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

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Abstract

Marine Protected Areas (MPAs) have been implemented globally as a conservation tool to improve the health and function of marine ecosystems. Research has focused on assessing MPA effectiveness, however certain habitats and communities are often avoided because they are difficult or expensive to monitor. Mesophotic (30-100m) rocky reef fish communities are a valuable commercial and recreational resource that is highly targeted but often overlooked in monitoring due to depth restricted sampling. We used two MPAs in California's statewide protection network, along with parried reference sites, to test how protection status along with environmental conditions influenced the abundance and biomass of three highly targeted species 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 and the influence of protection was mixed. This work highlights how species with high habitat affinities benefit differently from protection, as a function of depth and habitat representation within the MPA/reference pair. To accurately evaluate MPAs, and the network as a whole, researchers must recognize organism-habitat relationships and incorporate them when assessing conservation efforts.

Introduction

Marine Protected Areas (MPAs) have been implemented globally as a means of protecting marine ecosystems from anthropogenic pressures (Gleason et al. 2013; Sullivan-Stack et al. 2022; Maestro et al. 2019). 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 (Brown et al. 2022; Andradi-Brown et al. 2016; Brokovich et al. 2008).

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 (Baillon et al. 2012; Kahng et al. 2017; Giraldo-Ospina et al. 2020). These habitats also provide an important ontogenetic bridge between shallow

96 nursery habitats and deeper adult habitats (Love 2011; Swadling et al. 2022). Finally, these
97 deep habitats might be critical refuges from the effects of climate change, such as increases
98 in sea water temperature (MacDonald et al. 2016; Pereira et al. 2018). Together these
99 factors make mesophotic reefs important contributors to marine biodiversity and a
100 necessary component of an effective MPA network.

101 One of the expected benefits of MPAs is the buildup of targeted species within its
102 boundaries and consequently, an MPA's performance is often measured by its ability to
103 enhance the biomass and abundance of fisheries targets (Caselle et al. 2015; Lenihan et al.
104 2022). Recreational and commercial fisheries often have a number of targeted species that
105 utilize a wide breadth of habitats across the seascape (Region 2003; Scholz et al. 2006).
106 Effective MPA networks should protect habitats ranging from sand, sand-rock ecotone,
107 rocky reefs, and pelagic zones, while incorporating these habitats across an extensive depth
108 range (Young and Carr 2015). Despite the fact that MPAs are an ecosystem conservation
109 tool, it is unlikely any MPA can achieve a 'one-size fits all' design, instead, any single
110 MPA will likely be more effective at protecting some species compared to others. Factors
111 such as species movement, the availability of preferred habitat, oceanographic conditions,
112 predator and prey abundances, and recruitment dynamics will all influence an MPA's
113 ability to enhance particular targeted species (Moffitt et al. 2011).

114 With the purpose of better understanding the effects of MPAs on mesophotic rocky
115 reef fish communities, we implemented the use of BRUV camera systems at two
116 geographically distinct MPAs (and nearby reference areas) within California's Northern
117 Channel Islands (Figure 1): Carrington Point State Marine Reserve (SMR) at Santa Rosa
118 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; Hamilton et al. 2010; Caselle 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

142 protection status on the abundance and biomass of targeted fish species. These two focal
143 MPAs are nested into larger networks; first, a network within the Channel Islands (Figure
144 1B), which itself is nested into a large California statewide network of protected areas.
145 Previous studies have shown individual variation in MPA performance across the network
146 for shallow reefs and kelp forests (Caselle et al. 2015; Ziegler et al. 2023). Here we use
147 two MPAs to demonstrate the potential for individual MPA variation in performance in
148 presumably more stable, deeper water habitats.
149

150 Methods

151 *Sampling Design*

152 Our BRUV design was modified from existing designs used extensively to monitor a
153 variety of marine habitats in Australia (Willis and Babcock 2000; Goetze et al. 2021; Harvey et
154 al. 2021). We deployed BRUVs using a stratified random approach, using geological habitat
155 maps and bathymetry to target rocky reef habitat within our sampling depths (30-100m).
156 Because the Carrington Pt. SMR has very little habitat >50m deep, survey depths at this site
157 were generally limited to this maximum depth, while surveys at Anacapa extended to 100m
158 depth. A map showing each MPA/reference zone polygon can be found in Figure S1.
159 Sampling effort included both MPA and reference sites (where fishing is allowed)
160 on any single day to control for environmental variability between sampling days.
161 Sampling took place from August to October for four consecutive years (2019-2022). In
162 2020, we also sampled in June at Anacapa Island as a response to the shutdown of
163 commercial passenger fishing vessels (CPFV) at that location due to COVID-19. We
164 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. A more detailed description of BRUV sampling methods and tools can be found in supplemental materials Methods S1.

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 frame. In some instances, we were not able to accurately measure all individuals in a particular MaxN frame due to the camera angle or obstructions blocking one of the cameras. In this case, we measured as many individuals as possible from the MaxN frame. We estimated the biomass of individual fishes 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. We obtained length-weight fitting parameters from the literature and FishBase (Froese and Pauly 2000). Because not all fish in the MaxN frame can be measured (some individuals are not within view of both cameras) we used the mean of all individual weights in the MaxN frame, multiplied by the MaxN for each

188 individual species to estimate biomass. We classified species as targeted by fishing or non-
189 targeted by fishing using information from the CA Department of Fish and Wildlife as well
190 as local knowledge of the authors.

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

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

200

201 *Focal fish species*

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

209 California sheephead, which appeared on nearly half of our surveys, are the largest and
210 only targeted wrasse (*Labridae*) species that inhabits the study area. California sheephead are not

211 only highly targeted by recreational anglers, but also by a smaller live-fish commercial fishery
212 (Love 2011). As a protogynous hermaphrodite (female at birth with the potential to transition to
213 male later in life), fishing pressure has a more complex effect on the sex/size structure and the
214 reproductive potential of a local population (Hamilton et al. 2007).

215 With 21 unique species of rockfish observed in this study, we more closely
216 examined a sub-group of rockfish that we considered "targeted" and are more likely to
217 respond to protection from fishing. This grouping excludes small-bodied rockfish that are
218 infrequently caught and almost never retained by anglers such as halfbanded (*S.*
219 *semicinctus*) and calico rockfish (*S. dallii*). Three targeted species: vermilion (*S. miniatus*),
220 copper (*S. caurinus*), and blue rockfish (*S. mystinus*) made up over 70% of the targeted
221 rockfish observed on our surveys. Vermilion and copper rockfish are long-lived (50-60
222 years) high value species that have a significant recreational and commercial fishery,
223 increasing their potential to benefit from protection. Blue rockfish are a schooling, largely
224 planktivorous species, that is of moderate value to recreational and commercial fishing
225 (Love 2011).

226

227 *Abundance and Biomass Modeling*

228 Generalized linear models (GLM) were used to understand how differences in habitat
229 type, depth, and MPA status influenced fish abundance and biomass. To account for species-
230 specific habitat preference and other potential traits (e.g. movement patterns) we ran models on
231 targeted rockfish, ocean whitefish, and California sheephead separately. We also ran separate
232 models for each island because the depth ranges differed (Carrington Pt. SMR ranged from 30m
233 - 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 median 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 S5) 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 S5). 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 S6. 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 S6). 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 S7). 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 S7). The patterns at Carrington Pt. were less consistent, with depth only being a significant predictor of biomass (p-value = 0.02, Figure 3 & Table S7), 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 S7 & 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 S7).

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 S8). 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 S8). We did not find a significant interaction term between MPA status and habitat type for either ocean whitefish metric (Figure S4 & Table S8). 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 S8).

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 S9). 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 S9), and had significantly lower biomass on 'soft' vs 'hard' habitat at Anacapa ('soft' p-value = 0.05; Figure 5 & Table S9). 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

349 from this result. At Anacapa, we found a significant negative MPA effect for the abundance and
350 biomass of sheephead, with greater values in the reference area (MaxN p-value = 0.01, estimate
351 = 1.01; biomass p-value = 0.03, estimate = 1.09; Figure 5 & Table S9).
352
353 Deviance Explained
354 Across all species and both metrics, the model framework performed slightly better at
355 Anacapa compared to Carrington Pt., with the deviance explained ranging from 0.46 – 0.22 at
356 Anacapa and 0.22 – 0.17 at Carrington Pt. (Tables S7 – S9). This is likely related to the larger
357 available depth range at Anacapa and that depth was a significant predictor of abundance and
358 biomass for all three species in this study. The highest deviance explained was for California
359 sheephead at Anacapa (DE = 0.46 for MaxN; DE = 0.45 for Biomass; Table S9) and is most
360 likely related to the smaller range in MaxN and biomass values associated with the California
361 sheephead data compared to the larger range associated with targeted rockfish and ocean
362 whitefish.
363
364 *Focal Species Size Structure*
365 We plotted the density of individual fish total lengths in MPAs and reference areas
366 for the five most common targeted species in our study; copper rockfish (n = 506),
367 vermilion rockfish (n = 459), blue rockfish (n = 1760), ocean whitefish (n = 5767), and
368 California sheephead (n = 603) (Figure 6). Copper rockfish were generally larger inside the
369 MPAs at both Anacapa and Carrington Pt., with the MPA containing more individuals
370 >400mm TL (Figure 6A). Vermilion rockfish had a bimodal size structure with multiple
371 size classes present at Carrington Pt. and Anacapa (Figure 6B). Inside the Anacapa MPA,

372 the population size structure is dominated by smaller sized individuals (<20cm), with
373 proportionally fewer adult fishes. While the population size structure patterns for
374 vermillion rockfish at Carrington Pt. appear to be more related to protection from fishing,
375 with proportionally larger individuals inside the MPA. The smaller-bodied schooling blue
376 rockfish had similar population size structure across protection zones at Carrington Pt. and
377 Anacapa (Figure 6C). Ocean whitefish and California Sheephead showed similar patterns
378 at Anacapa and Carrington, with a greater proportion of larger individuals inside the MPA
379 at each location (Figure 6D & E).
380
381 Discussion
382 In this study we show that environmental drivers, such as depth and habitat availability,
383 need to be considered when assessing the ability of MPAs to enhance the biomass and
384 abundance of targeted species. MPA effectiveness, in both tropical and temperate marine
385 ecosystems, has been linked to benthic features such as the amount of consolidated hard bottom,
386 reef complexity, and habitat continuity (Dames et al. 2020). Individual species have been shown
387 to respond differently to such features, hence species-habitat associations must be considered
388 during MPA implementation, when defining MPA goals, and when assessing performance.
389 Studies have shown that a lack of preferred habitat inside the protection zone can limit the ability
390 of MPAs to enhance species and functional diversity (Navarro-Martínez et al. 2023). MPAs are
391 designed as ecosystem management tools, with broad goals of protecting biodiversity, yet
392 individual species can have widely varying habitat requirements. Many MPA design processes,
393 especially for MPA networks, try to encompass habitat replication and representation (Roberts et
394 al. 2003; Halpern et al. 2010; Saarman et al. 2013), but in practice, it is impossible to design

395 optimally for every species. Thus, accounting for habitat in post implementation monitoring and
396 choice of reference areas, can help to set realistic expectations for MPA performance.
397 The Carrington Pt. MPA and adjacent reference area had similar amounts of continuous
398 hard substrate, which indicated that the greater biomass of targeted rockfishes in the MPA was
399 likely related to protection more than habitat. Rockfish (family *Sebastes*) are generally
400 characterized as a demersal, rock associated and heavily fished family, and it appears that the
401 Carrington Pt. MPA is well designed for their protection. Inside the Anacapa MPA, there was a
402 notable lack of continuous hard substrate, particularly at depth, that appears to limit the
403 performance of the MPA at that location for this rock-associated fish group and makes
404 comparisons with the paired reference area challenging. However, the Anacapa MPA is likely
405 more effective at enhancing the ocean whitefish population, a more mobile species that is
406 associated with the sand-rock ecotone (Bellquist et al. 2008). Habitat maps and *in situ*
407 observations from Anacapa MPA and reference area showed that these locations were dominated
408 by a mix of soft, sandy habitat and isolated patch reefs. Ocean whitefish abundance and biomass
409 was also strongly associated with depth, but unlike targeted rockfish, ocean whitefish are more
410 abundant in shallower areas, with the majority of observations occurring shallower than 60m.
411 The examples above, comparing very different fish species groups, demonstrate how
412 scientific guidelines and a network approach to MPA design can help meet ecosystem goals and
413 protect populations of different species across a variety of habitats. The creation of networks,
414 with numerous reserves spread across various habitats, has become the standard by which to
415 structure marine no-take zones, both at the local and global scale. The California Marine Life
416 Protection Act (MLPA) established the network of MPAs throughout California with the goals of
417 protecting ecosystem biodiversity and protecting and rebuilding populations of key species. This

418 process relied on MPA design guidelines from a scientific advisory committee and chief among
419 those guidelines was 'habitat representation' throughout the network (Saarman et al. 2013). At
420 the network level, this was achieved by including a variety of major habitat types such as; rocky
421 intertidal zones, estuaries, and shallow and deep subtidal habitat. Here we show that a more
422 nuanced treatment of habitat within an MPA can provide critical information on individual MPA
423 performance for key species (Young and Carr 2015).

424 By incorporating habitat availability in and out of the MPAs and studying deeper zones
425 than previously explored, we found several results that differed from prior studies and/or our
426 expectations. Contrary to our predictions and prior studies of shallower reefs in the area (Caselle
427 et al. 2015; Honeyman et al. 2023), California sheephead abundance and biomass at these deeper
428 depths was significantly greater in the Anacapa reference area which is open to fishing. Active
429 tracking data has shown that California sheephead use a variety of habitats, but tend to favor
430 rocky-reefs, spending 50% - 70% of their time on hard, consolidated substrate (Topping et al.
431 2005). The deep-water habitat within the Anacapa MPA is lacking this hard substrate, which is
432 more abundant in the shallow kelp forests of the Anacapa MPA. This illustrates the importance
433 of surveying the full range of depths for species of interest when evaluating MPA performance
434 or advising fisheries management. A more comprehensive approach to MPA design and
435 management can be achieved by filling gaps in our knowledge of how MPAs may differentially
436 enhance fish communities at all depths and habitat types.

437 To measure the ecological effects of a marine protected areas, especially without data for
438 that site prior to MPA implementation, researchers often use a nearby fished area (reference site)
439 as a control by which hypotheses about the cessation of fishing can be tested. Selection of these
440 'control' sites must weigh numerous factors such as; habitat type, depth range, species

441 composition, and seasonal oceanographic characteristics, when deciding on location and scale.
442 Often the easiest way to broadly control for various environmental factors is by placing the
443 reference area in close proximity to the MPA. However, unlike strictly controlled lab
444 experiments, MPAs are expected to affect control areas by design. Adjacent placement of
445 reference areas, while often meeting goals of controlling for environmental conditions and
446 perhaps even habitat, creates a scientific design challenge, with the likelihood that reference sites
447 will be affected by the presence of a nearby MPA through the redistribution of fishing effort, and
448 potential "spillover" of fish coming from the MPA (Caselle et al. 2015; Di Lorenzo et al. 2016).
449 Anacapa Island presents an interesting case study in reference site selection. Previous
450 studies of very deep water habitats using Remotely Operated Vehicles excluded the Anacapa
451 MPA from analyses, citing a lack of appropriate reference area (Karpov et al. 2012). This
452 exclusion comes despite containing one of the oldest MPAs in the Northern Channel Islands
453 network, with the Anacapa eastern SMR established in 1978. Here we chose the reference
454 location as immediately offshore of, and deeper than, long-standing reference sites used for
455 shallower rocky reef and kelp forest studies (Caselle et al. 2015; White et al. 2021). While shown
456 to be appropriate for shallow rock reef, we found that in deeper waters, the reference area
457 contained more deep rock than in the MPA, potentially limiting our ability to detect an MPA
458 effect on rock-associated species (e.g., targeted rockfish, California sheephead). However, both
459 reference area and MPA contained similar amounts of deep sand-rock ecotone habitat favored by
460 ocean whitefish, the most numerous species of fish in our study. Hence tradeoffs exist where
461 reference site selection must incorporate species-habitat associations, assess MPA goals, work to
462 inform management decisions, and are beholden to the realities of field studies.
463 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 (Mumby et al. 2021; Bejarano et al. 2019; Taylor and McIlwain 2010). 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

487 across this gradient (Luo et al. 2020; Lombardo et al. 2020; Thorburn et al. 2021). We observed
488 a distinct break in suitable rockfish habitat within the Anacapa MPA complex, with very little
489 deep habitat (>70m) present. Not only does this reduce the overall available habitat for adult
490 rockfish, it likely reduces the potential for this MPA to provide a valuable ontogenetic bridge for
491 species with high habitat affinity. An MPA that contains contiguous habitats within a species full
492 depth range is better equipped to protect that species at all stages of life, enhancing the benefits
493 experienced by protection from fishing.

494 The protection of connected depth gradients is also likely to provide resilience for fish
495 populations faced with environmental stressors including seasonal changes in water temperature,
496 short-term temperature anomalies (marine heat waves), and long-term changes resulting from
497 global climate change. In an ever-warming global ocean, it has become necessary for fish
498 communities to adapt to rising sea temperatures, often through range shifts in latitude or depth
499 (Perry et al. 2005; Dahms and Killen 2023; Chaikin et al. 2022). Access to deep refuge habitat
500 can improve the resilience of some fish communities and allow them to survive shallow water
501 stressors (MacDonald et al. 2016; Pereira et al. 2018). Inversely, global climate change has been
502 shown to reduce deep-water dissolved oxygen, creating upward pressure on fish communities
503 escaping oxygen minimum zones (OMZ) (Ross et al. 2020). This has been observed around
504 Southern California's Channel Islands, with some rockfish communities shifting to shallower
505 depths as a response to OMZ shoaling (Meyer-Gutbrod et al. 2021). Spatial protections such as
506 MPAs can provide corridors of protected habitat across depth zones to allow for this type of
507 adaptive migratory process. The combined effects of large-scale environmental stressors and
508 species-specific life histories on habitat use across depth gradients have the potential to alter an
509 MPAs effectiveness in the near and long-term.

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

The California MPA network will continue to work towards protecting marine biodiversity and populations of key fished species across the state. Our results demonstrate the 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.

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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. 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. 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. 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

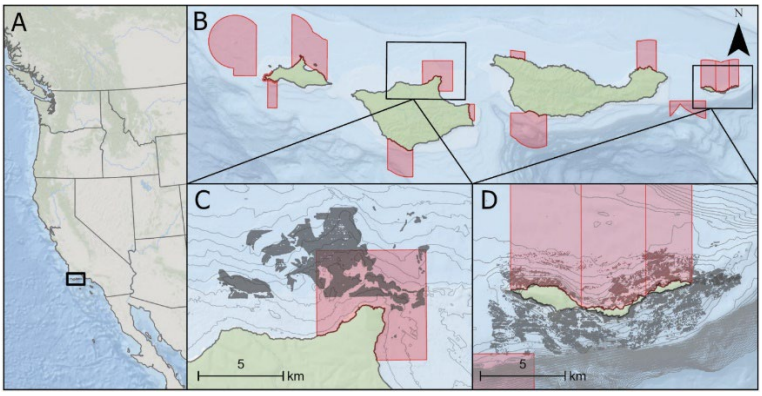


Figure 2

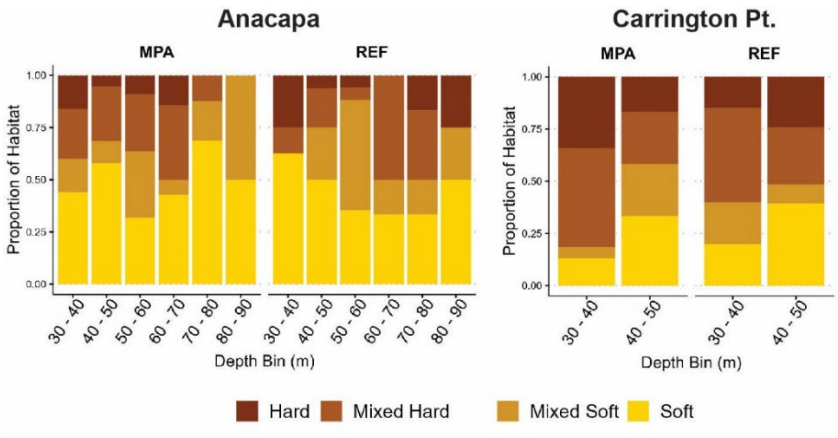

Anacapa
MPA
REF
Carrington Pt.
MPA
REF
Proportion of Habitat
1.00
0.75
0.50
0.25
0.00
30 - 40
40 - 50
50 - 60
60 - 70
70 - 80
80 - 90
Depth Bin (m)
Hard
Mixed Hard
Mixed Soft
Soft

Figure 3

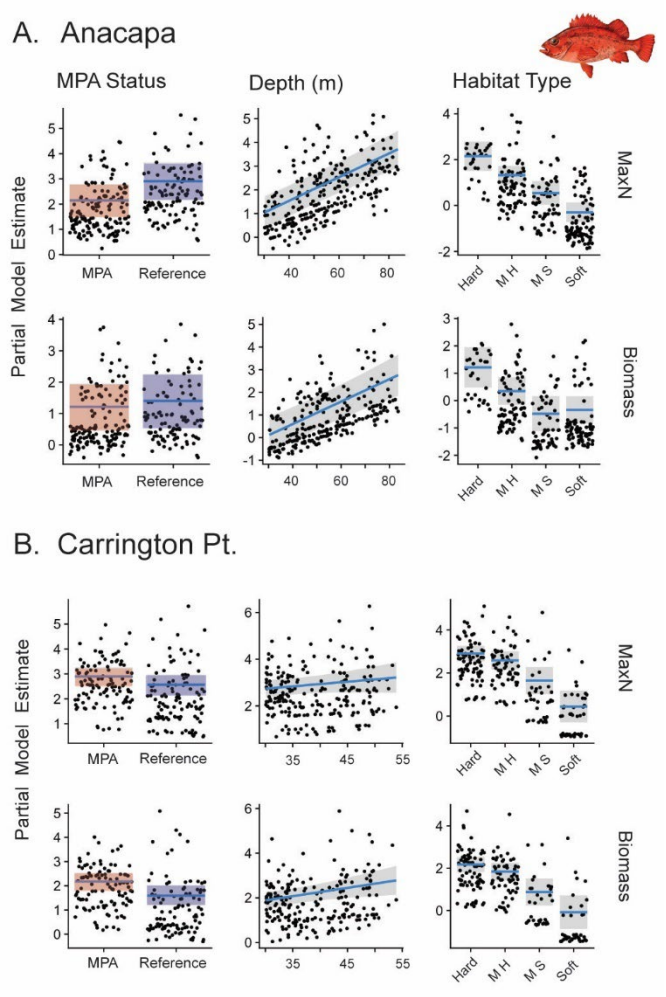

A. Anacapa
MPA Status
Depth (m)
Habitat Type
Partial Model Estimate
MaxN
Biomass
MPA
Reference
Hard
M H
M S
Soft
B. Carrington Pt.

Figure 4

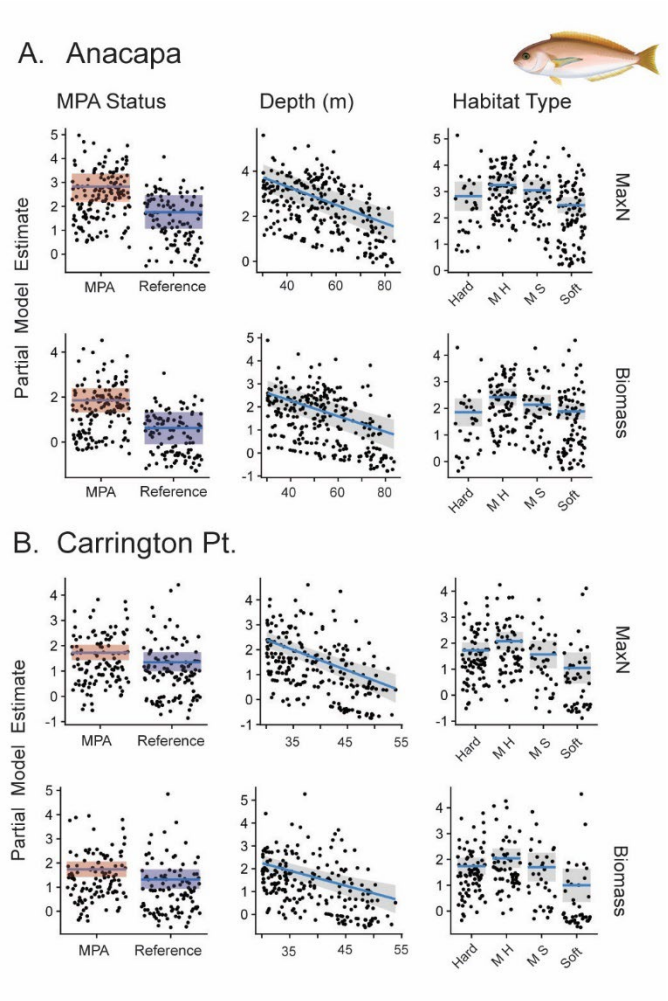

A. Anacapa
MPA Status
Depth (m)
Habitat Type
Partial Model Estimate
MaxN
Biomass
MPA
Reference
Hard
M H
M S
Soft
B. Carrington Pt.

Figure 5

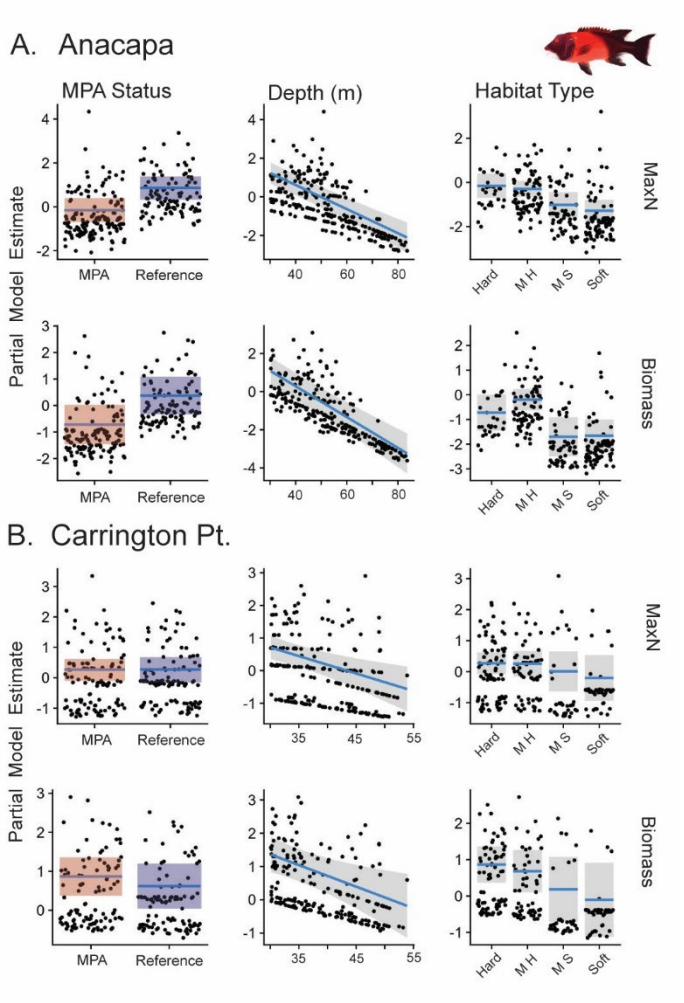
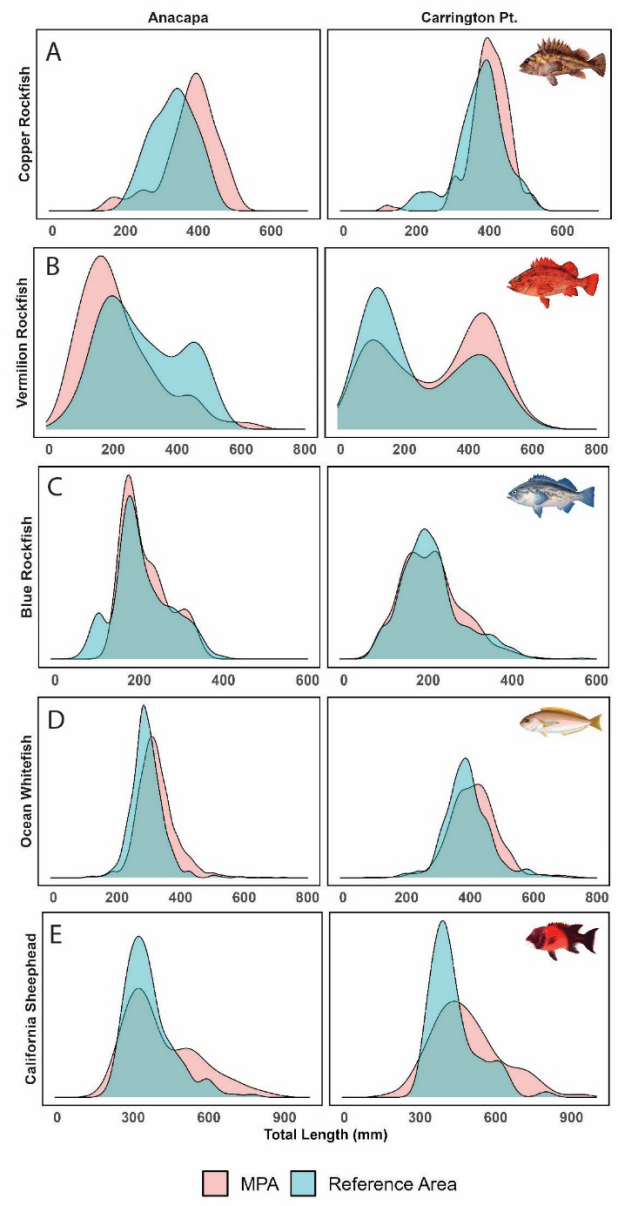

A. Anacapa
MPA Status
Depth (m)
Habitat Type
Partial Model Estimate
MaxN
Biomass
MPA
Reference
Hard
M H
M S
Soft
B. Carrington Pt.

Figure 6


Anacapa
Carrington Pt.
A
Copper Rockfish
B
Vermilion Rockfish
C
Blue Rockfish
D
Ocean Whitefish
E
California Sheephead
Total Length (mm)
MPA
Reference Area