Title: Understanding organism-habitat relationships and critically evaluating reference areas is key to marine protected area assessment

Authors: Conner Jainese[I], Peter M. Carlson[I], Katelin Seeto[I], Lyndsey McNeill[I], Kelly Sivertson[I], Jennifer E. Caselle[I]

Affiliation: Marine Science Institute, University of California Santa Barbara[I]

Corresponding Author:

Conner Jainese, connerjainese@ucsb.edu

University of California, Santa Barbara

Marine Science Institute, Bld. 520

Santa Barbara, California

Key Words/Phrases: Baited Remote Underwater Video, mesophotic, Marine Protected Area, fish, stereo-video, California, MPA network

Abstract

Marine Protected Areas (MPAs) have been implemented globally as a conservation tool for improving the overall health and function of fisheries and marine ecosystems impacted by human activities. Thorough consideration of habitat and depth representation within MPAs is crucial for comprehensive evaluation of existing MPAs, as well as the implementation of new MPAs. Mesophotic (30-100m) rocky reef fish communities are a valuable commercial/recreational resource, though the effects of MPAs on this community remain relatively understudied. We tested the effects of environmental conditions and protection from fishing on demersal fish communities living on mesophotic rocky reefs utilizing Baited Remove Underwater Video (BRUV) surveys at two MPAs in California's Statewide MPA network. We examined the primary drivers of abundance and biomass for three targeted (i.e. fished) species groups with varying life histories and habitat preferences. Depth and habitat were strong predictors for all groups; ocean whitefish (*Caulolatilus princeps*), California sheephead (*Semicossyphus pulcher*), and targeted rockfish (*Sebastes spp*). The pattern of these effects however, differed between the species groups, providing context to how they responded to fishing cessation. The influence of protection was mixed, with positive MPA effects on abundance when the availability of a species preferred habitat was distributed similarly between MPA and reference sites. This work highlights how species with high habitat affinities benefit differently from protection, as a function of depth and habitat representation within an MPA. With this in mind, continued monitoring of the valuable fish community that inhabits mesophotic rocky reefs would provide resource managers a more nuanced understanding of MPA performance and inform future MPA design.

Introduction

Marine Protected Areas (MPAs) have been implemented globally as a means of protecting marine ecosystems from anthropogenic pressures (Fox et al. 2012; Gleason et al. 2013; Kirlin et al. 2013; Maestro et al. 2019; Sullivan-Stack et al. 2022). The primary goal of most MPAs is to conserve and maintain marine biodiversity, with secondary benefits, such as increased catch rates outside of protection zones and economic stability for local communities, also predicted to occur (Murray et al. 1999; Sala and Giakoumi 2018). There is strong evidence that an MPA network, opposed to a single MPA, is more effective at broadly protecting a diverse suite of species across various life stages and habitats (Gaines et al. 2010; Grorud-Colvert et al. 2014). Well-designed MPA networks are able to incorporate nursery areas, account for ontogenetic habitat shifts, recognize different species-habitat associations, and protect vulnerable spawning grounds (Grüss et al. 2014; Olson et al. 2019). Monitoring all of these habitats is difficult and it is rare that all habitats within a single MPA or across an MPA network are effectively monitored. Monitoring priority is often given to those habitats more easily or cheaply accessed (shallow water reefs, grass beds, shorelines, etc.), while more challenging habitats are often data-poor (Field et al. 2007; Noble-James et al. 2023).

Mesophotic (30-100m) reefs represent one habitat that has been historically difficult to monitor and a growing body of research acknowledges our relatively incomplete understanding of these communities globally (Kahng et al. 2017; James et al. 2017; Cerrano et al. 2019). Mesophotic reefs support a diverse suite of commercially valuable species and it is estimated that a significant portion of commercial groundfish harvest falls within this depth zone (Miller et al. 2017; Jacquemont et al. 2024). As a result,

these fishes are left under-surveyed and relatively data poor, while simultaneously being highly targeted. Along the west coast of California many of the mesophotic fisheries are actively managed, with enforcement agencies frequently revising depth restrictions and species-specific take limits. Active management requires monitoring data from these depths and a combination of fisheries-dependent and independent data has been shown to provide a robust measure of stock size (Dennis et al. 2015; Howard et al. 2023). Baited remote underwater video (BRUV) systems have opened new opportunities for better understanding mesophotic reefs in temperate and tropical ecosystems by providing a fisheries-independent, non-destructive sampling technique that can operate at depths beyond recreational or even most scientific SCUBA diving limits (Brokovich et al. 2008; Pearson and Stevens 2015; Andradi-Brown et al. 2016; Abesamis et al. 2018; Brown et al. 2022).

Mesophotic reefs represent an ecologically important habitat that contains distinct invertebrate and fish communities (Williams et al. 2019; Honeyman et al. 2023; Bell et al. 2024). Below 30m depth, solar irradiance begins to attenuate, limiting photosynthesis and algal growth that characterizes shallower reefs. At these depths, structure forming sessile invertebrate, many themselves of conservation concern, such as gorgonians, anemones, calcareous algae, and bryozoans dominate the benthos (Ponti et al. 2018). In the Northern hemisphere, the mesophotic temperate reef fish community is dominated by Rockfishes (genus *Sebastes*), a diverse assemblage of ecologically and economically important fishes that includes >100 recognized species (Love et al. 2002; Love and Yoklavich 2006; Love 2011). The mesophotic depth zone offers a relatively stable set of environmental conditions that can function as nursery habitat and a refuge space for species that were historically

found along wider depth gradients (Marliave et al. 2009; Baillon et al. 2012; Kahng et al. 2017; Giraldo-Ospina et al. 2020). These habitats also provide an important ontogenetic bridge between shallow nursery habitats and deeper adult habitats (Love 2011; Swadling et al. 2022). Finally, these deep habitats might be critical refuges from the effects of climate change, such as increases in sea water temperature (MacDonald et al. 2016; Pereira et al. 2018). Together these factors make mesophotic reefs important contributors to marine biodiversity and a necessary component of an effective MPA network.

One of the expected benefits of MPAs is the buildup of targeted species within its boundaries and consequently, an MPA's performance is often measured by its ability to enhance the biomass and abundance of fisheries targets (Caselle et al. 2015; Lenihan et al. 2022). Recreational and commercial fisheries often have a number of targeted species that utilize a wide breadth of habitats across the seascape (Scholz et al. 2006). Effective MPA networks should protect habitats ranging from sand, sand-rock ecotone, rocky reefs, and pelagic zones, while incorporating these habitats across an extensive depth range (Young and Carr 2015). Despite the fact that MPAs are an ecosystem conservation tool, it is unlikely any MPA can achieve a 'one-size fits all' design, instead, any single MPA will likely be more effective at protecting some species compared to others. Factors such as species movement, the availability of preferred habitat, oceanographic conditions, predator and prey abundances, and recruitment dynamics will all influence an MPA's ability to enhance particular targeted species (Moffitt et al. 2011).

With the purpose of better understanding the effects of MPAs on mesophotic rocky reef fish communities, we implemented the use of BRUV camera systems at two geographically distinct MPAs (and nearby reference areas) within California's Northern

Channel Islands (Figure 1): Carrington Point State Marine Reserve (SMR) at Santa Rosa Island and Anacapa Island SMR/State Marine Conservation Area (SMCA). Straddled across a biogeographic transition zone, where cool southern-flowing waters of the California Current meet warmer northern-flowing waters from the Southern California Counter Current (Horn and Allen 1978), these two MPAs are characteristically distinct, occupying opposite ends of a strong environmental gradient that exists across the Northern Channel Islands. The primary variation along this gradient is in sea surface temperature (SST), accompanied by other related factors including productivity, frequency of disturbance/wave exposure, algal species persistence, and level of human interaction (Harms and Winant 1998; Blanchette et al. 2006; Hamilton et al. 2010; Caselle et al. 2015; Fewings et al. 2015).

We utilized stereo BRUV surveys because they are well suited for capturing fish community data across this under-sampled depth range and are useful for a variety of habitat types (Cappo et al. 2004; Heyns-Veale et al. 2016; Whitmarsh et al. 2017). Additional advantages of assessing fish communities using BRUVs include its non-destructive nature as a sampling technique (essential for MPA monitoring), the ability to collect highly accurate fish measurements for biomass calculations, the creation of a video record that can be re-analyzed to extract novel information or correct for inter-observer biases, the ability to observe species targeted by fishing and non-targeted species, and the opportunity to collect visual data on species habitat associations (Cappo et al. 2006; Langlois et al. 2010; Bennett et al. 2016). BRUV systems have become a widely implemented technique in many parts of the world as a non-destructive, fishery independent data collection tool for monitoring marine protected areas (Rees et al. 2004; Langlois et al. 2006; Kelaher et al. 2014) but are still in the early stages of use

in California.

Using BRUV survey data from Carrington Pt. SMR and Anacapa SMCA/SMR and nearby reference areas we measured the importance of habitat type, depth, and protection status on the abundance and biomass of targeted fish species. These two focal MPAs are nested into larger networks; first, a network within the Channel Islands (Figure 1B), which itself is nested into a large California statewide network of protected areas. Previous studies have shown individual variation in MPA performance across the network for shallow reefs and kelp forests (Caselle et al. 2015; Ziegler et al. 2023). Here we use two MPAs to demonstrate the potential for individual MPA variation in performance in presumably more stable, deeper water habitats.

Methods

Sampling Design and Tools

Our BRUV design was modified from existing designs used extensively to monitor a variety of marine habitats in Australia (Willis and Babcock 2000; Goetze et al. 2021; Harvey et al. 2021). Our BRUV stereo camera systems consist of a trapezoidal steel frame with two GoPro cameras (medium FOV, 30fps, 1080p) mounted in a calibrated stereo configuration. Each BRUV unit is equipped with two underwater dive lights to augment typically low ambient light conditions and a perforated PVC bait canister located in front of the camera array.

We deployed BRUVs using a stratified random approach, using geological habitat maps and bathymetry to target rocky reef habitat within our sampling depths (30-100m). We created a fishnet grid of 100m x 100m cells (ArcGIS Pro2.1) applied across each

MPA and its respective reference area. Grid cells were allocated into three depth bins (30-50m, 50-70m, and 70-100m), and habitat maps from the California Seafloor Mapping Program (Golden and Cochrane 2013) were used to calculate the amount of hard bottom within each grid cell. 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 eligible sampling locations. Deeper grid cells (70-100m) contained considerably less hard bottom and required the lower criteria to ensure an even number of potential sampling grid cells across the depth bins. Because the Carrington Pt. SMR has very little habitat >50m deep, survey depths at this site were generally limited to this maximum depth, while surveys at Anacapa extended to 100m depth.

To compare the overall amount of hard bottom in our depth ranges between the MPA and reference areas we calculated the number of eligible grid cells within each particular depth bin (30-50m, 50-70m, and 70-100m). We also report the total study area of each MPA and reference area from which all grid cells, hard and soft, were analyzed. MPA area was calculated from defined MPA boundaries and, for the inshore boundary, the 30m isobath. Calculating the area of the reference zone was somewhat subjective because the eastern and western boundaries are not designated as they are for the MPA. At Anacapa, we used the 30m and 100m isobaths for the inshore and offshore boundary respectively, and for eastern and western boundaries we estimated the area along the reef contours. At Carrington Pt., we followed a similar protocol, however the northern/offshore boundary was set by the 50m isobath. A map showing each MPA/reference zone polygon can be found in Figure S1.

We selected daily BRUV sampling locations haphazardly from the pool of

qualifying grids cells, making sure that surveys were set at a minimum distance of 250m between units to minimize the effects of bait plume and reduce the likelihood of fish being resampled. We baited BRUVs with whole, moderately scored mackerel (*Scomber japonicas*), which was replenished before each survey (Dorman et al. 2012; Jones et al. 2020, 2021), and deployed each BRUV for a minimum of 30 minutes (Harasti et al. 2015). Sampling effort included both MPA and reference sites (where fishing is allowed) on any single day to control for environmental variability between sampling days. Sampling took place from August to October for four consecutive years (2019-2022). In 2020, we also sampled in June at Anacapa Island as a response to the shutdown of commercial passenger fishing vessels (CPFV) at that location due to COVID-19. We tested for seasonal or COVID related affects and finding none, this data was included in all analyses unless otherwise noted. A map of all sampling locations, by year is available in Figure S2.

Video Processing

We analyzed video files using observation logging and 3D measurement software SeaGIS EventMeasure (www.seagis.com.au). We identified all observed fishes to the lowest taxonomic group possible. In order to quantify the relative abundance of fishes we recorded MaxN, the maximum number of individuals of a species present in a single video frame (Willis and Babcock 2000) using the first 30 minutes of each BRUV survey (Harasti et al. 2015), for every species observed. 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 BRUV surveys (Langlois et al. 2020).

We also measured the total length for every fish observed in the MaxN video

208 frame. To ensure accurate length measurements in EventMeasure, we calibrated cameras
209 before and after each sampling season (Harvey and Shortis 1998). In some instances, we
210 were not able to accurately measure all individuals in a particular MaxN frame due to the
211 camera angle or obstructions blocking one of the cameras. In this case, we measured as
212 many individuals as possible from the MaxN frame. We estimated the biomass of
213 individual fishes using an allometric length-weight conversion: $W = aTL^b$, where
214 parameters a and b are species specific constants, TL is total length in cm, and W is weight
215 in grams. We obtained length-weight fitting parameters from the literature and FishBase
216 (Froese and Pauly 2000). Because not all fish in the MaxN frame can be measured (some
217 individuals are not within view of both cameras) we used the mean of all individual
218 weights in the MaxN frame, multiplied by the MaxN for each individual species to
219 estimate biomass. We classified species as targeted by fishing or non-targeted by fishing
220 using information from the CA Department of Fish and Wildlife as well as local
221 knowledge of the authors.

222 In order to understand the influence of habitat on MPA effectiveness, and because
223 we cannot control the precise view of the forward facing BRUV cameras, we classified
224 habitat based on substrate characteristics within the field of view of the cameras. The four
225 habitat classifications were "Hard", "Mixed-Hard", "Mixed-Soft", and "Soft" (Categories
226 defined in Table S1).

227 In order to standardize the quality of videos used in analysis, we quantified the
228 "usability" of each video. All videos were assigned a "usability" score that considered the
229 amount of visible substrate and video length (Table S2). Any videos where the BRUV unit
230 did not remain upright for the entire 30 min (i.e., scores of 3 or 4) were removed from

analyses.

Focal fish species

In addition to groupings of all targeted species and all non-targeted species, we also analyzed patterns of biomass and MaxN for specific focal species. Ocean whitefish, the most abundant species observed in our study, are a medium size (39-56 cm TL at sexual maturity) tilefish (*Malacanthidae*) common in Southern California and Baja, Mexico. Typically residing at the periphery of rocky reefs, ocean whitefish primarily feed on small invertebrates often in nearby sandy flats (Elorduy-Garay and Caraveo-Patiño 1994; Love 2011). This species is a staple for the recreational fishery in the heart of its geographic range and is likely to benefit from fishing protection.

California sheephead, which appeared on nearly half of our surveys, are the largest and only targeted wrasse (*Labridae*) species that inhabits the study area. California sheephead are not only highly targeted by recreational anglers, but also by a smaller live-fish commercial fishery (Lucas 1994; Love 2011). As a protogynous hermaphrodite (female at birth with the potential to transition to male later in life), fishing pressure has a more complex effect on the sex/size structure and the reproductive potential of a local population (Hamilton et al. 2007).

With 21 unique species of rockfish observed in this study, we more closely examined a sub-group of rockfish that we considered "targeted" and are more likely to respond to protection from fishing. This grouping excludes small-bodied rockfish that are infrequently caught and almost never retained by anglers such as halfbanded (*S. semicinctus*) and calico rockfish (*S. dallii*). Three targeted species: vermilion (*S. miniatus*), copper (*S. caurinus*), and blue rockfish (*S. mystinus*) made up over 70% of the targeted

rockfish observed on our surveys. Vermilion and copper rockfish are long-lived (50-60 years) high value species that have a significant recreational and commercial fishery, increasing their potential to benefit from protection. Blue rockfish are a schooling, largely planktivorous species, that is of moderate value to recreational and commercial fishing (Love 2011).

Abundance and Biomass Modeling

Generalized linear models (GLM) were used to understand how differences in habitat type, depth, and MPA status influenced fish abundance and biomass. To account for species-specific habitat preference and other potential traits (e.g. movement patterns) we ran models on targeted rockfish, ocean whitefish, and California sheephead separately. We also ran separate models for each island because the depth ranges differed (Carrington Pt. SMR ranged from 30m - 60m depth; Anacapa SMCA/SMR ranged from 30m – 90m depth). Predictor variables were MPA status, depth, and habitat type, as well as the interaction between MPA status and habitat type to test if the effect of MPA status is similar across different habitat types.

All statistical models and model diagnostics were run using R version 4.3.0. Data from each species and metric (biomass and MaxN) combination was zero inflated, and the fitdistrplus package and descdist() function were used to determine the best fit distribution. Each data combination was fit to a negative binominal distribution and the models were run using the glm.nb function in the lme4 package. Randomized quantile residuals were calculated and tested for overdispersion using the DHARMa package and all dispersions statistics were <1. The 'visreg' package was used to visualize how each model parameter influenced a particular metric and represents each model estimate when all other predictors are held constant. We standardized

the visualizations by setting MPA status to 'MPA', habitat type to 'Hard', and depth as the mean depth from a particular island. Each regression plot shows a model prediction, 95% confidence interval, and the partial residuals of the model. We calculated the precent deviance explained for each model to understand how well our predictors explained the variation in the data.

Population Size Structure

To understand how protection from fishing alters the demographics of targeted fish populations, we plotted the size density histograms of the three most common targeted rockfishes (copper, vermillion, and blue rockfish), ocean whitefish, and California sheephead.

Results

We completed 280 and 341 BRUV surveys at Carrington Pt. and Anacapa Island respectively for a total of 621 surveys. Of those 621 surveys, 493 were classified as 'usable' (79% usable) and were included in analyses (Table S3) In general, two conditions resulted in unusable video; these were very strong currents and/or highly rugose habitat causing the BRUV system to not land upright, or tip over at some point during the video survey.

Habitat Description

We found differences in amount and type of rock at the two islands. When rock was present at Anacapa, the habitat was characterized by a patchy reef system with most video classified as 'mixed soft' or 'mixed hard' (Fig. 2, Table S4). In addition, the Anacapa MPA contained more 'soft' habitat classifications than the other island/MPA groupings. Carrington Pt. was characterized by more consistent hard bottom, with most videos classified as 'hard' or 'mixed

hard' (Figure 2, Table S4).

Similar to the video observations, benthic habitat maps showed a disparity between the amount of rocky substrate present in the Anacapa MPA and reference area, with 3-5 times more eligible grid cells in the reference area. Although the reference area was twice as large as the MPA, there still appears to be proportionally more abundant hard bottom habitat in the reference area. This is particularly true for the deepest zone (70-100m), which had 5 times as many eligible grid cells (MPA = 33 vs Reference = 167, Table 1) in the reference area. Carrington Pt. had a relatively similar number of eligible grid cells within the 30m - 50m depth bin, with the reference area only being slightly larger (Table 1). Overall, the benthic habitat maps used to identify eligible grid cells generally agreed with the observed habitat data from BRUV surveys, with Carrington Pt containing more consistent hard bottom and Anacapa containing more sand-rock ecotone habitat.

Species Observed

We observed a total of 65 fish species on the BRUV surveys across four years and both locations. Total summed MaxN and frequency of occurrence for each species are shown in Table S5. A single species, ocean whitefish, accounted for 32% of the summed MaxN values. These fish had the highest abundance across our study and were present on 84% of all surveys. Two species, copper rockfish and California sheephead had both high MaxN values and high frequency of occurrence at both islands. Copper rockfish occurred on 48% of surveys while California sheephead occurred on 49% of surveys (Table S5). Four schooling species: jack mackerel (*Trachurus symmetricus*), blacksmith (*Chromis punctipinnis*), halfbanded rockfish, and blue rockfish were abundant when observed but

occurred less frequently (4-27% of all surveys).

The BRUVs were able to observe species rarely seen in other surveys in California (e.g., SCUBA, ROV, submersible). These included species of concern including giant sea bass (*Stereolepis gigas*) (50 individual observations), bocaccio (*Sebastes paucispinis*) (79 individuals) and bat rays (*Myliobatis californica*) (11 individuals) as well as various species of the more cryptic flatfishes (including California 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.

Abundance and Biomass

Targeted Rockfish -

At both islands, targeted rockfishes showed similar patterns with habitat type and depth being significant predictors of both biomass and abundance. Generally, both biomass and abundance increased as the availability of hard substrate increased, with 'hard' vs. 'mixed soft' and 'soft' being highly significant (all eight comparisons across island, metric, hard vs. mixed hard, and hard vs. soft had a p-value <0.001; Figure 3 & Table S6). At Anacapa, depth was a significant predictor for targeted rockfish abundance and biomass, with both metrics increasing with depth (MaxN p-value = <0.001; biomass p-value = <0.001; Figure 3 & Table S6). The patterns at Carrington Pt. were less consistent, with depth only being a significant predictor of biomass (p-value = 0.02, Figure 3 & Table S6), most likely related to the limited depth range at this location compared to Anacapa. Interestingly, the interaction between soft habitat and MPA status was almost significant for targeted

rockfish biomass at Anacapa. Here, soft habitat was the only habitat type predicted to have greater targeted rockfish biomass inside the MPA compared to the reference area (p-value = 0.06, estimate = -1.43; Table S6 & Figure S3A). This interaction term indicates that the model estimate for soft bottom habitats in the MPA was greater compared to reference areas, while in other habitats (e.g., 'Hard', 'Mixed Hard', and 'Mixed-soft') the reference area estimate was larger. The only significant MPA effect, beyond the influence of habitat and depth, was for targeted rockfish biomass inside the Carrington Pt. MPA (p-value = 0.03; Figure 3 & Table S6).

Ocean Whitefish -

Depth was a strong predictor of ocean whitefish biomass and abundance with higher abundance and biomass found in shallower waters (p-value = < 0.001 for all comparisons of MaxN and biomass at both islands; Figure 4 & Table S7). The only significant habitat predictor was for soft habitats at Carrington Pt., with both abundance and biomass significantly lower on sandy, soft bottom habitats compared to hard substrate (p-value = 0.05; Figure 4 & Table S7). We did not find a significant interaction term between MPA status and habitat type for either ocean whitefish metric (Figure S4 & Table S7). Anacapa showed a significant MPA effect, with the abundance and biomass of ocean whitefish greater inside the MPA (MaxN p-value = 0.02; biomass p-value = 0.01; Figure 4 & Table S7).

California Sheephead -

Similar to ocean whitefish, depth was found to be a strong predictor of California sheephead biomass and abundance, with higher levels found in the shallower waters (Carrington Pt. and

Anacapa MaxN p-value <0.001; Carrington Pt. biomass p-value = <0.01; Anacapa biomass p-value = <0.001; Figure 5 & Table S8). California sheephead were significantly less abundant on two habitat types at Anacapa, 'mixed soft' and 'soft', compared to 'hard' substrate ('mixed soft' p-value = 0.03; 'soft' p-value = <0.01; Figure 5 & Table S8), and had significantly lower biomass on 'soft' vs 'hard' habitat at Anacapa ('soft' p-value = 0.05; Figure 5 & Table S8). At Carrington Pt., habitat alone was not found to be a significant predictor of sheephead abundance or biomass. We did find a significant interaction term for sheephead biomass and abundance between 'soft' habitat and MPA status at Carrington Pt., however these results had very few observations of sheephead on soft habitat across protection zones, limiting inference from this result. At Anacapa, we found a significant negative MPA effect for the abundance and biomass of sheephead, with greater values in the reference area (MaxN p-value = 0.01, estimate = 1.01; biomass p-value = 0.03, estimate = 1.09; Figure 5 & Table S8).

Deviance Explained

Across all species and both metrics, the model framework performed slightly better at Anacapa compared to Carrington Pt., with the deviance explained ranging from 0.46 – 0.22 at Anacapa and 0.22 – 0.17 at Carrington Pt. (Tables S6 – S8). This is likely related to the larger available depth range at Anacapa and that depth was a significant predictor of abundance and biomass for all three species in this study. The highest deviance explained was for California sheephead at Anacapa (DE = 0.46 for MaxN; DE = 0.45 for Biomass; Table S8) and is most likely related to the smaller range in MaxN and biomass values associated with the California sheephead data compared to the larger range associated with targeted rockfish and ocean whitefish.

392

393 *Focal Species Size Structure*

394 We plotted the density of individual fish total lengths in MPAs and reference areas
395 for the five most common targeted species in our study; copper rockfish (n = 506),
396 vermilion rockfish (n = 459), blue rockfish (n = 1760), ocean whitefish (n = 5767), and
397 California sheephead (n = 603) (Figure 6). Copper rockfish were generally larger inside the
398 MPAs at both Anacapa and Carrington Pt., with the MPA containing more individuals
399 >400mm TL (Figure 6A). Vermilion rockfish had a bimodal size structure with multiple
400 size classes present at Carrington Pt. and Anacapa (Figure 6B). Inside the Anacapa MPA,
401 the population size structure is dominated by smaller sized individuals (<20cm), with
402 proportionally fewer adult fishes. While the population size structure patterns for
403 vermillion rockfish at Carrington Pt. appear to be more related to protection from fishing,
404 with proportionally larger individuals inside the MPA. The smaller-bodied schooling blue
405 rockfish had similar population size structure across protection zones at Carrington Pt. and
406 Anacapa (Figure 6C). Ocean whitefish and California Sheephead showed similar patterns
407 at Anacapa and Carrington, with a greater proportion of larger individuals inside the MPA
408 at each location (Figure 6D & E).

409

410 Discussion

411 In this study we show that environmental drivers, such as depth and habitat availability,
412 need to be considered when assessing the ability of MPAs to enhance the biomass and
413 abundance of targeted species. MPA effectiveness, in both tropical and temperate marine
414 ecosystems, has been linked to benthic features such as the amount of consolidated hard bottom,

415 reef complexity, and habitat continuity (Dames et al. 2020). Individual species have been shown
416 to respond differently to such features, hence species-habitat associations must be considered
417 during MPA implementation, when defining MPA goals, and when assessing performance.
418 Studies have shown that a lack of preferred habitat inside the protection zone can limit the ability
419 of MPAs to enhance species and functional diversity (Navarro-Martínez et al. 2023). MPAs are
420 designed as ecosystem management tools, with broad goals of protecting biodiversity, yet
421 individual species can have widely varying habitat requirements. Many MPA design processes,
422 especially for MPA networks, try to encompass habitat replication and representation (Roberts et
423 al. 2003; Halpern et al. 2010; Saarman et al. 2013), but in practice, it is impossible to design
424 optimally for every species. Thus, accounting for habitat in post implementation monitoring and
425 choice of reference areas, can help to set realistic expectations for MPA performance.
426 The Carrington Pt. MPA and adjacent reference area had similar amounts of continuous
427 hard substrate, which indicated that the greater biomass of targeted rockfishes in the MPA was
428 likely related to protection more than habitat. Rockfish (family *Sebastes*) are generally
429 characterized as a demersal, rock associated and heavily fished family, and it appears that the
430 Carrington Pt. MPA is well designed for their protection. Inside the Anacapa MPA, there was a
431 notable lack of continuous hard substrate, particularly at depth, that appears to limit the
432 performance of the MPA at that location for this rock-associated fish group and makes
433 comparisons with the paired reference area challenging. However, the Anacapa MPA is likely
434 more effective at enhancing the ocean whitefish population, a more mobile species that is
435 associated with the sand-rock ecotone (Bellquist et al. 2008). Habitat maps and *in situ*
436 observations from Anacapa MPA and reference area showed that these locations were dominated
437 by a mix of soft, sandy habitat and isolated patch reefs. Ocean whitefish abundance and biomass

438 was also strongly associated with depth, but unlike targeted rockfish, ocean whitefish are more
439 abundant in shallower areas, with the majority of observations occurring shallower than 60m.
440 The examples above, comparing very different fish species groups, demonstrate how
441 scientific guidelines and a network approach to MPA design can help meet ecosystem goals and
442 protect populations of different species across a variety of habitats. The creation of networks,
443 with numerous reserves spread across various habitats, has become the standard by which to
444 structure marine no-take zones, both at the local and global scale. The California Marine Life
445 Protection Act (MLPA) established the network of MPAs throughout California with the goals of
446 protecting ecosystem biodiversity and protecting and rebuilding populations of key species. This
447 process relied on MPA design guidelines from a scientific advisory committee and chief among
448 those guidelines was 'habitat representation' throughout the network (Saarman et al. 2013). At
449 the network level, this was achieved by including a variety of major habitat types such as; rocky
450 intertidal zones, estuaries, and shallow and deep subtidal habitat. Here we show that a more
451 nuanced treatment of habitat within an MPA can provide critical information on individual MPA
452 performance for key species (Young and Carr 2015).
453 By incorporating habitat availability in and out of the MPAs and studying deeper zones
454 than previously explored, we found several results that differed from prior studies and/or our
455 expectations. Contrary to our predictions and prior studies of shallower reefs in the area (Caselle
456 et al. 2015; Honeyman et al. 2023), California sheephead abundance and biomass at these deeper
457 depths was significantly greater in the Anacapa reference area which is open to fishing. Active
458 tracking data has shown that California sheephead use a variety of habitats, but tend to favor
459 rocky-reefs, spending 50% - 70% of their time on hard, consolidated substrate (Topping et al.
460 2005). The deep-water habitat within the Anacapa MPA is lacking this hard substrate, which is

more abundant in the shallow kelp forests of the Anacapa MPA. This illustrates the importance of surveying the full range of depths for species of interest when evaluating MPA performance or advising fisheries management. A more comprehensive approach to MPA design and management can be achieved by filling gaps in our knowledge of how MPAs may differentially enhance fish communities at all depths and habitat types.

To measure the ecological effects of a marine protected areas, especially without data for that site prior to MPA implementation, researchers often use a nearby fished area (reference site) as a control by which hypotheses about the cessation of fishing can be tested. Selection of these 'control' sites must weigh numerous factors such as; habitat type, depth range, species composition, and seasonal oceanographic characteristics, when deciding on location and scale. Often the easiest way to broadly control for various environmental factors is by placing the reference area in close proximity to the MPA. However, unlike strictly controlled lab experiments, MPAs are expected to affect control areas by design. Adjacent placement of reference areas, while often meeting goals of controlling for environmental conditions and perhaps even habitat, creates a scientific design challenge, with the likelihood that reference sites will be affected by the presence of a nearby MPA through the redistribution of fishing effort, and potential "spillover" of fish coming from the MPA (Caselle et al. 2015; Di Lorenzo et al. 2016).

Anacapa Island presents an interesting case study in reference site selection. Previous studies of very deep water habitats using Remotely Operated Vehicles excluded the Anacapa MPA from analyses, citing a lack of appropriate reference area (Karpov et al. 2012). This exclusion comes despite containing one of the oldest MPAs in the Northern Channel Islands network, with the Anacapa eastern SMR established in 1978. Here we chose the reference location as immediately offshore of, and deeper than, long-standing reference sites used for

shallower rocky reef and kelp forest studies (Caselle et al. 2015; White et al. 2021). While shown to be appropriate for shallow rock reef, we found that in deeper waters, the reference area contained more deep rock than in the MPA, potentially limiting our ability to detect an MPA effect on rock-associated species (e.g., targeted rockfish, California sheephead). However, both reference area and MPA contained similar amounts of deep sand-rock ecotone habitat favored by ocean whitefish, the most numerous species of fish in our study. Hence tradeoffs exist where reference site selection must incorporate species-habitat associations, assess MPA goals, work to inform management decisions, and are beholden to the realities of field studies.

A consistent MPA effect was observed in the size structure of three targeted rockfish species, ocean whitefish and California sheephead, with the greater proportion of larger individuals inside the protection zone. This is not surprising as one of the earliest effects of a cessation of fishing is to allow larger individuals to grow and persist (McClanahan et al. 2007; Taylor and McIlwain 2010; Bejarano et al. 2019; Mumby et al. 2021). The notable exception was for vermillion rockfish inside the Anacapa MPA, which contained fewer large individuals than the reference area. Interestingly, the size structure for vermilion rockfish at both study sites reveal distinct cohorts at two size classes. This likely indicates periodic strong recruitment/survivorship for this species and provides an opportunity to track these cohorts over time. Repeated annual sampling such as done here allows the tracking of these types of population demographics through time to better understand year to year variability in recruitment dynamics for valuable fishery species. The ability to collect size structure data, with tools such as stereo BRUVs, can provide important additional insight into the effects of protection on these populations and is particularly important for the management of long-lived species like rockfishes.

The ability of MPAs to conserve and rebuild fish communities has been shown to improve with the protection of habitat across a wide range of depths (Curley et al. 2002; Goetze et al. 2021). Many species of fish utilize different depth zones and habitats across life stages, often with juvenile fish recruiting to relatively protected shallow nursery habitats and moving to deeper offshore habitats as they mature (Gibson et al. 2002; Aburto-Oropeza et al. 2009; Li et al. 2022). This ontogenetic movement is common with a number of the rockfish species observed in this study (Love et al. 1991) and should be considered in the context of MPA performance. The availability of suitable habitat along the ontogenetic depth profile likely influences the distribution of rockfish at varying life stages. Additionally, seasonal spawning migrations across depth gradients are observed globally and emphasize the significance of providing protection across this gradient (Luo et al. 2020; Lombardo et al. 2020; Thorburn et al. 2021). We observed a distinct break in suitable rockfish habitat within the Anacapa MPA complex, with very little deep habitat (>70m) present. Not only does this reduce the overall available habitat for adult rockfish, it likely reduces the potential for this MPA to provide a valuable ontogenetic bridge for species with high habitat affinity. An MPA that contains contiguous habitats within a species full depth range is better equipped to protect that species at all stages of life, enhancing the benefits experienced by protection from fishing.

The protection of connected depth gradients is also likely to provide resilience for fish populations faced with environmental stressors including seasonal changes in water temperature, short-term temperature anomalies (marine heat waves), and long-term changes resulting from global climate change. In an ever-warming global ocean, it has become necessary for fish communities to adapt to rising sea temperatures, often through range shifts in latitude or depth (Perry et al. 2005; Dulvy et al. 2008; Nye et al. 2009; Chaikin et al. 2022; Dahms and Killen

530 2023). Access to deep refuge habitat can improve the resilience of some fish communities and
531 allow them to survive shallow water stressors (MacDonald et al. 2016; Pereira et al. 2018).
532 Inversely, global climate change has been shown to reduce deep-water dissolved oxygen,
533 creating upward pressure on fish communities escaping oxygen minimum zones (OMZ) (Ross et
534 al. 2020). This has been observed around Southern California's Channel Islands, with some
535 rockfish communities shifting to shallower depths as a response to OMZ shoaling (Meyer-
536 Gutbrod et al. 2021). Spatial protections such as MPAs can provide corridors of protected habitat
537 across depth zones to allow for this type of adaptive migratory process. The combined effects of
538 large-scale environmental stressors and species-specific life histories on habitat use across depth
539 gradients have the potential to alter an MPAs effectiveness in the near and long-term.

540 We used the same model framework across two species and one species group to
541 understand the importance of MPA status, habitat type, and depth in determining patterns of
542 abundance and biomass. Across all models, the model performance indicated that these factors
543 were important in explaining the observed patterns, however other aspects of the system could be
544 incorporated to more accurately evaluate conservation efforts. Future studies will work to
545 integrate factors such as distance to reserve edge, presence of other ephemeral habitats (e.g.
546 ophiuroid or urchin barrens), and oceanographic parameters. BRUVs are particularly well suited
547 to adaptive monitoring programs, in that they are deployable in multiple habitats, relatively
548 inexpensive to operate and provide a video record that can be reassessed over time (Langlois et
549 al. 2010; Whitmarsh et al. 2017).

550 The California MPA network will continue to work towards protecting marine
551 biodiversity and populations of key fished species across the state. Our results demonstrate the
552 realized benefits of a well-designed and well enforced protection network, with a nuanced look

at how two geographically distinct MPAs might effectively protect different fisheries targets. We also highlight the importance of acknowledging and describing the limitations of particular MPAs when assessing an MPA network to align expectations with realistic outcomes. Continued monitoring efforts will provide valuable ecological knowledge as MPAs age and management efforts adapt to preserve fisheries in the face of climate uncertainty.

Acknowledgements

This work would not be possible without funding support from the California Ocean Protection Council and California Seagrant (Grant Numbers R/MPA-43 and R/MPA- 48). Special thanks to C. Honeyman, A. Parsons-field, J. Kolda, B. Brock, B. Behar, P. Campbell, W. Horstmeyer, N. Castaneda, S. Jaeger, K. McCaffrey, S. Urgoiti Crespo, G. Hansen, and M. O'Connell for assistance with fieldwork. Thank you to Y. Chen, Y. Sha, T. Hozdic, G. Simmons, J. Zounes, and J. Eisaguirre for video analysis. Thank you to R. Starr, J. Lindholm, and J. Todd for advice and insightful discussions. Thanks to A. Giraldo Ospina and C. Free for help with data analysis.

References

Abesamis RA, Langlois T, Birt M, et al (2018) Benthic habitat and fish assemblage structure from shallow to mesophotic depths in a storm-impacted marine protected area. Coral Reefs 37:81–97. https://doi.org/10.1007/s00338-017-1635-0

Aburto-Oropeza O, Dominguez-Guerrero I, Cota-Nieto J, Plomozo-Lugo T (2009) Recruitment and ontogenetic habitat shifts of the yellow snapper (Lutjanus argentiventris) in the Gulf of California. Mar Biol 156:2461–2472. https://doi.org/10.1007/s00227-009-1271-5

Andradi-Brown DA, Macaya-Solis C, Exton DA, et al (2016) Assessing Caribbean Shallow and Mesophotic Reef Fish Communities Using Baited-Remote Underwater Video (BRUV) and Diver-Operated Video (DOV) Survey Techniques. PLOS ONE 11:e0168235. https://doi.org/10.1371/journal.pone.0168235

Baillon S, Hamel J-F, Wareham VE, Mercier A (2012) Deep cold-water corals as nurseries for fish larvae. Frontiers in Ecology and the Environment 10:351–356. https://doi.org/10.1890/120022

Bejarano S, Pardede S, Campbell SJ, et al (2019) Herbivorous fish rise as a destructive fishing practice falls in an Indonesian marine national park. Ecological Applications 29:e01981. https://doi.org/10.1002/eap.1981

Bell JJ, Micaroni V, Harris B, et al (2024) Global status, impacts, and management of rocky temperate mesophotic ecosystems. Conservation Biology 38:e13945. https://doi.org/10.1111/cobi.13945

Bellquist LF, Lowe CG, Caselle JE (2008) Fine-scale movement patterns, site fidelity, and habitat selection of ocean whitefish (*Caulolatilus princeps*). Fisheries Research 91:325–335. https://doi.org/10.1016/j.fishres.2007.12.011

Bennett K, Wilson S k., Shedrawi G, et al (2016) Can diver operated stereo-video surveys for fish be used to collect meaningful data on benthic coral reef communities? Limnology and Oceanography: Methods 14:874–885. https://doi.org/10.1002/lom3.10141

Blanchette CA, Broitman BR, Gaines SD (2006) Intertidal community structure and oceanographic patterns around Santa Cruz Island, CA, USA. Mar Biol 149:689–701. https://doi.org/10.1007/s00227-005-0239-3

Brokovich E, Einbinder S, Shashar N, et al (2008) Descending to the twilight-zone: changes in coral reef fish assemblages along a depth gradient down to 65 m. Marine Ecology Progress Series 371:253–262. https://doi.org/10.3354/meps07591

Brown K, Monk J, Williams J, et al (2022) Depth and benthic habitat influence shallow and mesophotic predatory fishes on a remote, high-latitude coral reef. PLOS ONE 17:e0265067. https://doi.org/10.1371/journal.pone.0265067

Cappo M, Harvey E, Shortis M (2006) Counting and measuring fish with baited video techniques-an overview. In: Australian Society for Fish Biology Workshop Proceedings. Australian Society for fish biology Tasmania, pp 101–114

Cappo M, Speare P, De'ath G (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great

Barrier Reef Marine Park. Journal of Experimental Marine Biology and Ecology 302:123–152. https://doi.org/10.1016/j.jembe.2003.10.006

Caselle JE, Rassweiler A, Hamilton SL, Warner RR (2015) Recovery trajectories of kelp forest animals are rapid yet spatially variable across a network of temperate marine protected areas. Sci Rep 5:14102. https://doi.org/10.1038/srep14102

Cerrano C, Bastari A, Calcinai B, et al (2019) Temperate mesophotic ecosystems: gaps and perspectives of an emerging conservation challenge for the Mediterranean Sea. The European Zoological Journal 86:370–388. https://doi.org/10.1080/24750263.2019.1677790

Chaikin S, Dubiner S, Belmaker J (2022) Cold-water species deepen to escape warm water temperatures. Global Ecology and Biogeography 31:75–88. https://doi.org/10.1111/geb.13414

Curley BG, Kingsford MJ, Gillanders BM (2002) Spatial and habitat-related patterns of temperate reef fish assemblages: implications for the design of Marine Protected Areas. Mar Freshwater Res 53:1197–1210. https://doi.org/10.1071/mf01199

Dahms C, Killen SS (2023) Temperature change effects on marine fish range shifts: A meta-analysis of ecological and methodological predictors. Global Change Biology 29:4459–4479. https://doi.org/10.1111/gcb.16770

Dames V, Bernard A, Floros C, et al (2020) Zonation and reef size significantly influence fish population structure in an established marine protected area, iSimangaliso Wetland Park, South Africa. Ocean & Coastal Management 185:105040. https://doi.org/10.1016/j.ocecoaman.2019.105040

Dennis D, Plagányi É, Van Putten I, et al (2015) Cost benefit of fishery-independent surveys: Are they worth the money? Marine Policy 58:108–115. https://doi.org/10.1016/j.marpol.2015.04.016

Di Lorenzo M, Claudet J, Guidetti P (2016) Spillover from marine protected areas to adjacent fisheries has an ecological and a fishery component. Journal for Nature Conservation 32:62–66. https://doi.org/10.1016/j.jnc.2016.04.004

Dorman SR, Harvey ES, Newman SJ (2012) Bait Effects in Sampling Coral Reef Fish Assemblages with Stereo-BRUVs. PLOS ONE 7:e41538. https://doi.org/10.1371/journal.pone.0041538

Dulvy NK, Rogers SI, Jennings S, et al (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. Journal of Applied Ecology 45:1029–1039. https://doi.org/10.1111/j.1365-2664.2008.01488.x

Elorduy-Garay JF, Caraveo-Patiño J (1994) Feeding habits of the ocean whitefish, Caulolatilus princeps Jenyns 1842 (Pisces: Branchiostegidae), in La Paz Bay, B.C.S., Mexico. Ciencias Marinas 20:199–218. https://doi.org/10.7773/cm.v20i2.961

Fewings MR, Washburn L, Ohlmann JC (2015) Coastal water circulation patterns around the Northern Channel Islands and Point Conception, California. Progress in Oceanography 138:283–304. https://doi.org/10.1016/j.pocean.2015.10.001

Field SA, O'connor PJ, Tyre AJ, Possingham HP (2007) Making monitoring meaningful. Austral Ecology 32:485–491. https://doi.org/10.1111/j.1442-9993.2007.01715.x

Fox HE, Soltanoff CS, Mascia MB, et al (2012) Explaining global patterns and trends in marine protected area (MPA) development. Marine Policy 36:1131–1138. https://doi.org/10.1016/j.marpol.2012.02.007

Froese R, Pauly D (2000) FishBase 2000: Concepts Designs and Data Sources. WorldFish

Gaines SD, White C, Carr MH, Palumbi SR (2010) Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences 107:18286–18293. https://doi.org/10.1073/pnas.0906473107

Gibson RN, Robb L, Wennhage H, Burrows MT (2002) Ontogenetic changes in depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground. Marine Ecology Progress Series 229:233–244. https://doi.org/10.3354/meps229233

Giraldo-Ospina A, Kendrick GA, Hovey RK (2020) Depth moderates loss of marine foundation species after an extreme marine heatwave: could deep temperate reefs act as a refuge? Proceedings of the Royal Society B: Biological Sciences 287:20200709. https://doi.org/10.1098/rspb.2020.0709

Gleason M, Fox E, Ashcraft S, et al (2013) Designing a network of marine protected areas in California: Achievements, costs, lessons learned, and challenges ahead. Ocean & Coastal Management 74:90–101. https://doi.org/10.1016/j.ocecoaman.2012.08.013

Goetze JS, Wilson S, Radford B, et al (2021) Increased connectivity and depth improve the effectiveness of marine reserves. Global Change Biology 27:3432–3447. https://doi.org/10.1111/gcb.15635

Golden NE, Cochrane GR (2013) California State Waters Map Series Data Catalog. U.S. Geological Survey

Grorud-Colvert K, Claudet J, Tissot BN, et al (2014) Marine Protected Area Networks: Assessing Whether the Whole Is Greater than the Sum of Its Parts. PLOS ONE 9:e102298. https://doi.org/10.1371/journal.pone.0102298

Grüss A, Robinson J, Heppell SS, et al (2014) Conservation and fisheries effects of spawning aggregation marine protected areas: What we know, where we should go, and what we need to get there. ICES Journal of Marine Science 71:1515–1534. https://doi.org/10.1093/icesjms/fsu038

Halpern BS, Lester SE, McLeod KL (2010) Placing marine protected areas onto the ecosystem-based management seascape. Proceedings of the National Academy of Sciences 107:18312–18317. https://doi.org/10.1073/pnas.0908503107

Hamilton SL, Caselle JE, Malone DP, Carr MH (2010) Incorporating biogeography into evaluations of the Channel Islands marine reserve network. PNAS 107:18272–18277. https://doi.org/10.1073/pnas.0908091107

Hamilton SL, Caselle JE, Standish JD, et al (2007) Size-Selective Harvesting Alters Life Histories of a Temperate Sex-Changing Fish. Ecological Applications 17:2268–2280. https://doi.org/10.1890/06-1930.1

Harasti D, Malcolm H, Gallen C, et al (2015) Appropriate set times to represent patterns of rocky reef fishes using baited video. Journal of Experimental Marine Biology and Ecology 463:173–180. https://doi.org/10.1016/j.jembe.2014.12.003

Harms S, Winant CD (1998) Characteristic patterns of the circulation in the Santa Barbara Channel. Journal of Geophysical Research: Oceans 103:3041–3065. https://doi.org/10.1029/97JC02393

Harvey ES, McLean DL, Goetze JS, et al (2021) The BRUVs workshop – An Australia-wide synthesis of baited remote underwater video data to answer broad-scale ecological questions about fish, sharks and rays. Marine Policy 127:104430. https://doi.org/10.1016/j.marpol.2021.104430

Harvey ES, Shortis MR (1998) Calibration stability of an underwater stereo-video system: implications for measurement accuracy and precision. Marine Technology Society Journal 32:3–17

Heyns-Veale ER, Bernard ATF, Richoux NB, et al (2016) Depth and habitat determine assemblage structure of South Africa's warm-temperate reef fish. Mar Biol 163:158. https://doi.org/10.1007/s00227-016-2933-8

Honeyman C, Carlson P, Jainese C, et al (2023) Correspondence among multiple methods provides confidence when measuring marine protected area effects for species and assemblages. Journal of Applied Ecology 60:2699–2712. https://doi.org/10.1111/1365-2664.14515

Horn MH, Allen LG (1978) A Distributional Analysis of California Coastal Marine Fishes. Journal of Biogeography 5:23–42. https://doi.org/10.2307/3038105

Howard RA, Ciannelli L, Wakefield WW, Haltuch MA (2023) Comparing fishery-independent and fishery-dependent data for analysis of the distributions of Oregon shelf groundfishes. Fisheries Research 258:106553. https://doi.org/10.1016/j.fishres.2022.106553

Jacquemont J, Loiseau C, Tornabene L, Claudet J (2024) 3D ocean assessments reveal that fisheries reach deep but marine protection remains shallow. Nat Commun 15:4027. https://doi.org/10.1038/s41467-024-47975-1

James LC, Marzloff MP, Barrett N, et al (2017) Changes in deep reef benthic community composition across a latitudinal and environmental gradient in temperate Eastern Australia. Marine Ecology Progress Series 565:35–52. https://doi.org/10.3354/meps11989

Jones RE, Griffin RA, Herbert RJH, Unsworth RKF (2021) Consistency Is Critical for the Effective Use of Baited Remote Video. Oceans 2:215–232. https://doi.org/10.3390/oceans2010013

Jones RE, Griffin RA, Januchowski-Hartley SR, Unsworth RKF (2020) The influence of bait on remote underwater video observations in shallow-water coastal environments associated with the North-Eastern Atlantic. PeerJ 8:e9744. https://doi.org/10.7717/peerj.9744

Kahng S, Copus JM, Wagner D (2017) Mesophotic Coral Ecosystems. In: Rossi S, Bramanti L, Gori A, Orejas C (eds) Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots. Springer International Publishing, Cham, pp 185–206

Karpov KA, Bergen M, Geibel JJ (2012) Monitoring fish in California Channel Islands marine protected areas with a remotely operated vehicle: the first five years. Marine Ecology Progress Series 453:159–172. https://doi.org/10.3354/meps09629

Kelaher BP, Coleman MA, Broad A, et al (2014) Changes in Fish Assemblages following the Establishment of a Network of No-Take Marine Reserves and Partially-Protected Areas. PLOS ONE 9:e85825. https://doi.org/10.1371/journal.pone.0085825

Kirlin J, Caldwell M, Gleason M, et al (2013) California's Marine Life Protection Act Initiative: Supporting implementation of legislation establishing a statewide network of marine protected areas. Ocean & Coastal Management 74:3–13. https://doi.org/10.1016/j.ocecoaman.2012.08.015

Langlois T, Chabanet P, Pelletier D, Harvey E (2006) Baited underwater video for assessing reef fish populations in marine reserves. Fisheries Newsletter-South Pacific Commission 118:53

Langlois T, Goetze J, Bond T, et al (2020) A field and video annotation guide for baited remote underwater stereo-video surveys of demersal fish assemblages. Methods in Ecology and Evolution 11:1401–1409. https://doi.org/10.1111/2041-210X.13470

Langlois TJ, Harvey ES, Fitzpatrick B, et al (2010) Cost-efficient sampling of fish assemblages: comparison of baited video stations and diver video transects. Aquatic Biology 9:155–168. https://doi.org/10.3354/ab00235

Lenihan HS, Fitzgerald SP, Reed DC, et al (2022) Increasing spillover enhances southern California spiny lobster catch along marine reserve borders. Ecosphere 13:e4110. https://doi.org/10.1002/ecs2.4110

Li L, Hollowed AB, Cokelet ED, et al (2022) Three-dimensional ontogenetic shifts of groundfish in the Northeast Pacific. Fish and Fisheries 23:1221–1239. https://doi.org/10.1111/faf.12679

Lombardo SM, Adams AJ, Danylchuk AJ, et al (2020) Novel deep-water spawning patterns of bonefish (Albula vulpes), a shallow water fish. Mar Biol 167:187. https://doi.org/10.1007/s00227-020-03799-3

Love MS (2011) Certainly more than you want to know about the fishes of the Pacific Coast: a postmodern experience. Really Big Press

Love MS, Carr MH, Haldorson LJ (1991) The ecology of substrate-associated juveniles of the genusSebastes. Environ Biol Fish 30:225–243. https://doi.org/10.1007/BF02296891

Love MS, Yoklavich M, Thorsteinson LK (2002) The rockfishes of the northeast Pacific. Univ of California Press

Love MS, Yoklavich MM (2006) CHAPTER 10. Deep Rock Habitats. In: CHAPTER 10. Deep Rock Habitats. University of California Press, pp 253–266

Lucas S (1994) History and status of commercial live fish fisheries in California and the United States West Coast

Luo J, Ault JS, Ungar BT, et al (2020) Migrations and movements of Atlantic tarpon revealed by two decades of satellite tagging. Fish and Fisheries 21:290–318. https://doi.org/10.1111/faf.12430

MacDonald C, Bridge TCL, Jones GP (2016) Depth, bay position and habitat structure as determinants of coral reef fish distributions: Are deep reefs a potential refuge? Marine Ecology Progress Series 561:217–231. https://doi.org/10.3354/meps11953

Maestro M, Pérez-Cayeiro ML, Chica-Ruiz JA, Reyes H (2019) Marine protected areas in the 21st century: Current situation and trends. Ocean & Coastal Management 171:28–36. https://doi.org/10.1016/j.ocecoaman.2019.01.008

Marliave JB, Conway KW, Gibbs DM, et al (2009) Biodiversity and rockfish recruitment in sponge gardens and bioherms of southern British Columbia, Canada. Mar Biol 156:2247–2254. https://doi.org/10.1007/s00227-009-1252-8

McClanahan TR, Graham NAJ, Calnan JM, MacNeil MA (2007) Toward Pristine Biomass: Reef Fish Recovery in Coral Reef Marine Protected Areas in Kenya. Ecological Applications 17:1055–1067. https://doi.org/10.1890/06-1450

Meyer-Gutbrod E, Kui L, Miller R, et al (2021) Moving on up: Vertical distribution shifts in rocky reef fish species during climate-driven decline in dissolved oxygen from 1995 to 2009. Global Change Biology 27:6280–6293. https://doi.org/10.1111/gcb.15821

Miller RR, Field JC, Santora JA, et al (2017) Spatial valuation of California marine fisheries as an ecosystem service. Can J Fish Aquat Sci 74:1732–1748. https://doi.org/10.1139/cjfas-2016-0228

Moffitt EA, Wilson White J, Botsford LW (2011) The utility and limitations of size and spacing guidelines for designing marine protected area (MPA) networks. Biological Conservation 144:306–318. https://doi.org/10.1016/j.biocon.2010.09.008

Mumby PJ, Steneck RS, Roff G, Paul VJ (2021) Marine reserves, fisheries ban, and 20 years of positive change in a coral reef ecosystem. Conservation Biology 35:1473–1483. https://doi.org/10.1111/cobi.13738

Murray SN, Ambrose RF, Bohnsack JA, et al (1999) No-take Reserve Networks: Sustaining Fishery Populations and Marine Ecosystems. Fisheries 24:11–25. https://doi.org/10.1577/1548-8446(1999)024<0011:NRN>2.0.CO;2

Navarro-Martínez ZM, de la Guardia E, Szelistowski WA, Angulo-Valdés JA (2023) Habitats diversity and MPA regulations are insufficient in promoting healthy coral reef fish assemblages in Punta Francés National Park (Cuba). Regional Studies in Marine Science 60:102826. https://doi.org/10.1016/j.rsma.2023.102826

Noble-James T, Bullimore R, McBreen F, et al (2023) Monitoring benthic habitats in English Marine Protected Areas: Lessons learned, challenges and future directions. Marine Policy 157:105852. https://doi.org/10.1016/j.marpol.2023.105852

Nye JA, Link JS, Hare JA, Overholtz WJ (2009) Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series 393:111–129. https://doi.org/10.3354/meps08220

Olson AM, Hessing-Lewis M, Haggarty D, Juanes F (2019) Nearshore seascape connectivity enhances seagrass meadow nursery function. Ecological Applications 29:e01897. https://doi.org/10.1002/eap.1897

Pearson R, Stevens T (2015) Distinct cross-shelf gradient in mesophotic reef fish assemblages in subtropical eastern Australia. Marine Ecology Progress Series 532:185–196. https://doi.org/10.3354/meps11351

Pereira PHC, Macedo CH, Nunes J de ACC, et al (2018) Effects of depth on reef fish communities: Insights of a “deep refuge hypothesis” from Southwestern Atlantic reefs. PLOS ONE 13:e0203072. https://doi.org/10.1371/journal.pone.0203072

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate Change and Distribution Shifts in Marine Fishes. Science 308:1912–1915. https://doi.org/10.1126/science.1111322

Ponti M, Turicchia E, Ferro F, et al (2018) The understorey of gorgonian forests in mesophotic temperate reefs. Aquatic Conservation: Marine and Freshwater Ecosystems 28:1153–1166. https://doi.org/10.1002/aqc.2928

Rees M, Heyward A, Cappo M, et al (2004) Ningaloo Marine Park-Initial survey of seabed biodiversity in intermediate and deeper waters (March 2004). Australian Government, Australian Institute of Marine Science and Natural Heritage Trust

Region M (2003) Review of some California fisheries for 2002: market squid, sea urchin, Dungeness crab, prawn, coastal pelagic finfish, albacore, ocean salmon, nearshore live-fish, Pacific herring, and recreational

Roberts CM, Andelman S, Branch G, et al (2003) Ecological Criteria for Evaluating Candidate Sites for Marine Reserves. Ecological Applications 13:199–214. https://doi.org/10.1890/1051-0761(2003)013[0199:ECFECS]2.0.CO;2

Ross T, Du Preez C, Ianson D (2020) Rapid deep ocean deoxygenation and acidification threaten life on Northeast Pacific seamounts. Global Change Biology 26:6424–6444. https://doi.org/10.1111/gcb.15307

Saarman E, Gleason M, Ugoretz J, et al (2013) The role of science in supporting marine protected area network planning and design in California. Ocean & Coastal Management 74:45–56. https://doi.org/10.1016/j.ocecoaman.2012.08.021

Sala E, Giakoumi S (2018) No-take marine reserves are the most effective protected areas in the ocean. ICES Journal of Marine Science 75:1166–1168. https://doi.org/10.1093/icesjms/fsx059

Scholz A, Steinback C, Mertens M, et al (2006) Commercial fishing grounds and their relative importance off the Central Coast of California. Report submitted to the California Marine Life Protection Act Initiative (May 4)

Sullivan-Stack J, Aburto-Oropeza O, Brooks CM, et al (2022) A Scientific Synthesis of Marine Protected Areas in the United States: Status and Recommendations. Front Mar Sci 9:. https://doi.org/10.3389/fmars.2022.849927

Swadling DS, Knott NA, Taylor MD, et al (2022) Seascape connectivity of temperate fishes between estuarine nursery areas and open coastal reefs. Journal of Applied Ecology 59:1406–1416. https://doi.org/10.1111/1365-2664.14157

Taylor BM, McIlwain JL (2010) Beyond abundance and biomass: effects of marine protected areas on the demography of a highly exploited reef fish. Marine Ecology Progress Series 411:243–258. https://doi.org/10.3354/meps08672

Thorburn J, Wright PJ, Lavender E, et al (2021) Seasonal and Ontogenetic Variation in Depth Use by a Critically Endangered Benthic Elasmobranch and Its Implications for Spatial Management. Front Mar Sci 8:. https://doi.org/10.3389/fmars.2021.656368

Topping DT, Lowe CG, Caselle JE (2005) Home range and habitat utilization of adult California

sheephead, Semicossyphus pulcher (Labridae), in a temperate no-take marine reserve. Marine Biology 147:301–311. https://doi.org/10.1007/s00227-005-1573-1

White JW, Yamane MT, Nickols KJ, Caselle JE (2021) Analysis of fish population size distributions confirms cessation of fishing in marine protected areas. Conservation Letters 14:e12775. https://doi.org/10.1111/conl.12775

Whitmarsh SK, Fairweather PG, Huveneers C (2017) What is Big BRUVver up to? Methods and uses of baited underwater video. Rev Fish Biol Fisheries 27:53–73. https://doi.org/10.1007/s11160-016-9450-1

Williams J, Jordan A, Harasti D, et al (2019) Taking a deeper look: Quantifying the differences in fish assemblages between shallow and mesophotic temperate rocky reefs. PLOS ONE 14:e0206778. https://doi.org/10.1371/journal.pone.0206778

Willis TJ, Babcock RC (2000) A baited underwater video system for the determination of relative density of carnivorous reef fish. Mar Freshwater Res 51:755–763. https://doi.org/10.1071/mf00010

Young M, Carr M (2015) Assessment of Habitat Representation across a Network of Marine Protected Areas with Implications for the Spatial Design of Monitoring. PLOS ONE 10:e0116200. https://doi.org/10.1371/journal.pone.0116200

Ziegler SL, Johnson JM, Brooks RO, et al (2023) Marine protected areas, marine heatwaves, and the resilience of nearshore fish communities. Sci Rep 13:1405. https://doi.org/10.1038/s41598-023-28507-1

Table 1. Table showing the number of qualifying grid cells by depth bin within the marine protected area (MPA) and reference area (REF) at Anacapa and Carrington Pt. and the total survey area for each MPA and reference area.

		Depth Bin (m)			Study Area (km^2)
		30-50	**50-70**	**70-100**	
Anacapa	**MPA**	50	45	33	12.03
	REF	167	179	167	24.02
Carrington Pt.	**MPA**	342	NA	NA	11.73
	REF	322	NA	NA	13.68

Figure 1. Maps showing the study region and the two focal MPAs in the Santa Barbara Channel, Northern Channel Islands (NCI). A) shows the location of the NCI along the West Coast of North America. B) shows the NCI with red polygons delineating the NCI MPAs within the state wide California Marine Protected Area Network. Panel C) shows Carrington Pt. MPA and associated reference area while D) shows Anacapa MPA complex and associated reference area. Both panels C) and D) have dark grey shading representing mapped hard bottom and 10m bathymetry lines in light grey. Locations of BRUV surveys by year are shown in Figure S2.

Figure 2. Stack bar plot showing the proportion of observed habitat by depth bin from Anacapa and Carrington Point. Habitat was classified from BRUV surveys and was categorized based on visible habitat in which a survey was conducted.

Figure 3. Partial model predictions from a negative binomial generalized linear model used to test the effect of MPA Status, depth, and habitat on the MaxN and biomass of targeted rockfishes for Anacapa (A) and Carrington Point (B). The blue line and shaded region represent the model predictions and 95% CI for a particular predictor variable when all other variables are held constant. The points represent the partial residuals of the model. To standardize the display across islands and metrics we set all predictions to 'MPA' and 'Hard' for MPA status and habitat, while depth was set to the median value for that particular data set. The habitat codes 'M H' and 'M S' represent mixed hard and mixed soft habitats respectively.

Figure 4. Partial model predictions from the negative binomial generalized linear model used to test the effect of MPA Status, depth, and habitat on the MaxN and biomass of ocean whitefish for Anacapa (A) and Carrington Point (B). The blue line and shaded region

represent the model predictions and 95% CI for a particular predictor variable when all other variables are held constant. The points represent the partial residuals of the model. To standardize the display across islands and metrics we set all predictions to 'MPA' and 'Hard' for MPA status and habitat, while depth was set to the median value for that particular data set. The habitat codes 'M H' and 'M S' represent mixed hard and mixed soft habitats respectively.

Figure 5. Partial model predictions from the negative binomial generalized linear model used to test the effect of MPA Status, depth, and habitat on the MaxN and biomass of sheephead for Anacapa (A) and Carrington Point (B). The blue line and shaded region represent the model predictions and 95% CI for a particular predictor variable when all other variables are held constant. The points represent the partial residuals of the model. To standardize the display across islands and metrics we set all predictions to 'MPA' and 'Hard' for MPA status and habitat, while depth was set to the median value for that particular data set. The habitat codes 'M H' and 'M S' represent mixed hard and mixed soft habitats respectively.

Figure 6. Species-specific density histograms for the five targeted fish species; Copper Rockfish (A), Vermillion rockfish (B), Blue rockfish (C), ocean whitefish (D), and California sheephead (E) from Anacapa and Carrington Pt. The red density histograms represent data from within the MPA, while blue density histograms represent the data form reference areas open to fishing.

Figure 1

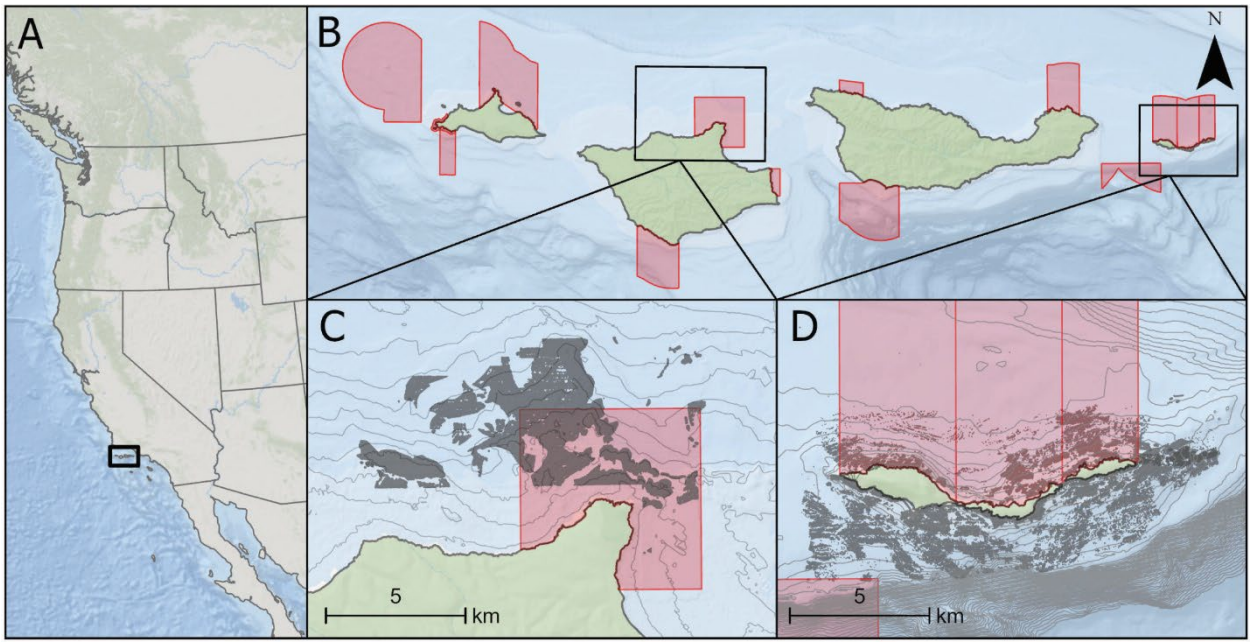


Figure 2

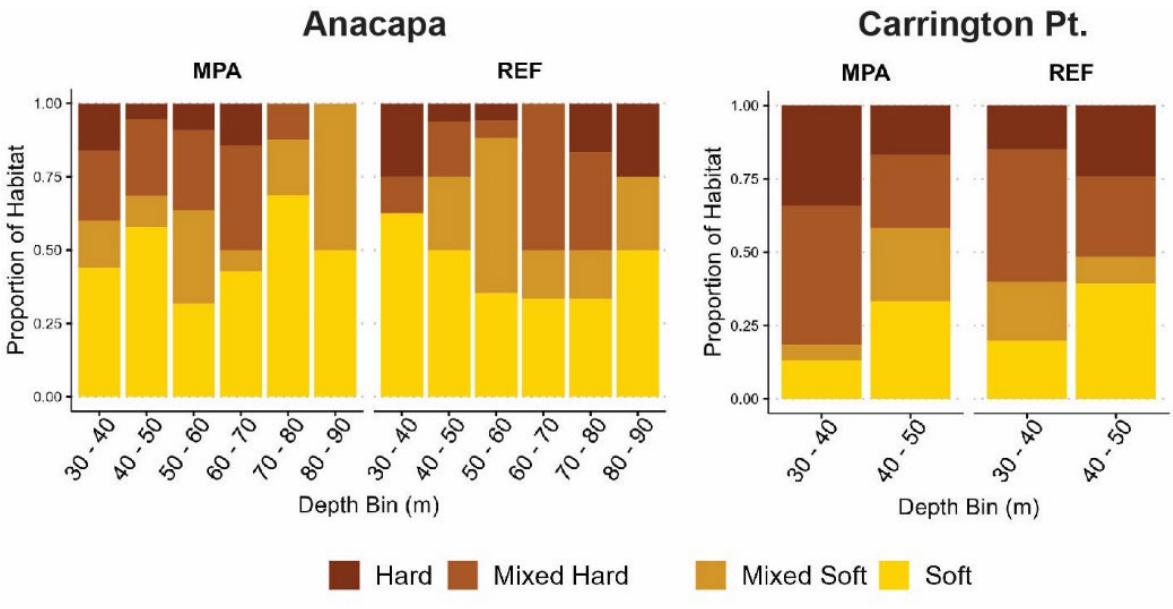

Anacapa
MPA
REF
Carrington Pt.
MPA
REF
Proportion of Habitat
1.00
0.75
0.50
0.25
0.00
30 - 40
40 - 50
50 - 60
60 - 70
70 - 80
80 - 90
Depth Bin (m)
Hard
Mixed Hard
Mixed Soft
Soft

Figure 3

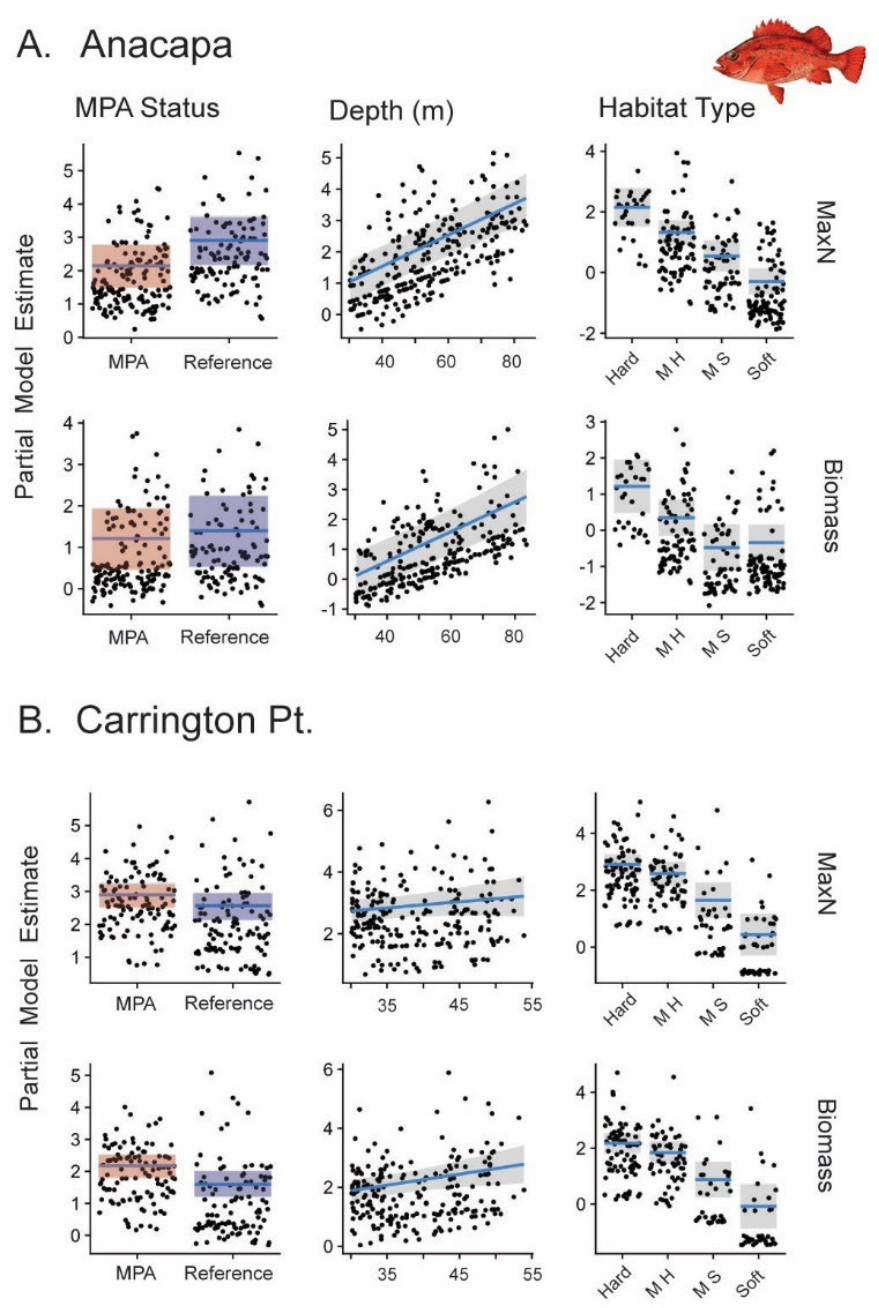

A. Anacapa
MPA Status
Depth (m)
Habitat Type
Partial Model Estimate
MaxN
Biomass
MPA
Reference
Hard
M H
M S
Soft
B. Carrington Pt.

Figure 4

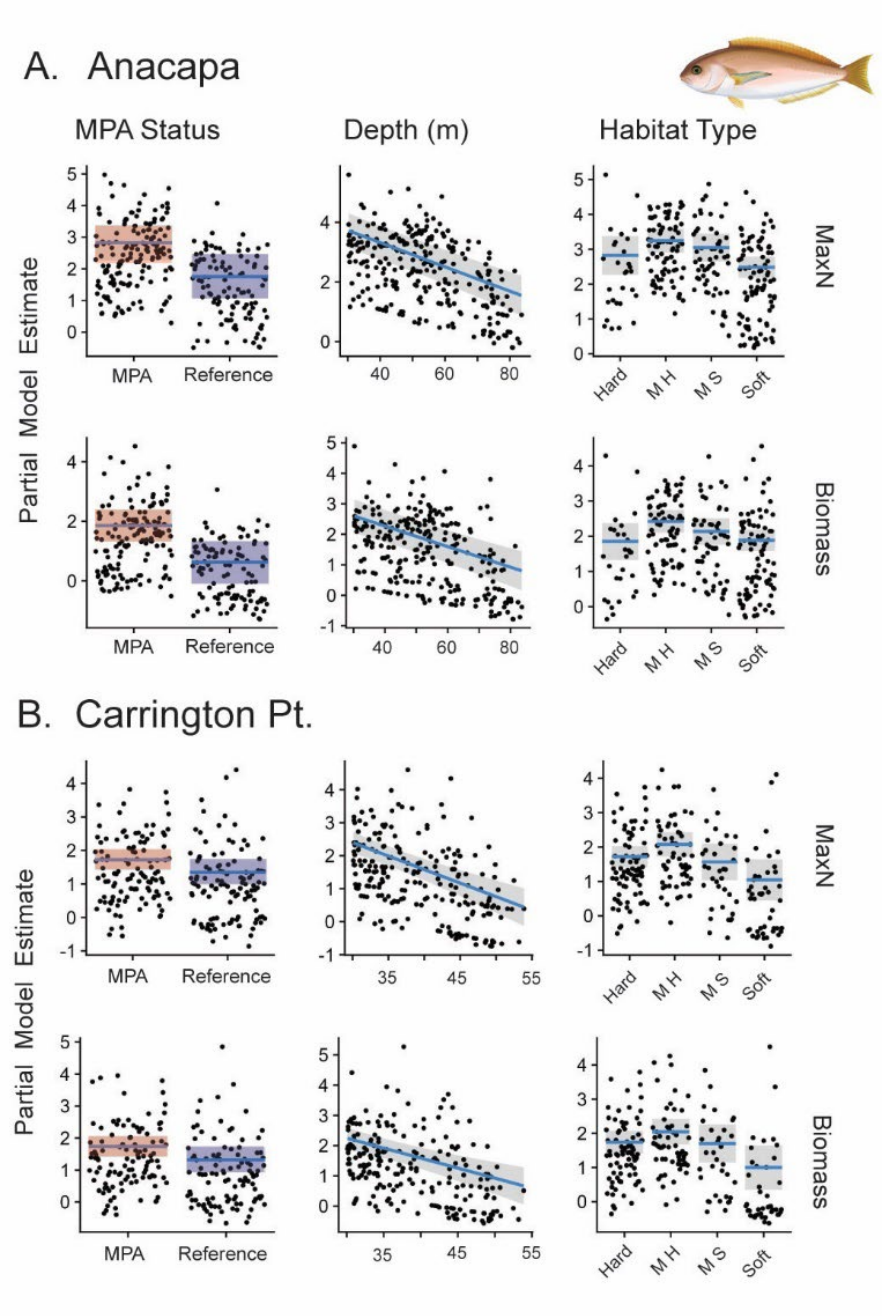

A. Anacapa
MPA Status
Depth (m)
Habitat Type
Partial Model Estimate
MaxN
Biomass
MPA
Reference
Hard
M H
M S
Soft
B. Carrington Pt.

Figure 5

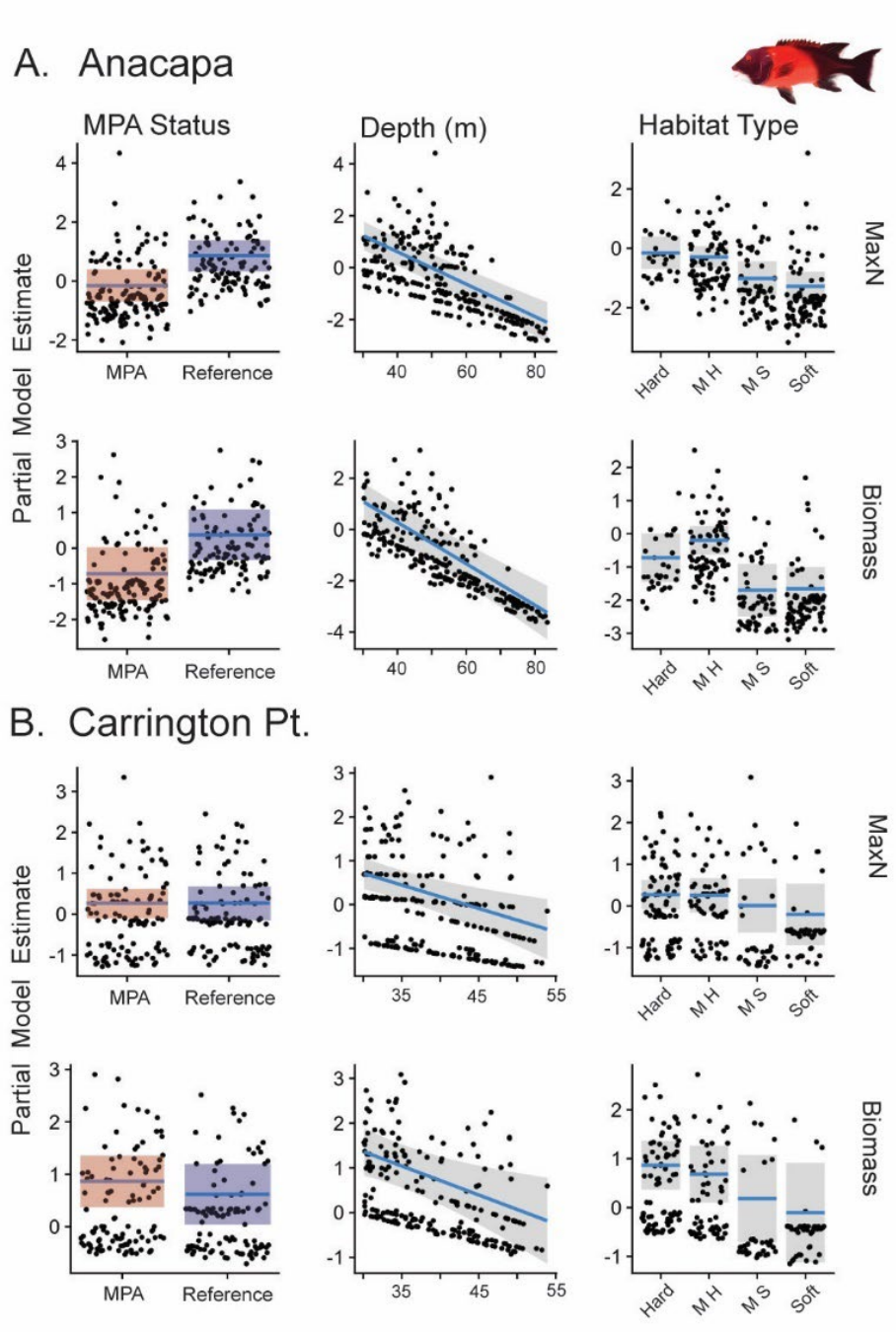
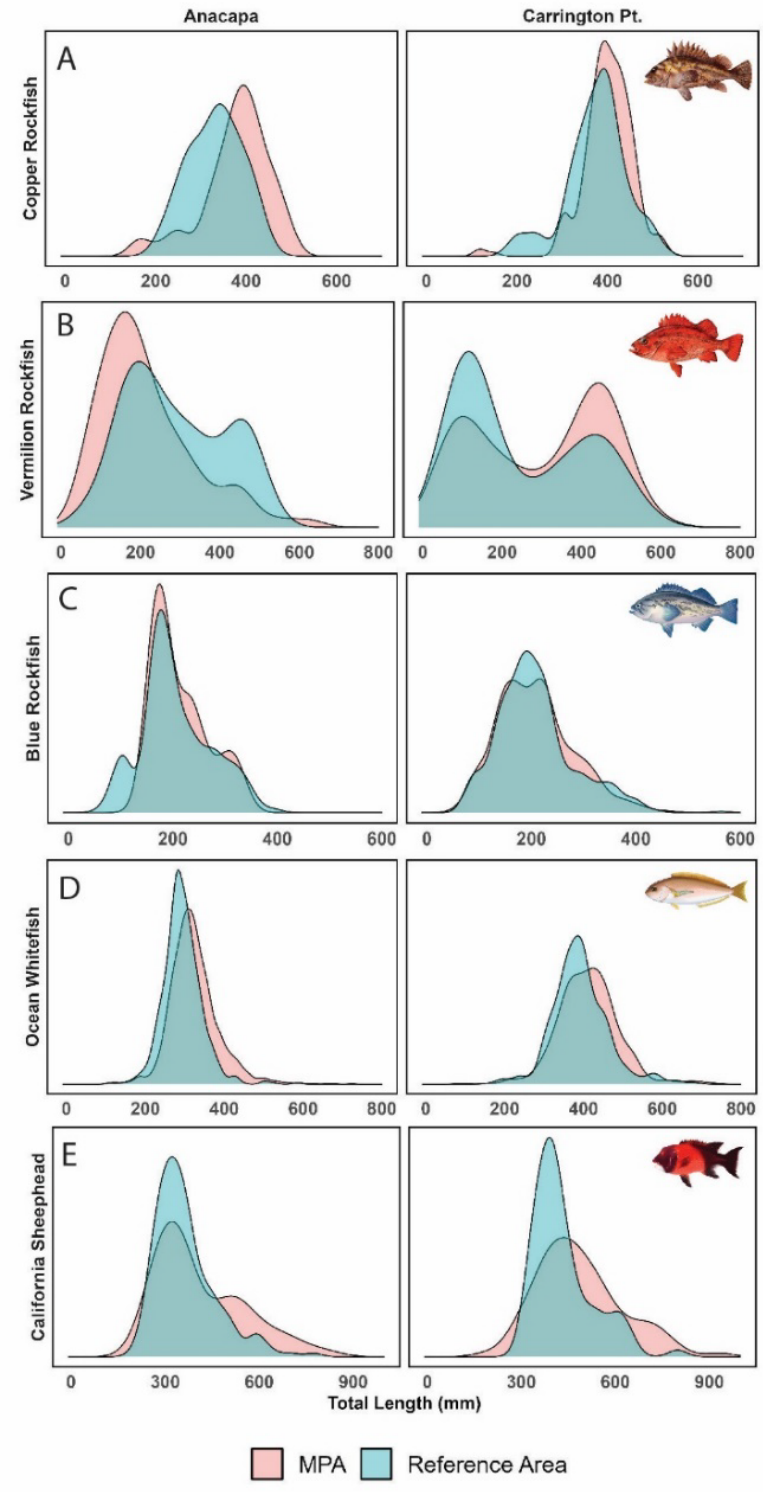

A. Anacapa
MPA Status
Depth (m)
Habitat Type
Partial Model Estimate
MaxN
Biomass
MPA
Reference
Hard
M H
M S
Soft
B. Carrington Pt.

Figure 6


Anacapa
Carrington Pt.
A
Copper Rockfish
B
Vermilion Rockfish
C
Blue Rockfish
D
Ocean Whitefish
E
California Sheephead
0
200
400
600
800
300
900
Total Length (mm)
MPA
Reference Area