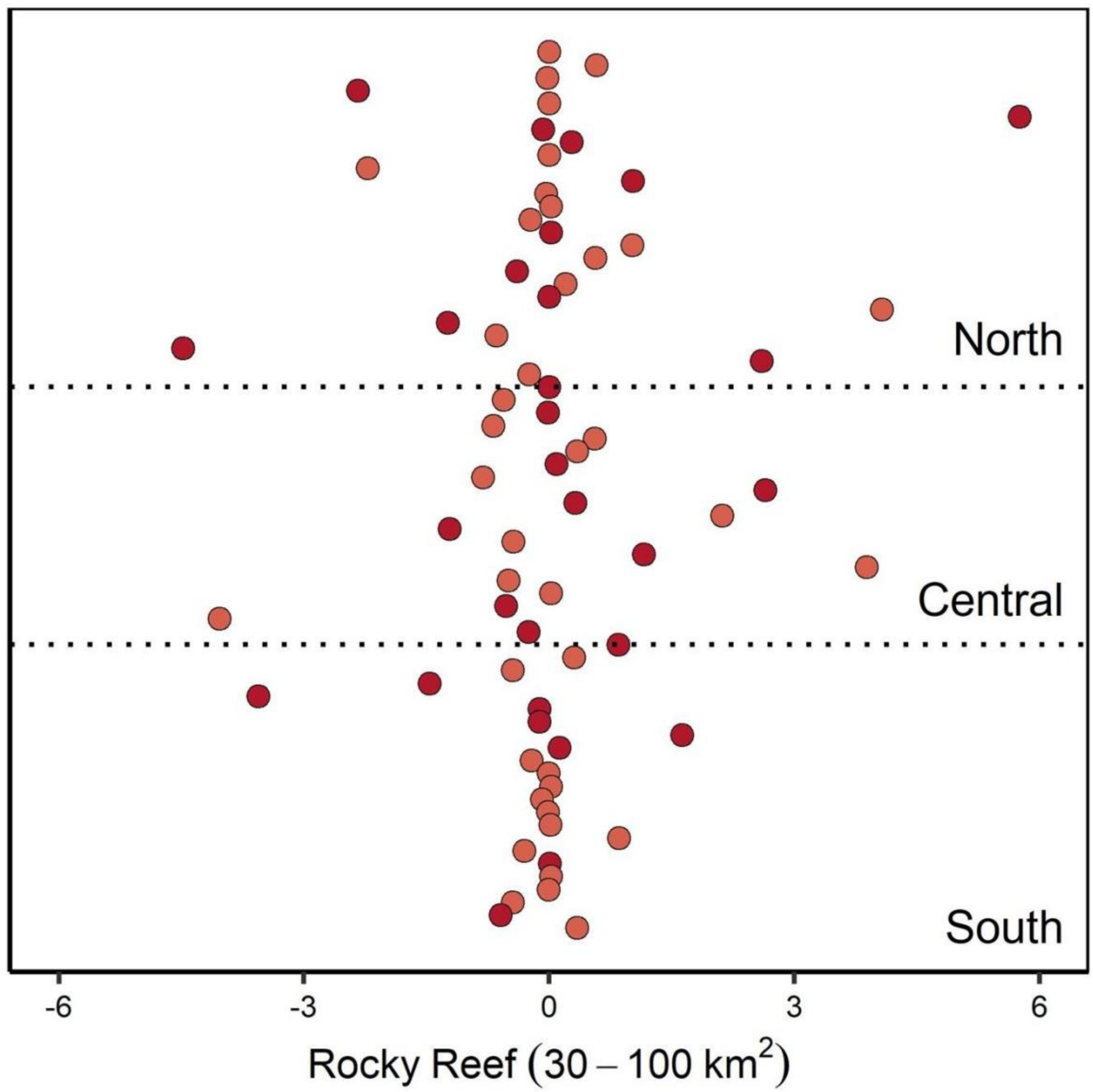


Figure 56. Difference plot depicting patterns in the differences between SMRs (dark red) and SMCAs (light red) with respect to the area (km^2) of deep rocky reef (30 –100 m), from north to south MPA regions.

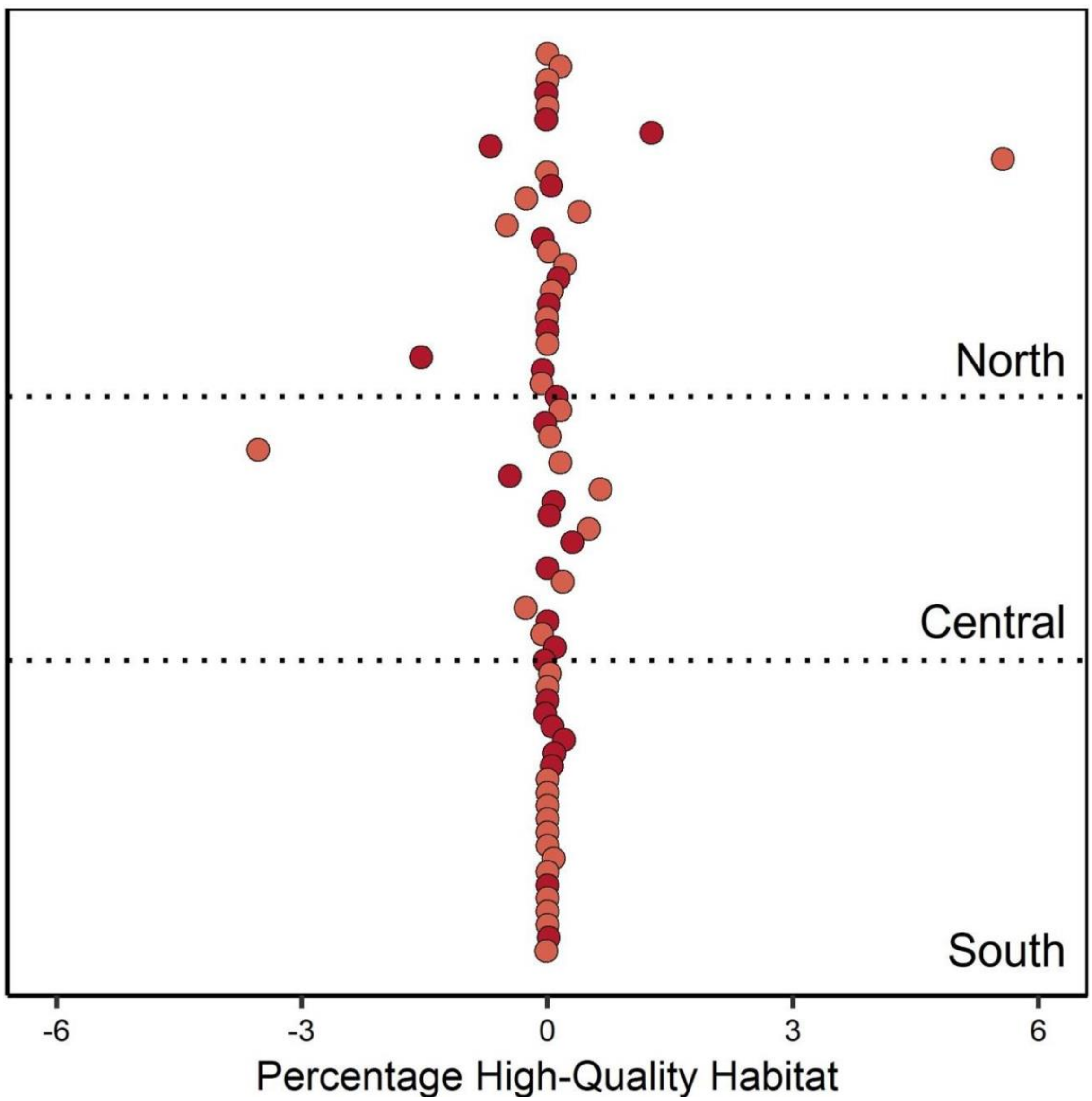


Figure 57. Difference plot depicting patterns in the differences between SMRs (dark red) and SMCAs (light red) with respect to the percentage of high-quality habitat (30 – 100 m) from north to south.

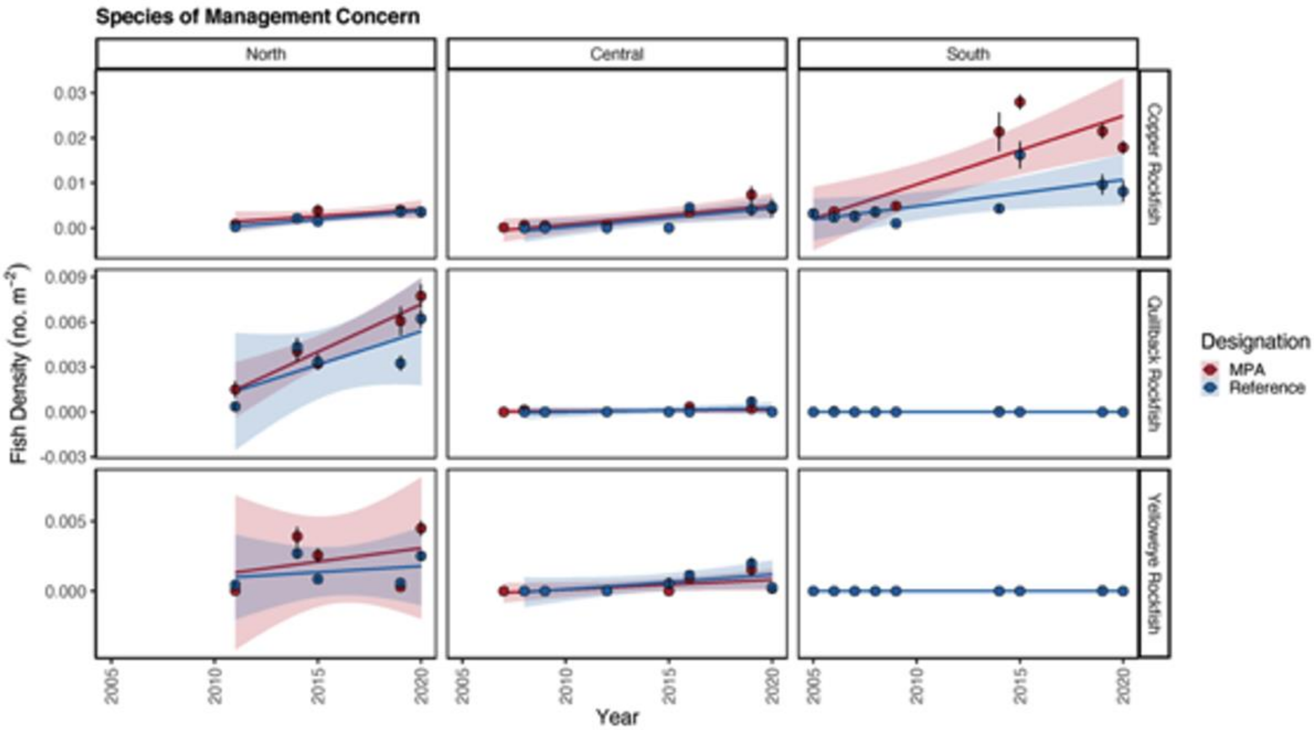


Figure 58. An interactive two-way ANCOVA to determine if the slopes of fish density were different between the MPAs and Reference sites in each management region.

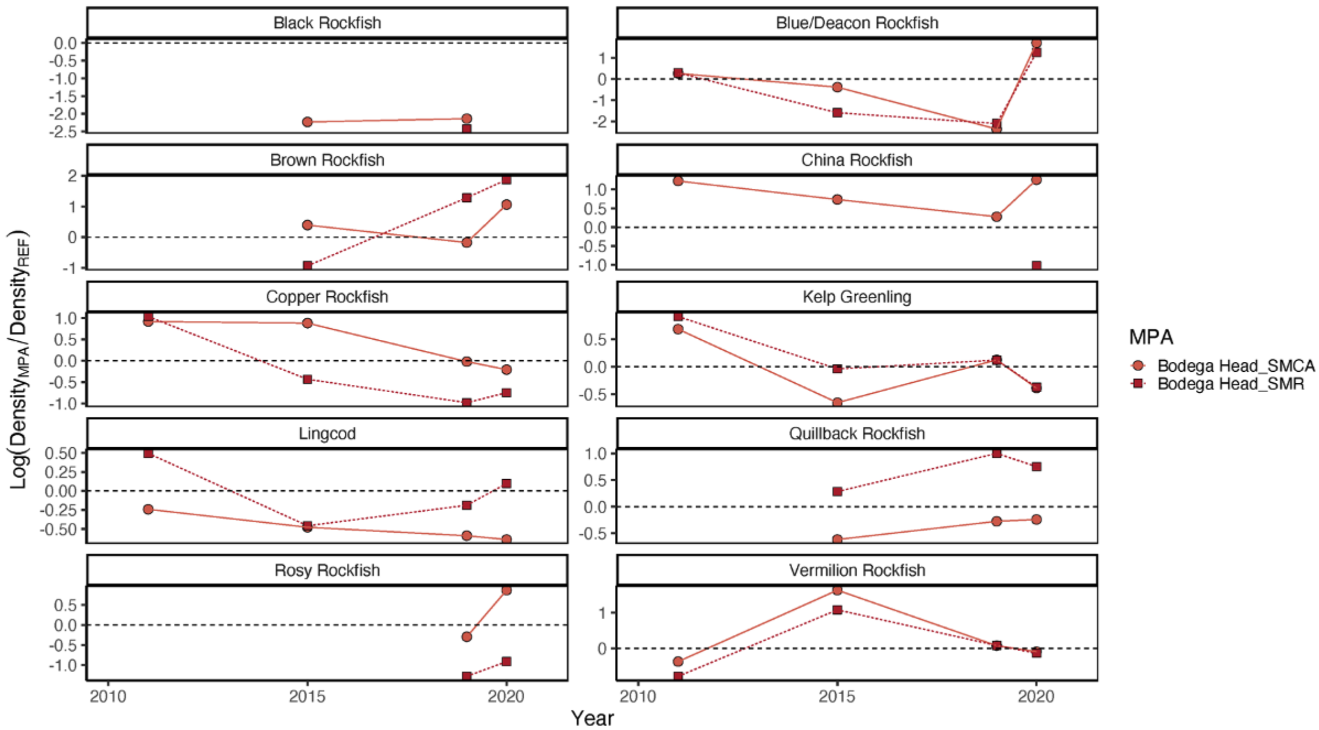


Figure 59. Density response ratios through time at Bodega Head SMCA and SMR. Fish densities in both Bodega Head SMCA and SMR had fairly similar trajectories.

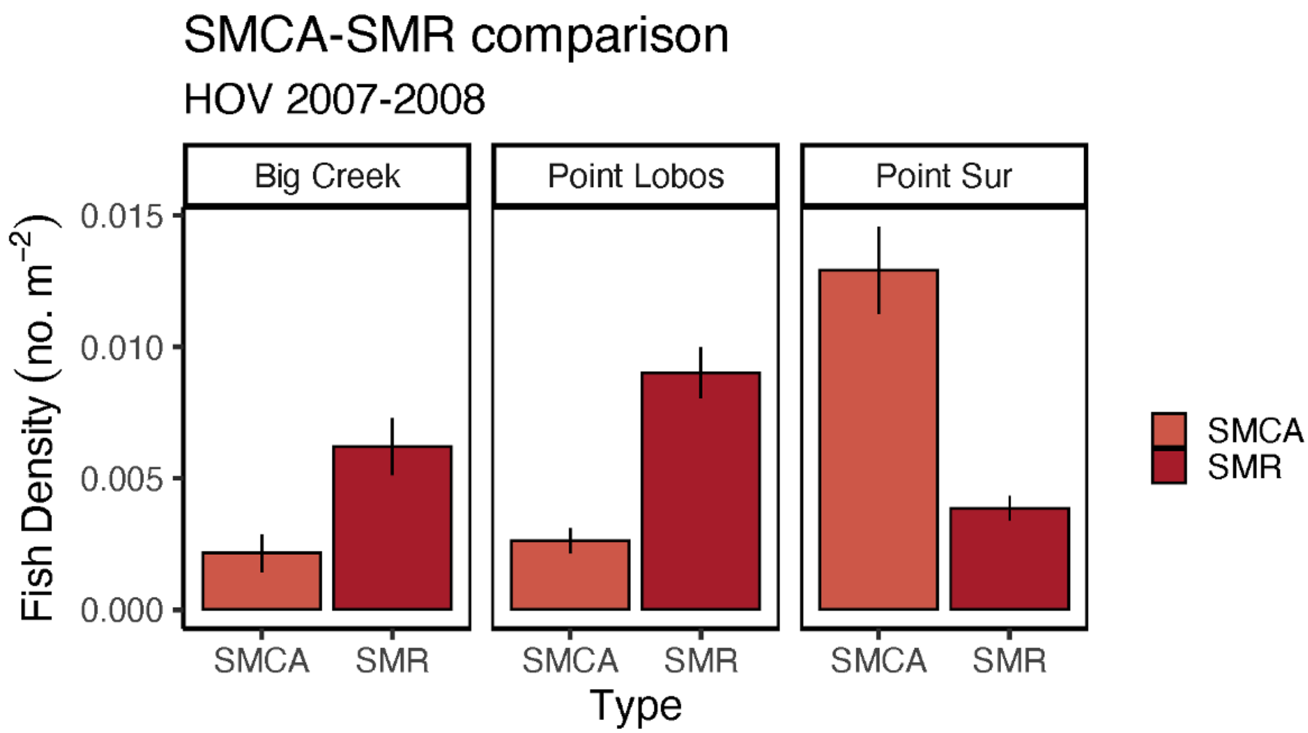


Figure 60. Differences in the density of fishes between SMCAs and SMRs, calculated from urveys at Big Creek, Point Lobos, and Point Sur in the years directly following MPA nentation (2007-2008).

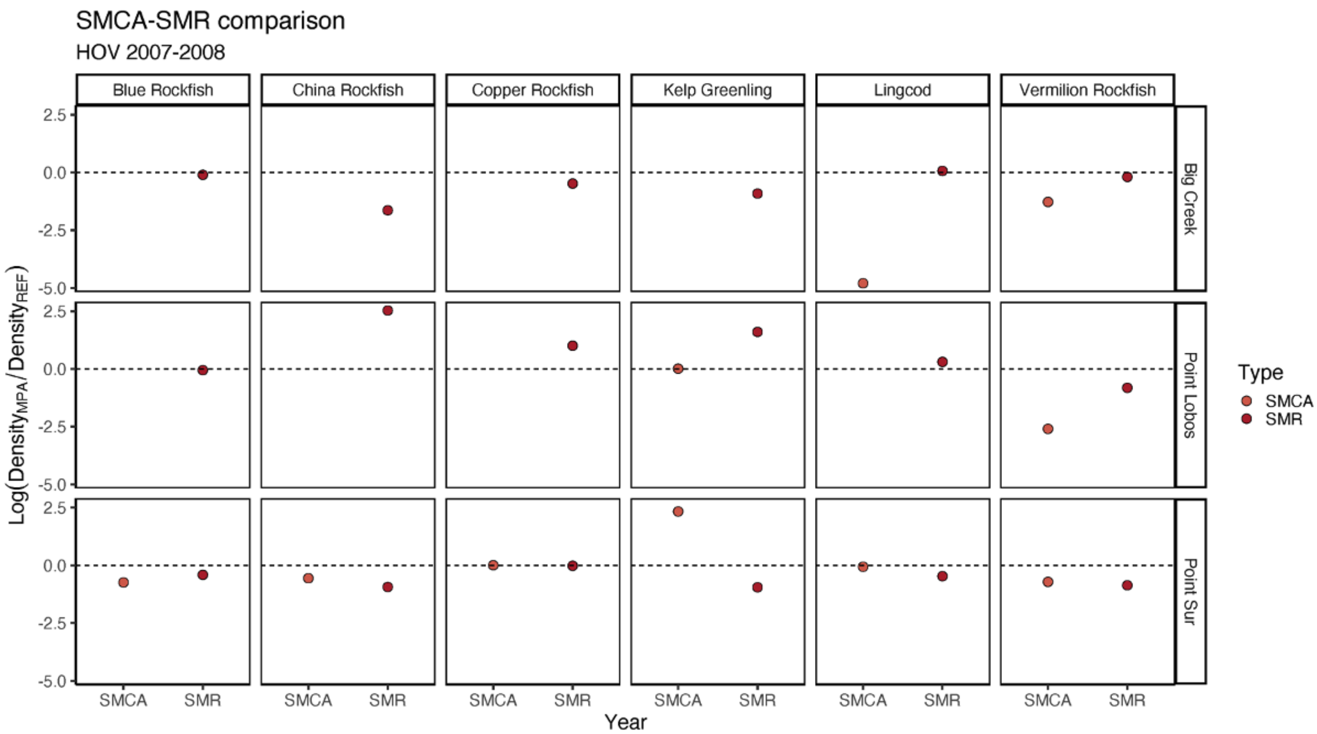


Figure 61. Species-specific MPA response ratios for 6 species inside both SMCAs and SMRs using the HOV Delta submersible data.

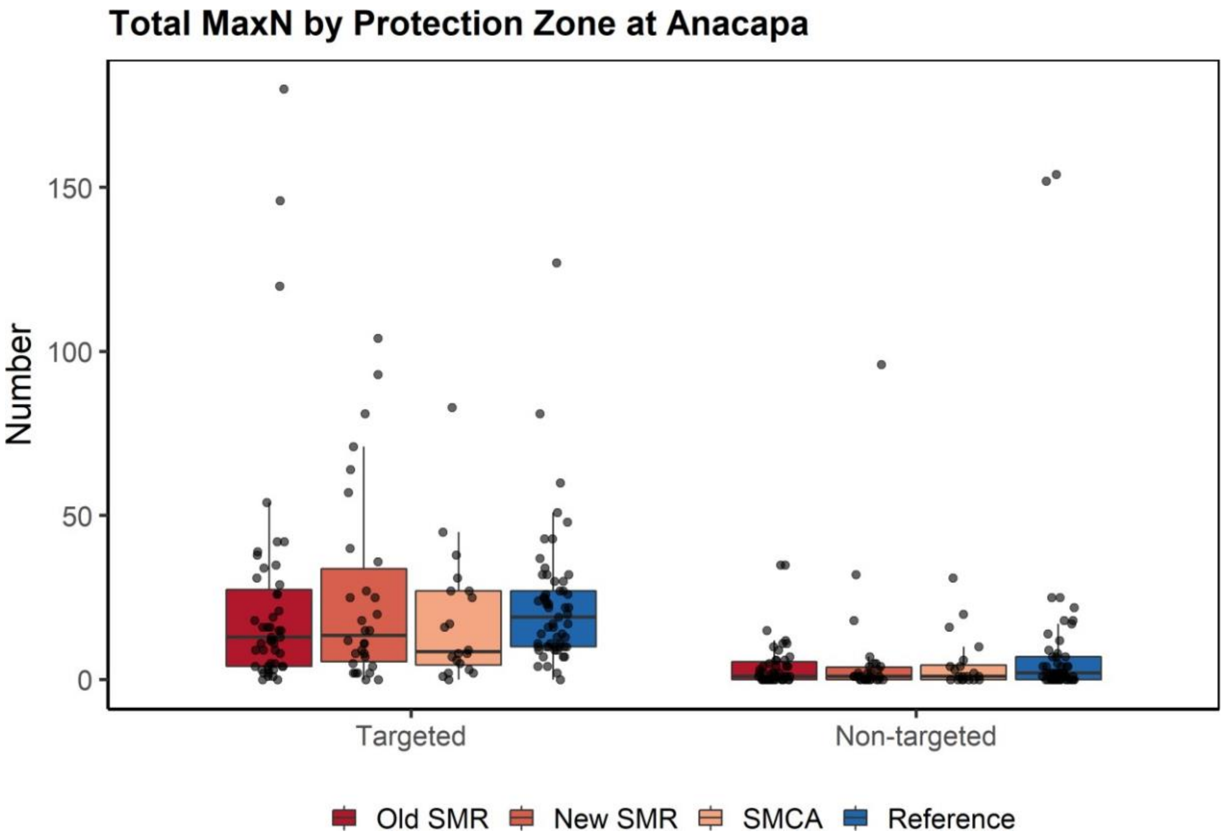


Figure 62. Summed total MaxN at each protection zone, calculated from BRUV surveys for targeted and non-targeted species at Anacapa Island.