

California State University, Northridge

Evidence for Food Limitation in Rebuilding Populations of a Fish in Marine Protected Areas

A thesis submitted in partial fulfillment of the requirements

for the degree of Master of Science in Biology

By Erika Nava

May 2019

The thesis of Erika Nava is approved:

Larry G. Allen, Ph.D.

Date

Scott L. Hamilton, Ph.D.

Date

Maria S. Adreani, Ph.D.

Date

Mark A. Steele, Ph.D., Chair

Date

California State University, Northridge

Acknowledgements

I would like to express my gratitude to the following people that made my research possible. First, I would like to thank my advisor and mentor Dr. Mark Steele for allowing me to join his lab of unique individuals. I appreciate his enthusiasm, support, friendship and confidence in my ability to succeed. Thank you to Dr. Mia Adreani, Dr. Scott Hamilton and Dr. Larry Allen for their guidance and knowledge that provide insight to my thesis project. Highest appreciation to all the individuals that helped me with field work and watching videos. I especially couldn't have survived my time at CSUN without my lab family. My lab was the harshest of critics but was also the most supportive. Lastly but not least I would like to thank my parents, for allowing me to dream big and motivating me every step of the way.

Table of Contents

Signature Page	ii
Acknowledgments	iii
Abstract	v
Introduction	1
Methods	4
Results	13
Discussion	20
References	26
Appendix A: Tables	29
Appendix B: Figures	31

Abstract

Evidence for Food Limitation in Rebuilding Populations of a Fish in Marine Protected Areas

By

Erika Nava

Master of Science in Biology

Marine protected areas (MPAs) are used to allow organisms and habitats to recover from anthropogenic impacts such as overfishing, which has significantly diminished populations of many exploited marine species. MPAs typically have higher biomass of harvested species within their borders than in fished area outside, which may cause intraspecific competition for limited resources upon population recovery. I evaluated evidence for whether a heavily fished species, California sheephead (*Semicossyphus pulcher*), becomes prey limited within MPAs given increasing duration since the cessation of fishing. I (1) verified that biomass of California sheephead was higher inside the MPAs than in nearby reference areas open to fishing; (2) tested the prediction that prey density would be lower in MPAs than reference sites outside; and (3) made foraging observations, to test whether foraging behavior of California sheephead differed inside versus outside of MPAs. I used the rock wrasse (*Halichoeres semicinctus*), an unfished, but taxonomically related species to test whether any differences in foraging behavior inside vs. outside of MPAs for California sheephead might not actually be caused by protection in MPAs. I studied three new MPAs in southern California established 2012 and three old MPAs established between 1971 and 1988. Underwater visual transect surveys conducted by scuba divers provided data on fish biomass and prey density. Foraging observations by divers quantified fish foraging behavior (foraging rate and time spent searching). Baited remote underwater videos (BRUVS)

were used to quantify fish abundance (MaxN), foraging rate, and time to attack bait. As expected, there were no apparent effects of MPAs on rock wrasse biomass or foraging behavior. In contrast, biomass of California sheephead was higher within MPAs than at reference sites outside and the difference in biomass inside vs. outside MPAs was higher in older MPAs than younger ones. Prey densities were lower for certain prey species within MPAs and generally correlated with California sheephead biomass and MPA age. California sheephead foraging behavior was different inside vs. outside of MPAs, although the magnitude of the behavioral differences depended on the MPA. At 5 of the 6 MPAs, California sheephead spent more time searching for food and foraged at a faster rate within MPAs. Higher foraging rates within MPAs were likely the result of consuming smaller, less valuable prey than at fished sites outside MPAs. BRUV observations revealed higher numbers of California sheephead attracted to bait stations within MPAs, despite diver transects revealing that sheephead densities were not higher in MPAs. BRUV observations also recorded higher foraging rates and faster attack times of bait in MPAs than at references sites outside. These results suggest that California sheephead may be food limited within MPAs, implying that as populations of harvested species rebuild within MPAs, they may become resource limited. This research documents unintended effects of MPAs.

Introduction

Marine organisms are facing numerous threats including overfishing, ocean acidification, eutrophication, and pollution. Such human-induced threats weaken the ability of marine ecosystems to recover from perturbations. Implementing effective management strategies can speed up recovery. Use of marine protected area (MPAs) is one such management strategy. MPAs are generally established to conserve biodiversity and protect habitats, but they include a variety of regulations and conservation strategies, which makes them vary in effectiveness (Mora et al. 2006).

MPAs have been shown to enhance density, biomass, species richness, size of individuals (Lester et al. 2009), but few studies have evaluated indirect effects of MPAs. As management strategies shift from single species protection to multispecies conservation, such as MPAs (Pikitch et al. 2004; Douvere 2008), research is needed to understand how key species respond to protection and how this affects their communities. Indirect effects of MPAs have been documented in foraging behavior of lobsters (Berriman et al. 2015), movements of fishes (Topping, Lowe, and Caselle 2005; Garcia, Mourier, and Lenfant 2015), and prey mortality (Selden et al. 2017). Recovery of predators can also indirectly influence primary production by affecting populations of herbivorous prey species (Pinnegar et al. 2000, Guidetti, 2006). Indirect effects that occur through cascading trophic interactions can take on the order of 10-15 years to occur in temperate MPAs (Babcock et al. 2010).

As populations rebuild within marine protected areas, little is known about whether the resulting higher biomasses of protected organisms will result in resource limitation. Increased biomass may lead to unforeseen intraspecific competition for resources, causing declines in growth rate or reproduction. As populations of harvested species recover, individuals may

change their foraging behavior to optimize foraging opportunities, if food becomes limited. Fish foraging decisions are based on multiple factors, presumably to obtain the maximum energy yield, such as where to feed, which items to feed on, and when to change search patterns (Godin, 1997; Allen, 2006). These decisions influence growth, survival, reproduction, and thus, overall fitness (Godin, 1997).

California sheephead (*Semicossyphus pulcher*) are a fish species that experienced heavy recreational and commercial fishing pressures between the 1980s to 1990s (Alonzo et al., 2004) and their population numbers declined, but recent studies have demonstrated that their population is recovering, most notably inside MPAs (Froeschke et al. 2006; Hamilton et al. 2010; Caselle et al. 2015; Friedlander et al. 2017). This species is a generalist carnivore that feeds mostly on invertebrates located on rocky reefs and soft bottoms (Cowen 1986; Hamilton et al. 2011). Although it has a broad diet, the diet can become specialized depending on the abundance of resources within a site (Cowen 1986; Hamilton et al. 2011). Foraging by California sheephead can be important for kelp forest health through predator control of sea urchin populations (Cowen 1983; Hamilton and Caselle 2015), which are favored prey of large individuals (Selden et al. 2017). Thus, population density and size structure of California sheephead can indirectly affect the abundance of primary producers such as giant kelp via a trophic cascade (Hamilton and Caselle 2015). When sea urchin populations build because they are not being controlled by predators such as California sheephead, they can virtually eliminate kelp beds (Cowen 1983; Estes and Duggins 2010). Selden et al. (2017) showed that mortality rates of purple and red sea urchins were higher inside MPAs compared to sites open to fishing because larger California sheephead are present inside MPAs (Selden et al. 2017).

Previous studies have demonstrated that populations of fishes within MPAs respond to protection distinctly, depending on species-specific fishing pressure before MPA implementation. Caselle et al. (2015) determined that targeted (fished) species within the Northern Channel Islands MPA network increased in biomass, whereas non-targeted species did not show any significant changes inside MPAs. I compared the fished California sheephead to the unfished rock wrasse (*Halichoeres semicinctus*) to aid in interpreting the potential causes of differences between MPA and non-MPA sites.

I tested the hypothesis that foraging behavior of California sheephead would be different inside MPAs than at reference sites outside, presumably as a result of food limitation due to higher biomass of sheephead in MPAs. Because foraging behavior could differ inside vs. outside of MPAs for reasons unrelated to higher population biomass, I also evaluated the foraging behavior of another species in the same family that is not targeted by fishers (Love 2011), the rock wrasse, as a phylogenetic control. I predicted that foraging behavior of California sheephead would differ inside vs. outside of MPAs but that foraging behavior of rock wrasse would not differ. I also tested the expectation that biomass of California sheephead would be higher within than outside MPAs, but that biomass of rock wrasse would not differ inside vs. outside of MPAs. I tested the prediction that prey density of sheephead would be lower in MPAs than at reference sites outside. Finally, I tested the hypothesis that differences in California sheephead biomass, foraging behavior, and prey density would be larger in older MPAs than in younger MPAs.

Methods

Study Area

To evaluate the potential for food limitation in rebuilding populations of a targeted species inside MPAs, I studied California sheephead and rock wrasse in MPAs and paired unprotected areas (non-MPAs) in the Southern California Bight, California, USA (Table 1). Paired sites were selected from six different locations in southern California: La Jolla, Laguna Beach, Long Point (Santa Catalina Island), East Blue Cavern (Santa Catalina Island), West Blue Cavern (Santa Catalina Island), and Anacapa Island. Thus, there were two mainland pairs and four island pairs. I selected three older MPAs that were established from 1971 to 1988, and three newer MPAs that were established in 2012 as part of the Marine Life Protection Act. All MPAs selected allowed no-take of any marine resources (California Fish and Wildlife Code). The older MPAs studied included the older portion of the Blue Cavern Onshore SMCA at Santa Catalina Island (est. 1988), the Anacapa SMR (est. 1978) at Anacapa Island, and the Matlahuayl SMR located off La Jolla Point (est. 1971). The newer MPAs studied included the newer portion of the Blue Cavern Onshore SMCA, the Long Point SCMA at Santa Catalina Island, and the Laguna Beach SMR. The six comparison, non-MPA sites were within 0.5 to 6.5 km from the paired MPA sites and on separate reefs structures sufficiently far to prohibit fish migration from the MPAs.

All study sites at Santa Catalina Island were located on the leeward (eastern) side. This island is located approximately 32 km off the California coast. The two MPA sites located within the Blue Cavern SMCA were Intake Pipes and Rock Quarry and the two proximate non-MPA sites outside were Isthmus Reef and Lion Head. The Long Point, Catalina, pair of sites were Italian Gardens (MPA) and Empire Landing (non-MPA). Anacapa Island is located 18 km off

the coast and 71km north of Santa Catalina Island. The MPA site here was located on the north side within the Anacapa SMR (Landing Cove). The comparison non-MPA site was on the south side (Fish Camp). The entire north side of Anacapa Island has some form of MPA protection, thus, it was not possible to have a non-MPA comparison site on the north side. Two MPA and non-MPA pairs of sites were located in coastal areas. In the Laguna Beach region, the MPA site was the Laguna Beach SMR and the paired non-MPA site was Crystal Cove. The southernmost sites were located within La Jolla region. The MPA site was within the Matlahuayl SMR (La Jolla Cove) and the non-MPA site was Boomer Beach.

Study Species

Both study species are wrasses (family Labridae) with broad diets composed of invertebrates. The diet of California sheephead consists of crabs, sea urchins, shrimps, barnacles, mollusks, polychaetes, bryozoans, brittle stars, and occasional fish (Cowen 1986; Hamilton et al., 2011). Rock wrasse consume smaller benthic invertebrates, such as small crustaceans, polychaetes, snails, brittle stars, ascidians, bivalves, and bryozoans (Love, 2011); and it occasionally cleans other fish by eating their ectoparasites (Hobson, 1976). California sheephead are found from the intertidal zone to 90 m depth, from Monterey Bay to the Gulf of California and Isla Guadalupe (Baja California) (Love, 2011). Rock wrasse are found from tidepools to about 40 m depth and range from Diablo Cove (central California) to southern Baja California.

I studied foraging behavior, which can be difficult to measure. Therefore selecting appropriate study species and methods is important. Both California sheephead and rock wrasse forage continually during the day and their foraging behavior is easily observed because they

quickly acclimate to the presence of divers. These two species were also chosen because of their taxonomic similarity and their similarity in behavioral characteristics and life histories. Both species are protogynous sex-changers.

Surveys of fishes, invertebrates, algae, and substrate characteristics

To quantify fishes, invertebrates, and habitat characteristics, I completed band transects on SCUBA. Transects were 30 x 2 x 2 m and n=6 were conducted at each site, with two at each of three depths (5, 8 and 14 m). I recorded densities, and size (total length, estimated visually to the nearest cm) of California sheephead, and rock wrasse. Each transect was categorized into one of four substrate types: rocky reef, boulder reef, sandy bottom, or cobble bed. After concluding fish surveys, I surveyed invertebrates that were potential prey for the two fishes. Invertebrates were surveyed using two methods: large invertebrates were counted along the entire 2 x 30 m transect, and small invertebrates were counted in five 0.25-m² quadrats placed randomly along the 30-m transect tape. Lastly, I quantified common macroalgae. The macroalgae enumerated were *Macrocystis pyrifera*, *Eisenia arborea*, and *Pterygophora californica*. *M. pyrifera* was quantified in two ways: number of individuals < 1-m tall and number of stipes of individuals > 1-m tall. All surveys were completed from June-October 2017.

Fish Foraging Observations by Divers

Foraging behavior was observed both by SCUBA divers and by baited remote underwater video (BRUV). Observing fish foraging in their natural habitat provides information on foraging tactics and feeding rates. Time budget observations were made on mature California sheephead

>160 mm total length (TL) and rock wrasse >120 mm TL (Cowen 1990). I quantified foraging rate, and time spent searching. Searching was defined as when the focal individual was either digging in the sand or its head was angled towards the substrate, apparently searching for food. Bites were defined as when the focal individual took a bite and consumed a prey item. Size and sex of each focal individual was recorded, and general feeding habitat noted. Preliminary observations were made to determine if feeding rates of California sheephead or rock wrasse changed throughout the day. Observations were made during three time periods (0500 to 0700, 1100 to 1300, and 1700 to 1900). Based on the results, the remaining observations were conducted between 0800 and 1300. Observations were made at depths of 3 to 18 m. To avoid selection bias, every second fish seen was observed. Each individual fish was observed for 5 minutes. Feeding observations only commenced after focal individual had acclimated to the observer; I gave each fish a 30 second acclimation period, which appeared sufficient. Observations were aborted if the focal individual fled or hid from the observer. Focal fish observations were made near the area sampled with transects, after completing the transects. I observed a total of 30 individuals of each species at each site. Observations that were incomplete (< 5 min) were removed from the statistical analysis. All observations were done during summer of 2017, except at Anacapa Island. Poor weather at Anacapa during summer of 2017 kept me from completing all observations, so I returned to Anacapa in summer 2018 to complete the observations on both fish species.

Baited Remote Underwater Video (BRUV) Observations

Baited Remote Underwater Video (BRUV) was used to observe fish foraging behavior in the absence of divers. I used BRUVs for two reasons: (1) the presence of divers may influence

fish foraging behavior differently inside vs. outside of MPAs; and (2) and it impossible to control for prey availability in observations of natural foraging behavior. I measured motivation to feed (a proxy for hunger) by presenting fish with standardized quantities of frozen squid and observing their reaction to this food, within MPAs and in fished areas. BRUVs were placed on or near (within 5 m) rocky reefs. Replicate BRUV deployments were spaced by at least 30 m apart to minimize the chances of observing the same individuals. Each replicate BRUV deployment lasted 15 minutes. As a control for attraction of fish to a disturbance rather than food, I deployed BRUV units without bait to observe the attraction towards the apparatus. I completed about 25 replicates of baited BRUVs and 15 controls at each site. I initiated BRUV observations in the summer of 2017 (10 baited and 10 non-baited) per site and completed the remaining observations in the summer of 2018 (15 baited and 5 non-baited) per site. Based on the low attraction towards the non-baited BRUV apparatus in the first summer, I reduced the sample size of that treatment the following year.

BRUV Video Analysis

Videos were analyzed using EventMeasure SeaGIS software. I measured time until initial approach, time until first bite, total number of bites, and MaxN for California sheephead and rock wrasse. MaxN is the maximum number of individuals of a species observed in a single frame; it is a conservative method to approximate density that avoids recounting individuals. I recorded the time to first bite of California sheephead, to determine if they were more willing to approach bait faster. Video quality was evaluated using modified criteria of Watson and

Huntington (2016) (Table 2). Videos with low quality scores were removed from the statistical analysis.

Statistical Analysis

I tested my expectation that biomass, density, and size of California sheephead would be higher in MPAs than non-MPAs in two separate ways. The first was with a two-way analysis of variance (ANOVA) with the factors *MPA* condition and *Location*, which included data from all 12 sites studied (6 MPAs and 6 non-MPA paired sites). MPA condition had two levels (MPA and non-MPA) and Location had six levels (Laguna Beach, Long Point, East Blue Cavern, West Blue Cavern, La Jolla, and Anacapa). The second approach also used the same model (two-way ANOVA with factors *MPA* condition and *Location*) but separate tests were done for locations with new MPAs (6 sites comprised of 3 MPA and non-MPA pairs) and older MPAs (the other 6 sites). The purpose of those two separate tests for older and newer MPAs were to evaluate whether the differences inside vs. outside of MPAs were similar between newer and older MPAs. The same models were used with data on rock wrasse.

Biomass of both species was estimated from weight-length equations (RecFin 2019). The weight of each individual observed was predicted from its estimated length and summed for each transect. For California sheephead, the equation used was $W = 0.0000002952L^{2.9066}$ (kg from mm TL); and for rock wrasse is was $W = 0.000000045L^{3.16}$. For all three response variables (biomass, density, and length) the assumption of normality was evaluated with quantile-quantile plots and the assumption of homogeneity of variances was evaluated with Levene's test. Biomass of both species was log (x+1) transformed to fit assumption of normality and homogeneity of

variance. Density and size of both species met the assumptions of normality and homogeneity of variance. All statistical analyses were done in RStudio.

I tested whether foraging behavior of two study species, based on diver observations, differed inside versus outside of MPAs with the same two-way ANOVA models described in the previous paragraph (factors *MPA* condition and *Location*). Foraging rate was square-root transformed and search time was arcsine transformed to meet normality assumptions. I combined data on foraging from 2017 and 2018 at Anacapa Island because the data from both years showed similar trends.

BRUV observations were used to test for differences inside versus outside of MPAs in foraging rate (bites within 15 min. intervals), MaxN, foraging rate/MaxN, and time to first bite for California sheephead and rock wrasse. Foraging rate/MaxN was examined to create a variable akin to per-capita foraging rate. Videos in which the focal species was seen but never attacked the bait were assigned a time to first bite of 15 minutes. The same two-way ANOVAs as described above were used for California sheephead MaxN, and time to first bite of bait. Because data on California sheephead foraging rate, and foraging rate/Max; and Rock wrasse MaxN, foraging rate and foraging rate/MaxN strongly violated the parametric assumptions of ANOVA, univariate permutational analysis of variance (PERMANOVA) on a Euclidean distance matrix was used with the same model terms (factors *MPA* condition and *Location*).

To determine whether any differences in foraging behavior, biomass, density, or size between MPAs and non-MPAs might be the result of systematic differences in habitat between MPAs and non-MPAs rather than true MPA effects (e.g., as would occur if MPAs were placed only at sites with good habitat), I tested whether habitat characteristics differed inside vs. outside MPAs. Because data on algae data did not meet the normality assumptions, I used permutational

multivariate analysis of variance (PERMANOVA). Data were transformed to $\log(x+1)$ to reduce the influence of very abundant species, while retaining some information on differences in abundance. PERMANOVA used the same two-way models described earlier (factors *MPA* condition and *Location*). Log-transformed data on macroalgae abundance was summarized with a Bray-Curtis dissimilarity matrix. P-values were generated from 999 permutations. All data tested with PERMANOVA were also tested for homogeneity of variance with PERMDISP, a multivariate analog of a Levene's test.

Benthic habitat characteristics were also compared between MPAs and outside areas. Because each transect was placed into a single benthic habitat category (rocky reef, boulder reef, sandy bottom, or cobble bed), a G-test was used to test for differences inside vs. outside MPAs and among locations. A 2 x 3 contingency table (factors *MPA* condition and *Substrate type*) was used.

Whether prey availability differed inside vs. outside MPAs was tested with multivariate and univariate analyses. Multivariate data were analyzed using PERMANOVA on a Bray-Curtis dissimilarity matrix constructed from $\log(x+1)$ transformed data to reduce the influence of very abundant taxa. I removed rare species that were observed less than six times across all 72 transects. The same two-factor PERMANOVA models described above was used (*MPA* and *Location*) to test the prediction that prey availability for California sheephead would be different inside versus outside of MPAs. To determine if prey species richness was lower in MPAs versus non-MPAs, I ran a two-way ANOVA with the same models (*MPA* condition and *Location*). The same univariate models were used for three prey species commonly consumed by California sheephead after detecting a significant multivariate difference. For California cone snail (*Conus*

californicus) and turban snails (*Tegula* spp.) ANOVA was used; but for purple sea urchin univariate PERMANOVA was used because the data did not meet the normality assumption.

Results

Algae and Substrate Characteristics

The macroalgal assemblage in MPAs was not consistently different from outside of them (PERMANOVA: MPA: $F_{1,60} = 0.96, p = 0.365$), although there were differences between paired sites inside vs. outside MPAs in some locations (MPA x Location: $F_{1,60} = 12.2, p = 0.001$). The dispersion of the macroalgae assemblage did not differ among MPAs (PERMDISP: $p = 0.08$). The differences in macroalgae between MPA and non-MPA sites was evident in locations with new MPAs (PERMANOVA: MPA: $F_{1,30} = 8.9, p = 0.0001$), but these differences were inconsistent (MPA x Location interaction: $F_{1,30} = 6.9, p = 0.003$). The locations with new MPAs also had unequal dispersion ($F_{1,34} = 4.13, p = 0.05$). Differences inside vs. outside of old MPA were inconsistent (MPA x Location: $F_{1,30} = 5.9, p = 0.001$) despite similar dispersions (PERMDISP: $p = 0.79$). An nMDS plot examining the 4 algae species quantified showed that MPA and non-MPA transect points overlapped considerably suggesting general similarity in algae abundance (Fig.1). Substrate characteristics were different inside vs. outside MPAs (G-test: $G = 9.5, df = 2, p = 0.0008$). MPAs more frequently had transects with cobble substratum, despite generally similar substrates in MPA and non-MPA sites.

Fish Biomass, Size, and Density

Biomass, size, and density of California sheephead tended to differ between paired sites inside and outside of MPAs, largely due to differences in old MPAs. Averaged across all six locations, biomass tended to be higher in MPAs than at reference sites outside, however this difference was marginally non-significant ($F_{1,60} = 3.6, p = 0.06$ Fig. 2), and the differences were statistically consistent among locations (MPA x Location interaction: $p = 0.30$). However, in old

MPAs biomass was significantly higher than in paired reference sites outside of MPAs ($F_{1,30} = 6.25, p = 0.02$), but that was not the case in newer MPAs ($F_{1,30} = 0.009, p = 0.92$). California sheephead density did not differ inside vs. outside MPAs ($F_{1,60} = 2.3, p = 0.13$, Fig. 3), despite the observed differences in biomass. Densities of California sheephead were significantly lower in older MPAs than outside ($F_{1,30} = 5.09, p = 0.03$), but no difference in density were detected inside vs. outside of younger MPAs ($F_{1,30} = 0.0, p = 1.0$). Averaged across locations, California sheephead size (length) was greater within MPAs compared to non-MPAs ($F_{1,166} = 13.0, p = 0.0004$), but this difference in mean size dependent on the location (MPA x Location interaction: $F_{1,166} = 5.9, p < 0.001$, Fig. 4). Older MPAs had larger sheephead inside than at references sites outside the MPA ($F_{1,100} = 30.5, p < 0.0001$), but that was not the case in locations with new MPAs ($F_{1,66} = 0.57, p = 0.45$).

As expected, there was no systematic difference in biomass, density, or size of the non-targeted species, rock wrasse, inside vs. outside MPAs. Averaged across all locations, MPAs did not contain higher biomass of rock wrasse ($F_{1,60} = 2.09, p = 0.15$, Fig. 2), nor was there an interaction between MPA status and Location (MPA x Location interaction: $F_{1,60} = 1.4, p = 0.20$). Accordingly, neither the model for locations with old MPAs or nor the model for ones with new MPAs detected significant differences in rock wrasse biomass inside vs. outside of MPAs (old MPAs: $F_{1,30} = 0.01, p = 0.90$; new MPAs: $F_{1,30} = 3.84, p = 0.06$). There were also no significant differences in rock wrasse density inside vs. outside MPAs across all locations ($F_{1,60} = 2.3, p = 0.14$; MPA x Location: $F_{1,60} = 1.54, p = 0.18$, Fig. 3); or in locations with old ($F_{1,30} = 1.0, p = 0.32$) or new MPAs ($F_{1,30} = 3.8, p = 0.06$). Likewise, size (length) of rock wrasse was not consistently different inside vs. outside of MPAs ($F_{1,288} = 0.06, p = 0.79$; Fig. 4), however the size differences depended on location (MPA x Location interaction: $F_{1,288} = 11.7, p = 0.0001$),

with rock wrasse being larger in size inside MPAs in some locations and larger in size outside MPAs in other locations. These differences primarily occurred in locations classified as being new MPAs (MPA x Location: $F_{1,192} = 10.3, p < 0.0001$), and not old MPAs ($F_{1,192} = 0.7, p = 0.37$).

Invertebrate Abundance

The invertebrate assemblage preyed upon California sheephead differed inside MPAs vs. outside them (PERMANOVA: $F_{1,60} = 7.7, p = 0.001$; Fig. 5). This difference was at least partly the result of the invertebrate assemblage inside MPAs being more variable than at paired reference sites outside, i.e., having greater dispersion (PERMDISP: $p = 0.036$). The difference in invertebrate assemblage was inside vs. outside MPAs depended on the location (MPA x Location interaction: $F_{1,60} = 3.7, p = 0.001$) and had unequal dispersion among MPAs (PERMDISP: $p = 0.04$), such that some MPA-Reference pair differed in invertebrate assemblages while others did not. PERMANOVA models testing new, and old MPAs separately, had similar results as all the MPAs combined. New MPAs showed differences inside and outside MPAs ($F_{1,30} = 3.2, p = 0.009$) in invertebrate assemblages and differences were inconsistent in all MPAs (MPA x Location interaction: $F_{1,30} = 2.6, p = 0.002$) and had equal dispersion by MPA (PERMDISP: $p = 0.12$). Old MPAs showed differences inside and outside MPAs ($F_{1,30} = 7.2, p = 0.001$), had inconsistent trends inside vs outside MPAs (MPA x Location interaction: $F_{1,30} = 5.5, p = 0.001$), and had equal dispersion by MPA (PERMDISP: $p = 0.10$). Despite greater dispersion of the invertebrate assemblage in MPAs, invertebrate species richness was lower in MPAs than outside of them (ANOVA: $F_{1,60} = 15.5, p = 0.0002$, Fig. 6). Differences in invertebrate species richness inside vs. outside MPAs were consistent across MPAs (MPA x Location interaction:

$F_{1,60} = 1.07, p = 0.38$). Locations with new and old MPAs both had lower species richness within MPAs (new MPAs: $F_{1,30} = 7.3, p = 0.01$; old MPAs: $F_{1,30} = 8.7, p = 0.006$).

The hypothesis that prey species commonly consumed by California sheephead would be less abundant within MPAs was supported only for some prey species. Purple sea urchins were significantly less abundant inside MPAs than at reference sites outside (univariate PERMANOVA: $F_{1,60} = 114.2, p = 0.001$; Fig. 7). Their abundance also differed inside vs. outside MPAs among locations (MPA x Location interaction: $F_{1,30} = 127.3, p = 0.001$). The difference in density of purple urchins inside vs. outside MPAs was greatest at Anacapa Island, where the difference in sheephead biomass was also greatest. Purple urchins were nearly absent from locations with new MPAs, except the Laguna Beach non-MPA and there was no difference in urchin density inside vs. outside of new MPAs ($F_{1,30} = 1.0, p = 1.0$). In contrast, locations with old MPAs had higher abundance of purple urchins outside of MPAs ($F_{1,30} = 115.3, p = 0.001$), though that varied by location (MPA x Location: $F_{1,30} = 140.2, p = 0.001$). Turban snail density was, on average, higher outside of MPAs ($F_{1,60} = 6.7, p = 0.01$, Fig. 8), a pattern that was statistically consistent among locations (MPA x Location: $F_{1,60} = 1.6, p = 0.16$). Locations with old MPAs had lower turban snail abundance within MPAs than outside of them ($F_{1,30} = 8.4, p = 0.006$). Locations with new MPAs had similar turban snail abundance inside and outside MPAs ($F_{1,30} = 0.6, p = 0.44$). In contrast cone snail density did not differ inside vs. outside MPAs ($F_{1,60} = 2.7, p = 0.10$), a trend that was consistent among all MPAs (MPA x Location interaction: $F_{1,60} = 0.8, p = 0.5$, Fig. 9). Cone snail density did not differ by MPA condition or location in locations with new MPAs (MPA x Location interaction: $F_{1,30} = 1.5, p = 0.3$) or old MPAs (MPA x Location interaction: $F_{1,30} = 0.4, p = 0.6$).

Fish Foraging

Diver observations

Five of six locations showed similar general patterns of California sheephead foraging behavior inside vs. outside MPAs. Averaged across all six locations, California sheephead search time did not significantly differ inside vs. outside MPAs ($F_{1,368} = 3.4, p = 0.064$, Fig. 10), but differences inside vs. outside MPAs depended on location (MPA x Location: $F_{1,368} = 9.1, p < 0.0001$). Locations with new MPAs had higher search time within MPAs ($F_{1,173} = 18.0, p < 0.001$) but that was not the case in locations with old MPAs ($F_{1,195} = 1.2, p = 0.26$). Similar trends were evident for five or six MPAs, but Anacapa MPA displayed the opposite trend. Foraging rate also did not significantly differ inside vs. outside MPAs ($F_{1,368} = 3.2, p = 0.082$, Fig. 11), however the differences inside vs. outside MPAs depended on location (MPA x Location: $F_{1,368} = 9.7, p < 0.001$). Locations with new MPAs had higher foraging rates within MPAs than at reference sites outside ($F_{1,173} = 15.7, p = 0.001$), but that was not the case in locations with old MPAs ($F_{1,195} = 3.2, p = 0.07$).

Most locations had similar foraging rates and searching times for rock wrasse inside and outside MPAs, but two regions, Anacapa and Laguna Beach, showed opposite trends (Figures 10 & 11). Searching behavior tended to differ inside vs. outside of MPAs for rock wrasse ($F_{1,355} = 4.5, p = 0.033$, Fig. 10), but this difference was not consistent among locations (MPA x Location: $F_{1,355} = 2.2, p = 0.004$). The differences in searching behavior of rock wrasse were driven by reduced search times for prey within new MPAs ($F_{1,172} = 4.6, p = 0.032$). Averaged across all MPAs, rock wrasse foraging rate was similar inside vs outside MPAs ($F_{1,355} = 1.6, p = 0.12$, Fig. 11), but the patterns depended upon location (MPA x Location: $F_{1,355} = 3.4, p = 0.004$).

BRUV Observations

California sheephead were observed frequently on the videos, whereas rock wrasse were observed less frequently. BRUV controls did not attract either of the study species. More California sheephead were recorded inside MPAs than outside of them (MaxN: $F_{1,244} = 11.1, p = 0.0009$; Fig. 12) but this pattern depended on the location surveyed (MPA x Location: $F_{1,244} = 2.2, p = 0.04$). In locations with new MPAs, MaxN was higher within the MPAs than outside of them (MaxN: $F_{1,131} = 8.6, p = 0.003$), a pattern that was consistent among locations ($F_{1,131} = 1.3, p = 0.25$). For old MPAs, MaxN did not differ significantly inside vs. outside of MPAs ($F_{1,113} = 2.7, p = 0.10$), but the patterns in MaxN were not consistent among locations ($F_{1,113} = 13.7, p < 0.0001$). For Old MPAs, MaxN was elevated inside MPAs at Anacapa and La Jolla, but not at West Blue Cavern.

Foraging rate of California sheephead at the BRUVs was higher inside MPAs than at reference sites outside (total bites by sheephead per 15 minutes: $F_{1,244} = 6.8, p = 0.013$, Fig. 13), a pattern that was statistically consistent among locations (MPA x Location: $F_{1,244} = 1.8, p = 0.11$). Approximate per-capita foraging rate was also significantly higher in MPAs (total bites per 15 minutes /MaxN: $F_{1,244} = 6.2, p = 0.015$, Fig. 14), but this pattern was depended upon location (MPA x Location: $F_{1,244} = 2.9, p = 0.02$). In old MPAs foraging rate was higher than in paired reference sites ($F_{1,113} = 4.6, p = 0.037$), as was per capita foraging rate ($F_{1,113} = 6.2, p = 0.015$); however, this pattern depended on location both for total (MPA x Location interaction: $F_{1,113} = 4.0, p = 0.018$) and per capita ($F_{1,113} = 5.4, p = 0.004$; MPA x Location interaction: $F_{1,113} = 6.5, p = 0.004$) foraging rate. In locations with new MPAs, California sheephead total foraging rate ($F_{1,131} = 3.0, p = 0.071$) and per capita foraging rate ($F_{1,2} = 2.8, p = 0.10$) did not differ

significantly inside vs. outside of MPAs. On average, California sheephead were also quicker to attack the bait within MPAs than at reference sites outside ($F_{1,244} = 12.7, p < 0.001$), but this pattern was inconsistent among locations (MPA x Location: $F_{1,244} = 4.7, p < 0.001$, Fig. 15), such that the magnitude of the response depended on the location. Quicker to attack bait within MPAs was noticeable within new ($F_{1,131} = 7.6, p = 0.006$) and old MPAs ($F_{1,113} = 5.0, p = 0.03$). But this pattern was inconsistent among locations in both new (MPA x Location: $F_{1,131} = 7.7, p < 0.001$) and old MPAs (MPA x Location: $F_{1,113} = 3.8, p = 0.02$).

In contrast and as expected, the non-targeted rock wrasse did not differ in numbers seen on videos (MaxN: $F_{1,244} = 1.4, p = 0.26$; Fig. 12) although this pattern was not the same at all locations (MPA x Location: $F_{1,244} = 2.3, p = 0.02$). Rock wrasse abundance did not differ in new ($F_{1,131} = 3.0, p = 0.08$) and old MPAs ($F_{1,113} = 2.3, p = 0.11$). Likewise, total foraging rate (total bites per 15 min: $F_{1,244} = 0.79, p = 0.44$, Fig. 13), or approximate per capita foraging rate did not differ inside vs. outside of MPAs (total bites per 15 min / MaxN ($F_{1,244} = 0.28, p = 0.74$, Fig. 14)). Rock wrasse per capita foraging rate did not differ significantly inside vs. outside MPAs in locations with old MPAs ($F_{1,113} = 1.8, p = 0.11$), and the response was consistent among locations (MPA x location interaction: $F_{1,113} = 0.5, p = 0.72$). In locations with new MPAs differences in rock wrasse per capita foraging rate depended on the location ($F_{1,131} = 3.6, p = 0.005$; MPA x Location: $F_{1,131} = 2.4, p = 0.04$), such that foraging was elevated outside of MPAs in some locations relative to inside MPAs. Total foraging rate of rock wrasse was higher at reference sites than inside new MPAs ($F_{1,131} = 3.6, p = 0.006$) and this difference was consistent among locations (MPA x Location: $F_{1,131} = 2.3, p = 0.06$). Total foraging rate of rock wrasse did not differ within vs. outside of old MPAs ($F_{1,113} = 2.7, p = 0.10$) and this pattern was consistent among locations ($F_{1,113} = 0.3, p = 0.72$).

Discussion

This study indicates that fish feeding behavior can be influenced by management measures such as the implementation of MPAs and that the time since MPA establishment is an important factor in determining how MPAs affect foraging behavior. As biomass and size structure of California sheephead has recovered within MPAs, food resources may become limited as preferred prey are consumed. This was reflected in lower invertebrate density and diversity within older MPAs, which had the highest biomass of California sheephead. Likely to compensate for lower prey abundances, California sheephead appeared to alter foraging behavior within MPAs, potentially by consuming larger quantities of abundant prey species with lower caloric value. Altered foraging behavior was observed both through *in situ* visual observations by divers and remote video.

Differences in biomass and size of California sheephead apparently take several years to develop. Older MPAs (~30-40 years old) had much greater differences in biomass and body size between paired MPA-reference sites, than the more recently established MPAs (5-6 years old). This is not surprising given that large California sheephead can be decades old and they do not reach a harvestable size (30 cm total length) until they are approximately 6 years old (Hamilton et al., 2011). MPA success depends on many factors such as size, age, and enforcement of protection (Claudet et al. 2008; Friedlander et al. 2017). Age of MPA had positive effects on commercially fished species and species richness in European MPAs (Claudet et al. 2008). Older MPAs may in part be more successful because of local enforcement and community awareness to maintain these areas as protected (Aburto-Oropeza et al. 2011), whereas limited public awareness of newly established MPAs, could reduce their effectiveness.

Higher biomass of California sheephead was caused by there being larger individuals within MPAs. MPAs often increase density, biomass, and size of targeted species (Tetreault 2007; Lester et al. 2009) . My research indicates that protection in MPAs lead to higher biomass and larger California sheephead, but density was unaffected. I included individuals of all sizes in my estimate of density, including juveniles. Froeschke and co-authors (2006), demonstrated that whereas densities of adult California sheephead and kelp bass were higher within an MPA, densities of sub-adults and juveniles did not differ. Rock wrasse had similar biomass, density, and size of individuals of within and outside of MPAs. This fits a documented pattern and expectation that exploited species show the greatest response for MPA implementation (Caselle et al. 2015). A study on the northern Channel Islands, California found that fished species consistently increased their biomass within MPAs and in areas proximate to them, indicating potential spill over (Caselle et al. 2015).

One MPA I studied stood out from the others, both in the magnitude of the differences in biomass and body size of sheephead: Landing Cove at Anacapa Island. This site also had differences in foraging behavior from the paired, non-MPA site that were opposite those at the other MPAs studied. Large California sheephead at Landing Cove appeared to have controlled purple urchin populations and other invertebrate species. The drastic differences in invertebrate abundance within vs. outside the MPA at Anacapa Island, apparently altered foraging behavior of California sheephead, but in a way different from other sites I studied. The Anacapa MPA had much lower diversity of prey species than the paired unprotected site (three vs. seven invertebrate prey species per transect). The density of purple sea urchins was ~2,200 times lower within the MPA than outside of it. Large sheephead within the Anacapa SMR likely control urchin abundance because they are physically capable to consume larger urchins, whereas

smaller sheephead outside the MPA cannot consume large urchins (Selden et al. 2017). Cowen (1983) demonstrated the impact that California sheephead can have on sea urchins in an experiment in which he removed all California sheephead from an area approximately 12,600 m² at San Nicholas Island, California, and maintained the removal for a year. Cowen monitored sea urchin density and microhabitat use in the absence of California sheephead, and found that sea urchins shifted to using exposed microhabitats and their populations increased by 26% over a year.

Invertebrate densities differed inside versus outside MPAs and these differences seemed to correlate with California sheephead biomass. Sheephead are generalist invertivores, which allows them to change their diet according to what is abundant and available (Cowen 1986). Purple urchins are a preferred prey species and their numbers seemed to be controlled within MPAs with higher biomass of California sheephead. Turban snails (*Tegula* spp.) seemed to be similarly impacted by predation by California sheephead. The La Jolla location had higher densities of purple urchins inside the MPA suggesting that sheephead there are consuming other prey species besides purple urchins. The La Jolla sites had noticeably high abundance of bryozoans on giant kelp blades, and I observed large male sheephead that were physically capable of consuming urchins, consuming portions of kelp blades instead. It seems likely that California sheephead are adjusting their diets to their resource availability, and consume invertebrates that remain abundant.

Lower invertebrate densities within MPAs appeared to change California sheephead foraging behavior. Time spent searching for food is related to its availability and physical ability to consume prey species in the area. Animals are expected to spend more time searching for food

and move farther in areas with limited food (Pyke 1984). California sheephead spent more time searching within all the MPAs except the Anacapa SMR.

This research verified that California sheephead within MPAs are usually larger, which can impact their foraging decisions. Bluegill sunfish, searching ability and prey handling ability increased with body size (Mittelbach 1981). Size-related differences of older California sheephead have the physical capacity to consume prey that will maximize biomass (energy) ingested and could potentially search longer to obtain that preferred food source. Larger individuals are capable of consuming a broader array of prey items. For example, the efficiency of Arctic char in eating macroinvertebrates increases with body size (Byström et al. 2006; Gilliam and Fraser 1988). In the case of California sheephead, only large individuals can consume sea urchins. Fish usually feed optimally, which includes consuming higher caloric prey, such as parrotfish that choose to maximize energetic yield by consuming prey with high caloric value (Lobel and Ogden 1981). Fish generally prefer prey species that maximize calorie intake, but ultimately are opportunistic feeders. Shifts in prey availability within home ranges will cause fish foraging behavior to change. Shifting to prey species with lower caloric value to maintain calorie acquisition in the face of food depletion will necessitate increased foraging rates to compensate. Likely, this is why California sheephead foraged at faster rates on natural prey items during diver observations inside MPAs. This possibility is consistent with Cowen's (1986) observations that in areas with high biomass of California sheephead, they switched to alternative, lower priority prey (i.e. bryozoan barnacles and encrusted algae). The results from BRUVs and diver observations, showed differences in California sheephead foraging behavior inside vs. outside of MPAs. Diver observations detected signs of hunger, with longer periods searching for food and potentially switching diet to lower priority prey, hence higher foraging

rates within MPAs. BRUVs revealed that California sheephead within MPAs were more willing to approach and attacked bait faster than those outside of them, and took more bites of bait, also suggesting hunger.

California sheephead were much more commonly recorded by BRUVs than the smaller rock wrasse, which only occasionally attacked bait. This difference between the two species could be because squid is not an ideal bait for rock wrasse, or possibly they were intimidated by larger fish attacking bait. A study conducted by Coghlan et al. (2017) investigated the potential bias of BRUVs for targeted species relative to non-targeted species. They found no evidence that large-bodied, targeted species, affected smaller conspecifics or smaller non-targeted species.

Differences in foraging behavior inside vs. outside MPAs was fairly consistent among locations, including at new MPA sites. However, new MPAs did not have significantly higher biomass, body size, or density of California sheephead. It is unclear what other threats or environmental factors might have altered foraging behavior even in newer MPAs. I would suggest studying other targeted species, such as *Paralabrax* spp. to evaluate if these differences in foraging behavior inside of young MPAs are consistently found in harvested species.

Potential resource limitation within MPAs affect marine organisms distinctly. Berriman et al. (2015) tested the hypothesis that marine reserves with higher densities of spiny lobster (*Panulirus interruptus*), would alter their attack behavior and consume a less palatable prey item, *Aplysia californica*. They conducted this experiment at four marine reserves and paired non-MPA comparison sites and found the less palatable prey species was only consumed in marine reserves. In contrast, diets of gopher rockfish did not differ within vs. outside old Point Lobos

MPA (Loury et al., 2015). Understanding which organisms are affected indirectly with limited resources in MPAs can improve management strategies.

This study indicates that foraging by a fished species that is rebuilding its biomass in MPAs can potentially reduce the abundance of preferred prey in MPAs. This could have cascading effects, e.g., in the case of reduced abundances of sea urchins, which can impact kelp forests via their herbivory. Reductions in densities of other prey species, e.g., *Tegula* snails, may also have cascading effects on the local community. Considering the consequences of altered trophic interactions within MPAs as populations of harvested species rebuild may be important for effective multi-species protection.

References

- Aburto-Oropeza, O., Erisman, B., Galland, G. R., Mascareñas-Osorio, I., Sala, E., & Ezcurra, E. (2011). Large recovery of fish biomass in a no-take marine reserve. *PLoS ONE*, 6(8). doi:10.1371/journal.pone.0023601
- Allen, L. G., Pondella, D. J., & Horn, M. H. (2006). *The ecology of marine fishes California and adjacent waters*. Berkeley: University of California Press.
- Alonso, Suzanne H, Meisha Key, and Teresa Ish. (2004). Status of the California sheephead stock. *California Department of Fish and Game* (April 2019).
- Babcock, R. C. et al. (2010). Decadal trends in marine reserves reveal differential rates of change in direct and indirect Effects. *Proceedings of the National Academy of Sciences* 107(43): 18256–61.
- Berriman, J., Kay, M., Reed, D., Rassweiler, A., Goldstein, D., & Wright, W. (2015). Shifts in attack behavior of an important kelp forest predator within marine reserves. *Marine Ecology Progress Series*, 522, 193-201. doi:10.3354/meps11157.
- Byström, P., Andersson, J., Kiessling, A., & Eriksson, L. (2006). Size and temperature dependent foraging capacities and metabolism: Consequences for winter starvation mortality in fish. *Oikos*, 115(1), 43-52. doi:10.1111/j.2006.0030-1299.15014.x.
- California Fish and Game Code of Regulations, Title 14, Section 632: Natural Resources, Division 1: Fish and Wildlife Code - Department of Fish and Game. Department of Fish and Wildlife. Accessed March 2019.
<https://www.wildlife.ca.gov/Conservation/Marine/MPAs/Network/Title-14-Section-632>.
- Caselle, Jennifer E, Andrew Rassweiler, Scott L Hamilton, and Robert R Warner. (2015). Recovery trajectories of kelp forest animals are rapid yet spatially variable across a network of temperate marine protected areas. *Nature Publishing Group* (September): 1–14. <http://dx.doi.org/10.1038/srep14102>.
- Claudet, Joachim et al. (2008). “Marine Reserves: size and age do matter.” *Ecology Letters* 11(5): 481–89.
- Coghlán, A. R., D. L. McLean, E. S. Harvey, and T. J. Langlois. (2017). Does fish behaviour bias abundance and length information collected by baited underwater video? *Journal of Experimental Marine Biology and Ecology* 497(May 2016): 143–51. <http://dx.doi.org/10.1016/j.jembe.2017.09.005>.
- Cowen, Robert K. (1986). Site-specific differences in the feeding ecology of the California sheephead, *semicossyphus pulcher* (labridae). *Environmental Biology of Fishes* 16(1–3): 193–203.
- Cowen, Robert K. (1983). Ecology on red sea urchin (*strongylocentrotus franciscanus*) Populations : An Experimental Analysis. *Oecologia* 58: 249–55.
- Cowen, Robert K. (1990). Sex change and life history patterns of the labrid , *semicossyphus pulcher* , across an environmental gradient. *Copeia* (3): 787–95.

- Douvere, Fanny. (2008). The importance of marine spatial planning in advancing ecosystem-based sea use management. *Marine Policy* 32(5): 762–71.
- Estes, James A, and David O Duggins. (2010). Sea otters and kelp forests in Alaska : generality and variation in a community ecological paradigm. *Ecological Monographs* 65(1): 75–100.
- Friedlander, Alan M. et al. (2017). Size, age, and habitat determine effectiveness of Palau's marine protected areas. *PLoS ONE* 12(3).
- Froeschke, John T, Larry G Allen, and Daniel J Pondella II. (2006). The fish assemblages inside and outside of a temperate marine reserve in southern California. *Bulletin of the Southern California Academy of Sciences* 105(3): 128–42.
<http://scholar.oxy.edu/cgi/viewcontent.cgi?article=1126&context=scas>.
- Garcia, Jessica, Johann Mourier, and Philippe Lenfant. (2015). Spatial behavior of two coral reef fishes within a Caribbean marine protected area. *Marine Environmental Research* 109(October 2017): 41–51. <http://dx.doi.org/10.1016/j.marenvres.2015.06.004>.
- Gilliam, J.F., and D. F. Fraser. (1988). Resource depletion and habitat segregation by competitors under predation hazard. *Size-structured Populations*.
- Godin, J. J. (1997). *Behavioural ecology of teleost fishes*. Oxford: Oxford University Press.
- Guidetti, Paolo. (2006). Marine reserves reestablish lost predatory interactions. *Ecological Applications* 16(3): 963–76.
- Hamilton, S. L., J. E. Caselle, D. P. Malone, and M. H. Carr. (2010). Incorporating biogeography into evaluations of the Channel Islands marine reserve network. *Proceedings of the National Academy of Sciences* 107(43): 18272–77.
- Hamilton, Scott L. et al. (2011). Extensive geographic and ontogenetic variation characterizes the trophic ecology of a temperate reef fish on southern California (USA) Rocky Reefs. *Marine Ecology Progress Series* 429(Power 1992): 227–44.
- Hamilton SL, Wilson JR, Ben-Horin T, Caselle JE (2011) Utilizing Spatial Demographic and Life History Variation to Optimize Sustainable Yield of a Temperate Sex-Changing Fish. *PLoS ONE* 6(9): e24580. doi:10.1371/journal.pone.0024580
- Hobson, Edmunds S. (1976). The rock wrasse, halichoeres semicinctus, as a cleaner fish. *California Fish and Game* 62(1): 73–78.
- Lester, Sarah E. et al. (2009). Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series* 384: 33–46.
- Love, M. S. (2011). *Certainly more than you want to know about the fishes of the Pacific Coast: A postmodern experience*. Santa Barbara, CA: Really Big Press.
- Lobel, P. S., and J. C. Ogden. (1981). Foraging by the herbivorous parrotfish sparisoma Radians. *Marine Biology* 64(2): 173–83.

- Loury, Erin K. et al. (2015). Trophic ecology of the gopher rockfish *Sebastodes carnatus* inside and outside of central California marine protected areas. *Marine Ecology Progress Series* 536: 229–41.
- Mach, Megan E. et al. (2017). Assessment and management of cumulative impacts in California's network of marine protected areas. *Ocean & Coastal Management* 137: 1–11. <https://www.sciencedirect.com/science/article/pii/S0964569116303647>.
- Mittelbach, Gary G. (1981). Foraging efficiency and body size : a study of optimal diet and Habitat Use by Bluegills. *Ecological Society of America* 62(5): 1370–86.
- Mora, Camilo et al. (2006). Coral reefs and the global network of marine protected areas. *Science* 312(5781): 1750–51.
- Pikitch, E.K, Santora C., Babcock E. A, Bakun A, Bonfil R. (2004). Ecosystem-based fishery management. 305(5682): 346–47.
- Pinnegar, J., Polunin, N., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M., Pipitone, C. (2000). Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environmental Conservation*,27(2), 179-200. doi:10.1017/s0376892900000205
- Pyke, G H. (1984). Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* 15(1): 523–75.
- Selden, Rebecca L et al. (2017). Protection of large predators in a Marine Reserve Alters Size-Dependent Prey Mortality.
- Tetreault, Irene. (2007). Temperate marine reserves enhance targeted but not untargeted fishes in multiple no-take MPAs. *Ecological Applications* 17(8): 2251–67.
- Topping, D. T., C. G. Lowe, and J. E. Caselle. (2005). Home range and habitat utilization of adult California sheephead, *semicossyphus pulcher* (Labridae), in a temperate no-take marine reserve. *Marine Biology* 147(2): 301–11.
- Watson, Jessica L., and Brittany E. Huntington. (2016). Assessing the performance of a cost-effective video lander for estimating relative abundance and diversity of nearshore fish assemblages. *Journal of Experimental Marine Biology and Ecology* 483: 104–11. <http://dx.doi.org/10.1016/j.jembe.2016.07.007>

Table 1. Summary of study sites

<i>Sites</i>	<i>Locations</i>	<i>MPA Condition</i>	<i>MPA Establishment</i>	<i>Coordinates</i>
<i>Empire Landing</i>	Long Point	Non-MPA		33.25.830° N, 118.26.302° W
<i>Lion Head</i>	East Blue Cavern	Non-MPA		33.27.345° N, 118.30.307° W
<i>Crystal Cove</i>	Laguna Beach	Non-MPA		33.34.118° N, 117.50.316° W
<i>Boomer Beach</i>	La Jolla	Non-MPA		32.51.159° N, 117.16.767° W
<i>Isthmus Reef</i>	West Blue Cavern	Non-MPA		33.26.942° N, 118.29.521° W
<i>Fish Camp</i>	Anacapa	Non-MPA		34.0.248° N, 119.23.235° W
<i>Italian Gardens</i>	Long Point	MPA	2012	33.24.670° N, 118.22.472° W
<i>Rock Quarry</i>	East Blue Cavern	MPA	2012	33.26.486° N, 118.27.910° W
<i>Laguna Beach</i>	Laguna Beach	MPA	2012	33.32.657° N, 117.47.658° W
<i>La Jolla Cove</i>	La Jolla	MPA	1971	32.51.174° N, 117.16.092° W
<i>Intake Pipes</i>	West Blue Cavern	MPA	1988	33.26.826° N, 118.29.092° W
<i>Landing Cove</i>	Anacapa	MPA	1978	34.1.176° N, 119.21.762° W

Table 2. Defined metrics used to score video quality by visibility, view, and primary habitat. Modified from Watson and Huntington 2016.

Metric	Class	Description
<i>Visibility</i>	0 = Unusable	view of surrounding substrate completely obscured; fish ID not possible
	1 = Poor	ID potentially compromised by visibility
	2 = Moderate	view limited but by variable turbidity but ID still possible
	3 = Good	view of surrounding substrate clear, ID readily possible
<i>View</i>	0 = Poor	obstructed or tipped upwards (cannot see benthos)
	1 = Moderate	partially obstructed; >50% of frame is obstructed, or BRUV tilted but benthos is visible
	2 = Good	not obstructed, orientated upright
<i>Primary Habitat</i>	Bedrock/Reef	substrate with almost continuous formations >1m
	Boulder	rock size 15 cm to 1 m
	Cobble (rocks and shells)	rock size 0.5 to 15 cm
	Sand	size < 0.5 cm
	Algae	majority of visible habitat is algae

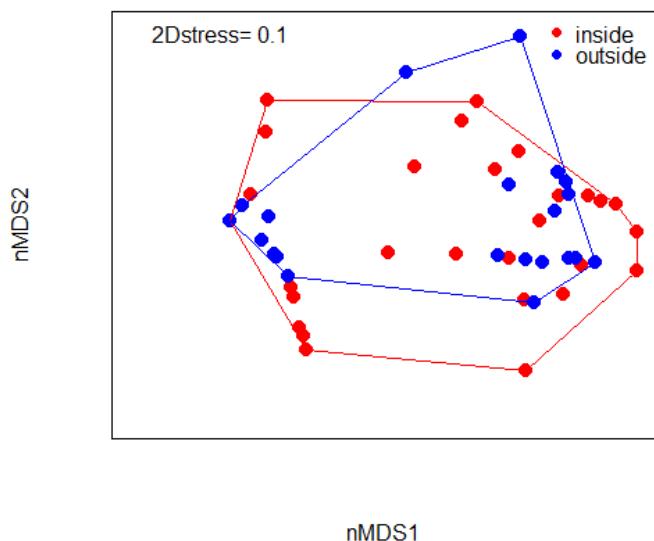
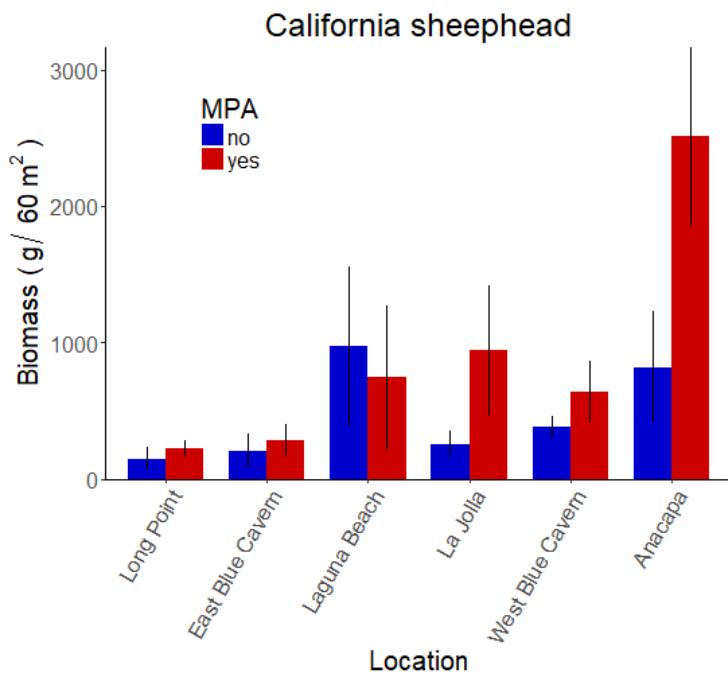


Figure 1. nMDS plot illustrating the algal assemblage inside versus outside MPAs in six locations. Ordination is based on four algae species. Each site was surveyed with six transects and each transect is represented by a point. MPA transects were not different from non-MPA transects Analysis was based on a Euclidean distance matrix calculated from log-transformed data.

A.



B.

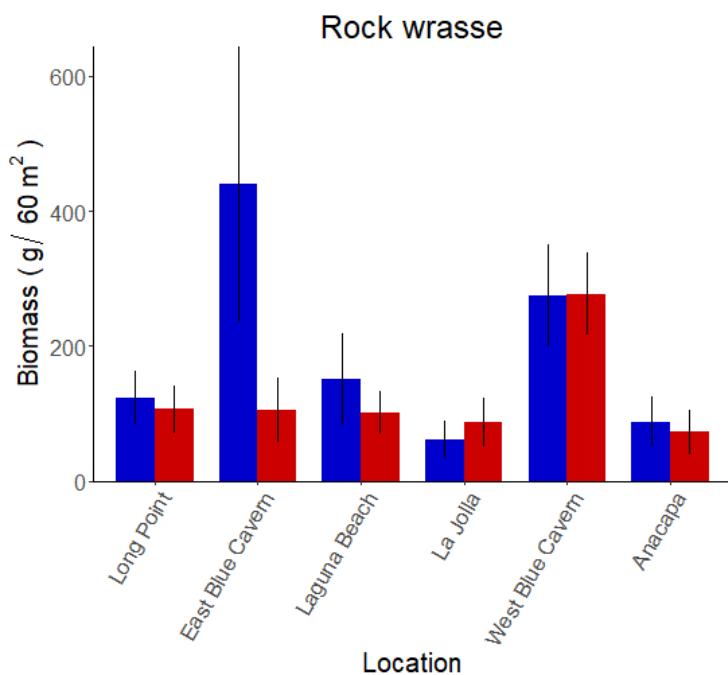
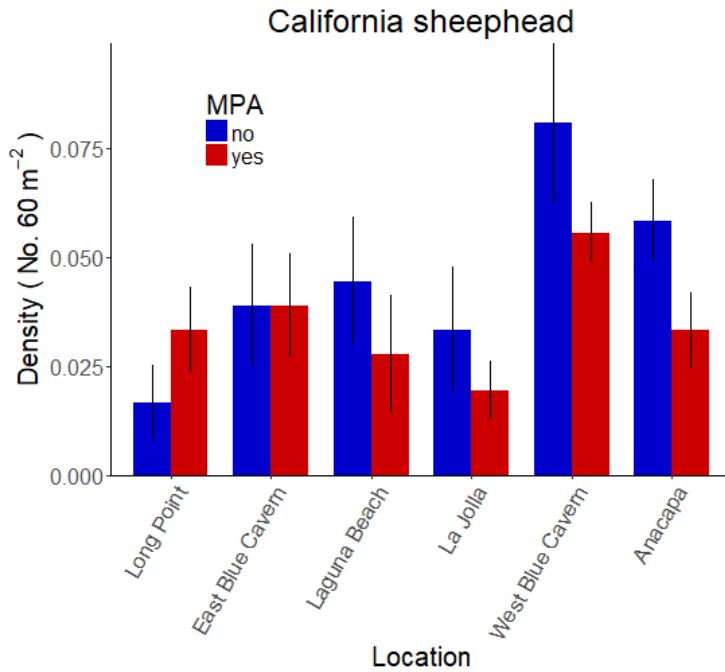


Figure 2. Biomass of two fishes inside (red) and outside (blue) of 6 MPAs in the Southern California Bight: (A) California sheephead (targeted by fishing); and (B) rock wrasse (not targeted by fishing). Means ± 1 SE are shown; $n = 6$ transects for each mean.

A.



B.

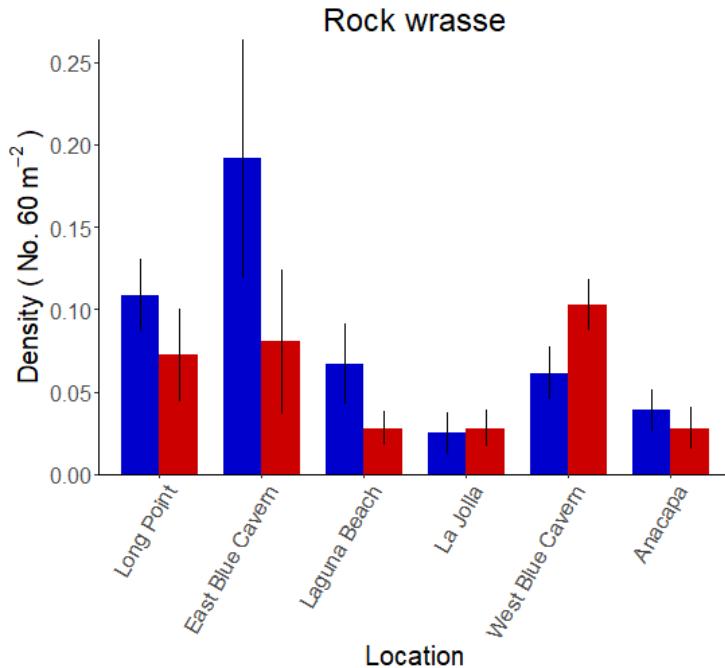
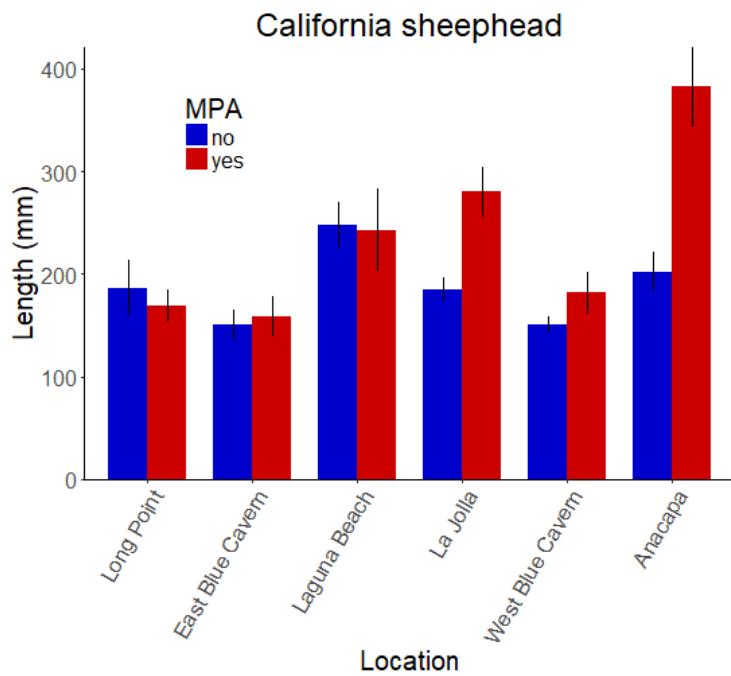


Figure 3. Density of two fishes inside (red) and outside (blue) of 6 MPAs in the Southern California Bight: (A) California sheephead (targeted by fishing); and (B) rock wrasse (not targeted by fishing). Means ± 1 SE are shown; $n = 6$ transects for each mean.

A.



B.

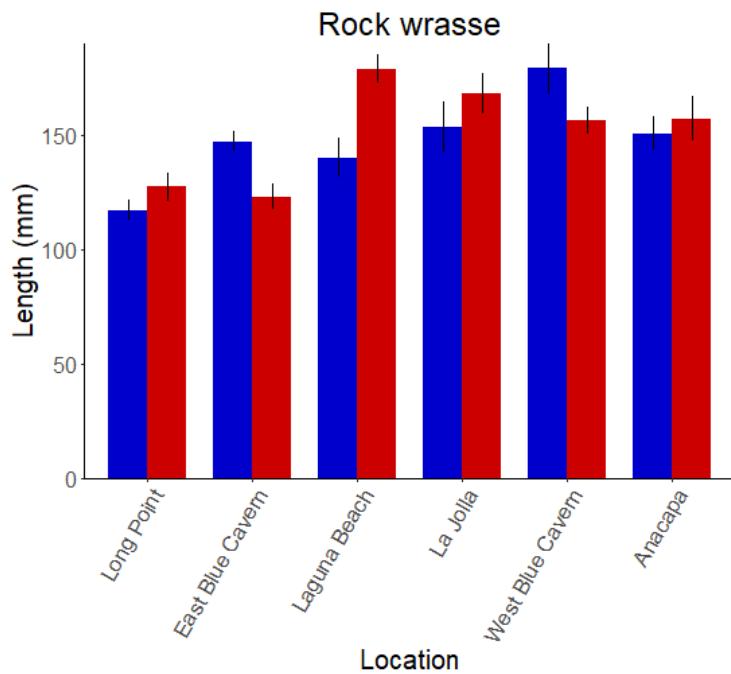


Figure 4. Size (total length mm) of two fishes inside (red) and outside (blue) of 6 MPAs in the Southern California Bight: (A) California sheephead (targeted by fishing); and (B) rock wrasse (not targeted by fishing). Means \pm 1 SE are shown; $n = 6$ transects for each mean.

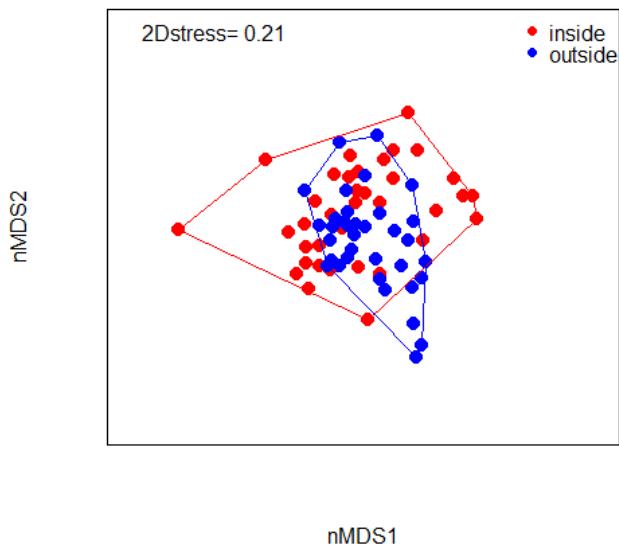


Figure 5. nMDS plot illustrating differences between transects inside versus outside all 6 MPAs. Ordination is based on invertebrate species (22 variables). Each site was surveyed 6 times and each replicate is represented by a point in the figure. MPA transects were significantly different from non-MPA transects. Analysis was based on Bray–Curtis similarity measure calculated from log-transformed data.

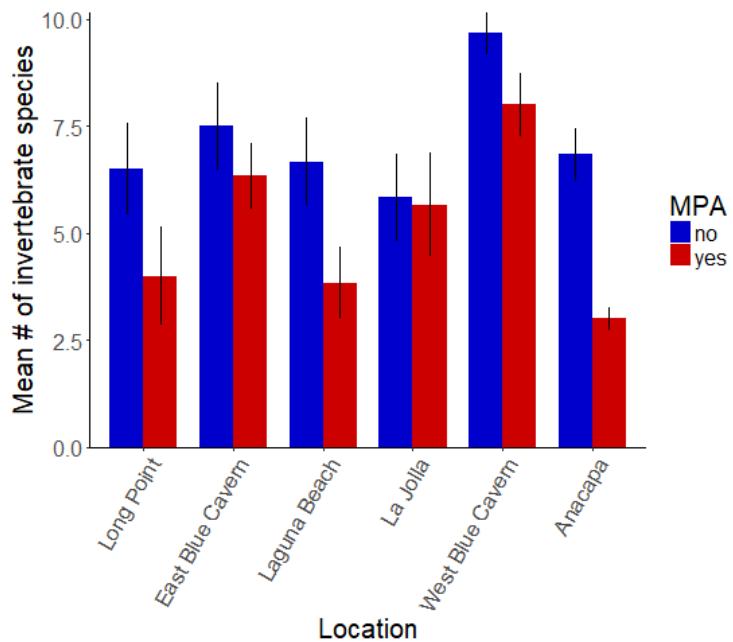


Figure 6. Invertebrate species richness inside (red) and outside (blue) of 6 MPAs in the Southern California Bight. Means \pm 1 SE are shown; n = 6 transects for each mean.

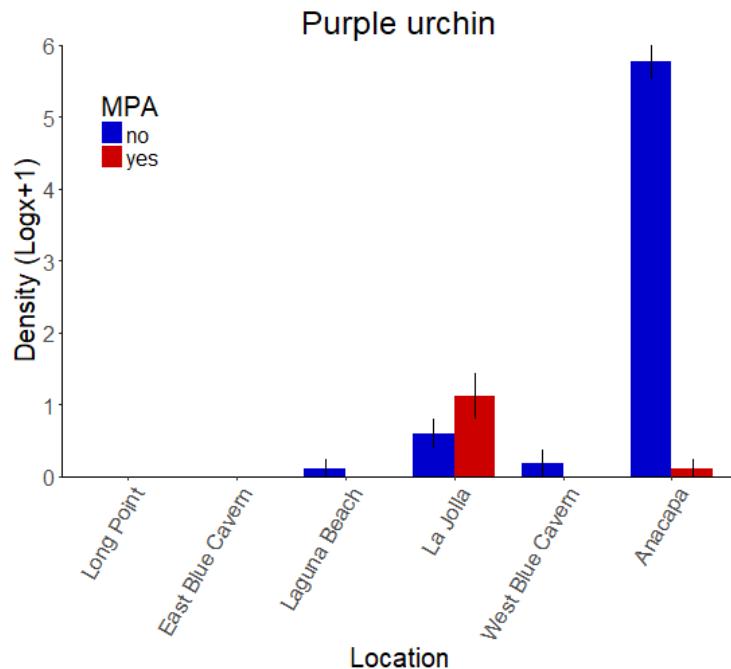


Figure 7. Density ($\log x+1$) of purple urchins inside (red) and outside (blue) of 6 MPAs in the Southern California Bight. Means ± 1 SE are shown; $n = 6$ transects for each mean.

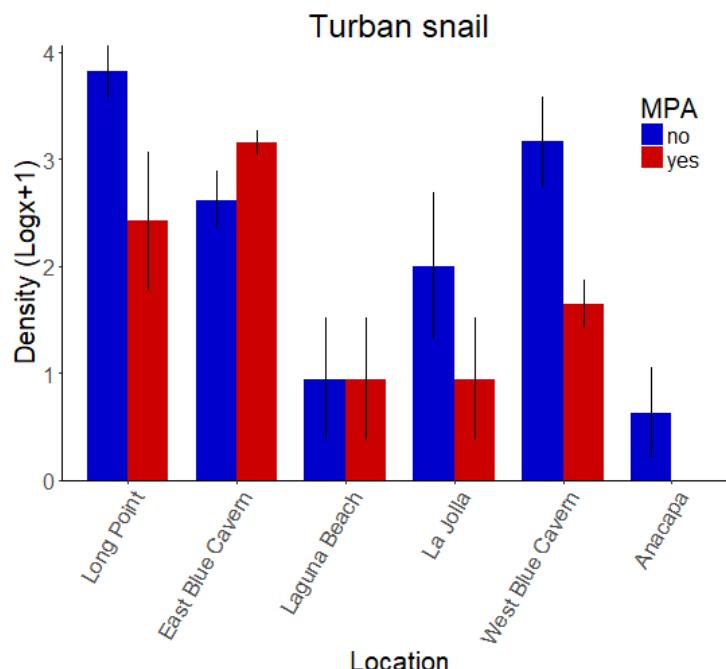


Figure 8. Density ($\log x+1$) of turban snails inside (red) and outside (blue) of 6 MPAs in the Southern California Bight. Means ± 1 SE are shown; $n = 6$ transects for each mean.

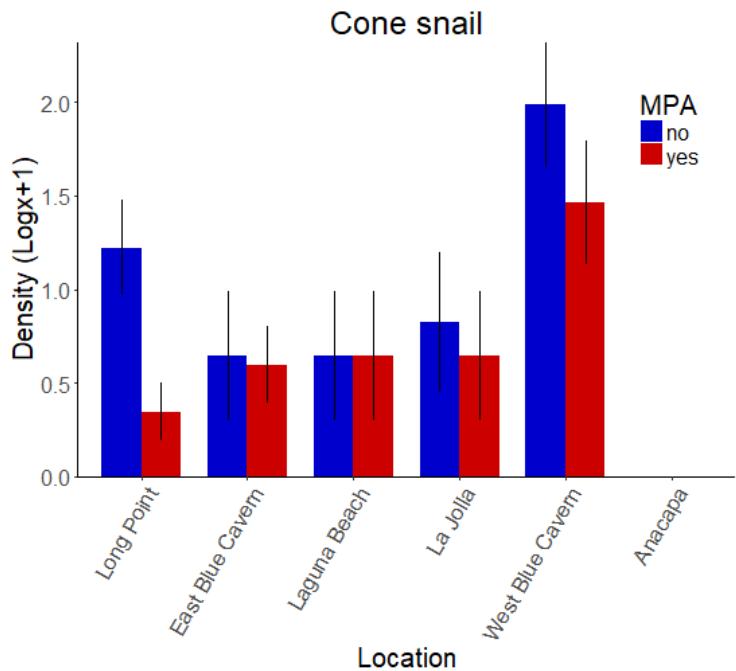
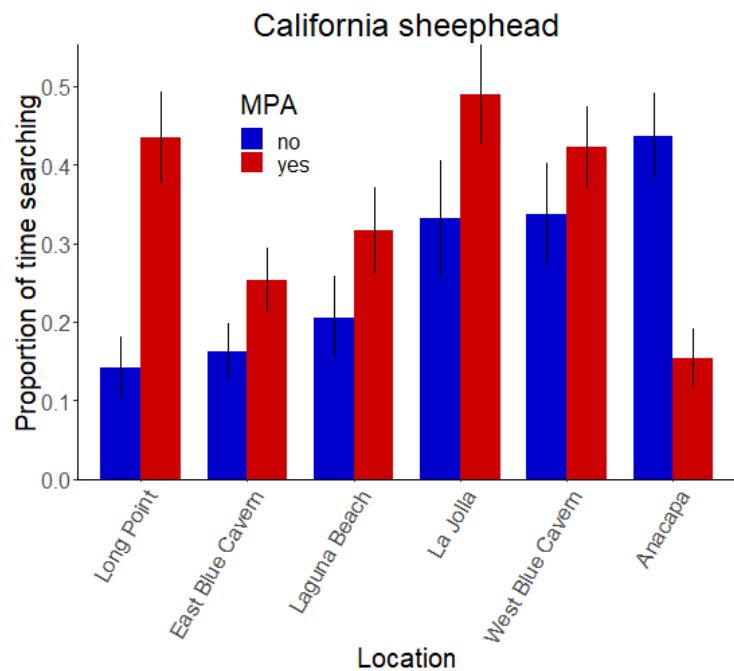


Figure 9. Density (log $x+1$) of cone snails inside (red) and outside (blue) of 6 MPAs in the Southern California Bight. Means \pm 1 SE are shown; n = 6 transects for each mean.

A.



B.

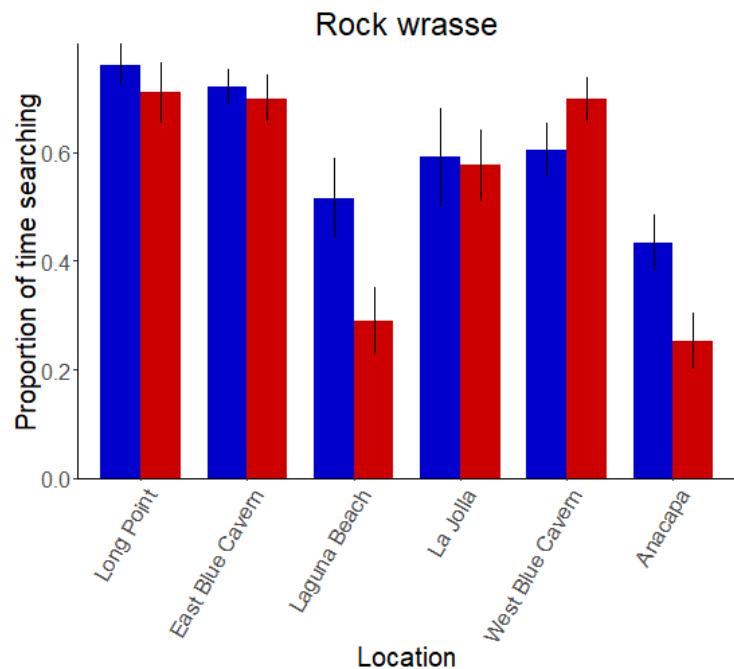
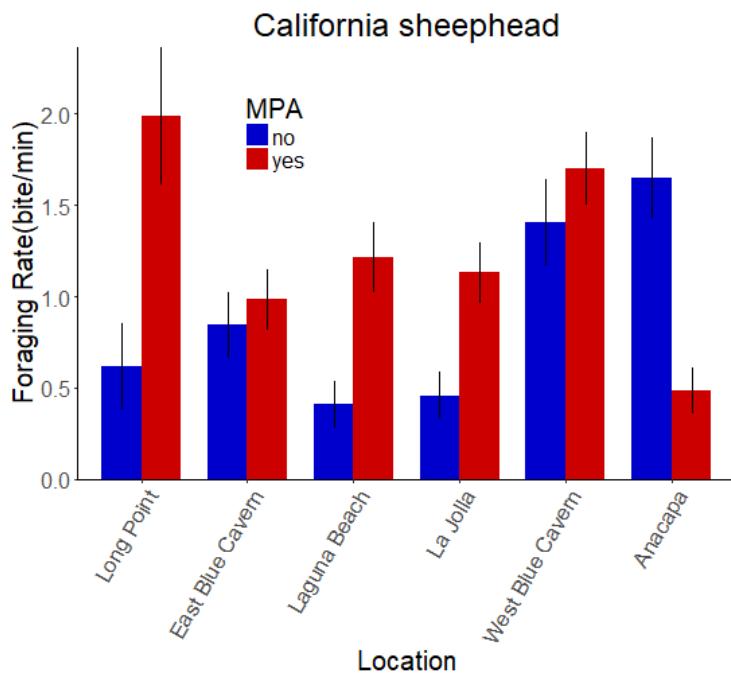


Figure 10. Natural search behavior of two fishes inside (red) and outside (blue) of 6 MPAs in the Southern California Bight: (A) California sheephead (targeted by fishing); and (B) rock wrasse (not targeted by fishing). Means \pm 1 SE are shown.

A.



B.

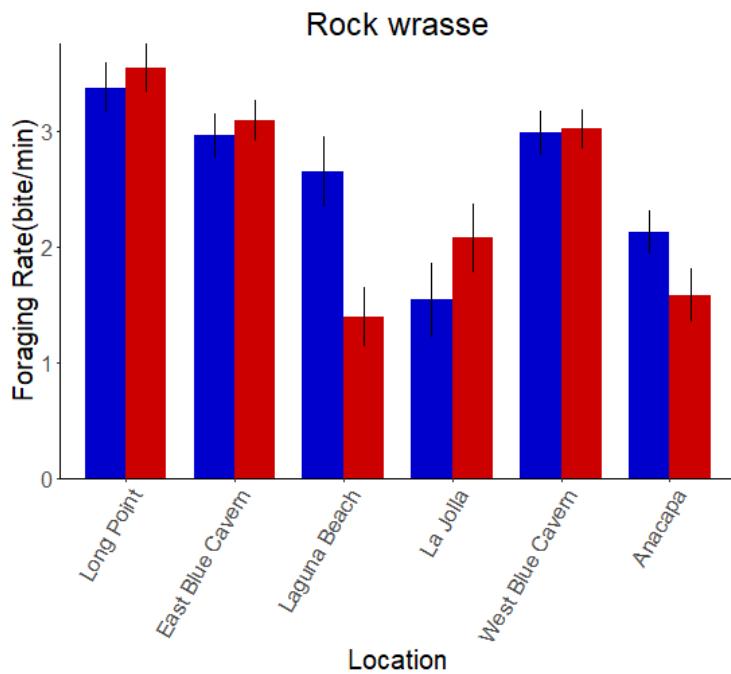
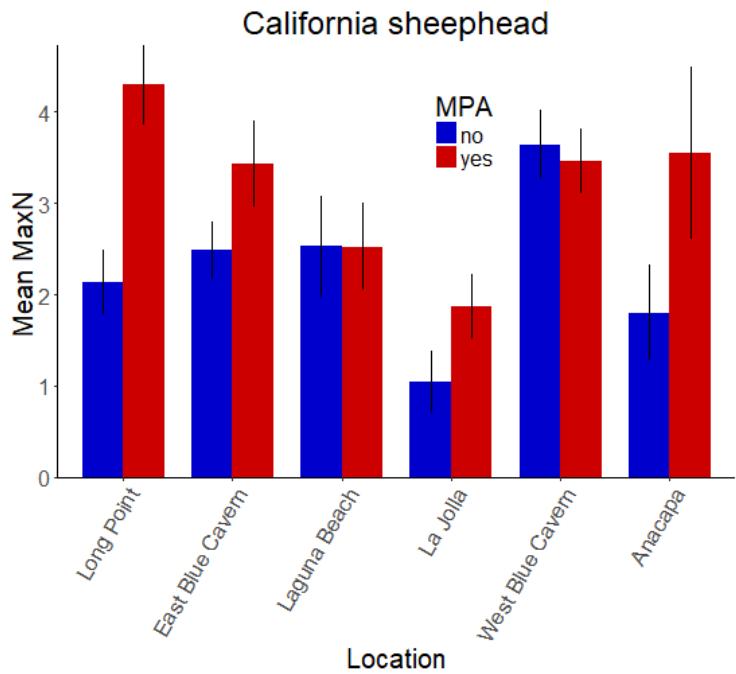


Figure 11. Natural foraging rate (bites/min) of two fishes inside (red) and outside (blue) of 6 MPAs in the Southern California Bight: (A) California sheephead (targeted by fishing); and (B) rock wrasse (not targeted by fishing). Means \pm 1 SE are shown.

A.



B.

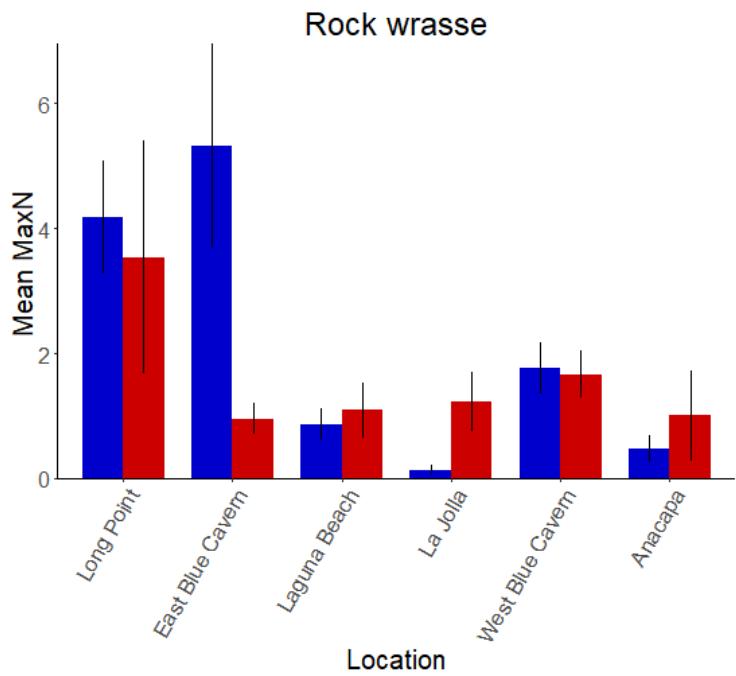
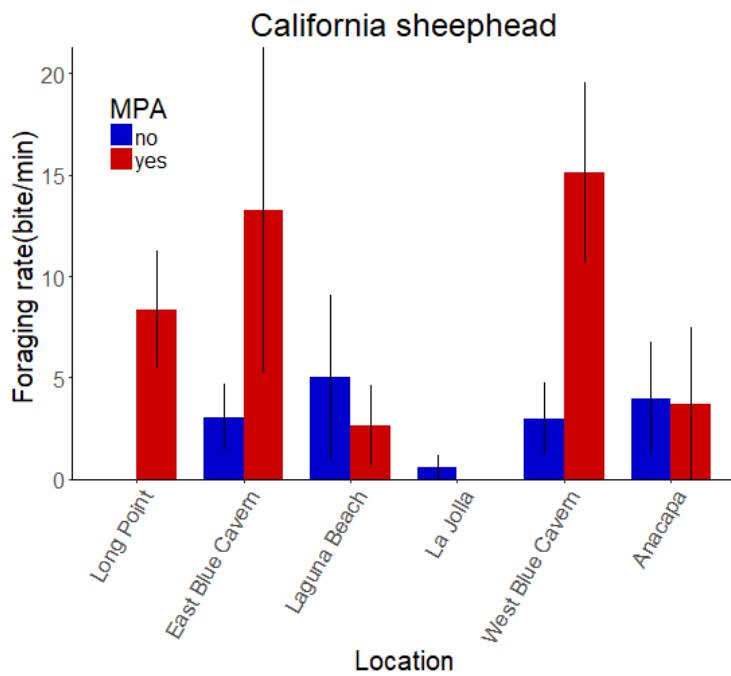


Figure 12. MaxN of two fishes inside (red) and outside (blue) of 6 MPAs in the Southern California Bight: (A) California sheephead (targeted by fishing); and (B) rock wrasse (not targeted by fishing). Means \pm 1 SE are shown; $n = 35$ for each mean.

A.



B.

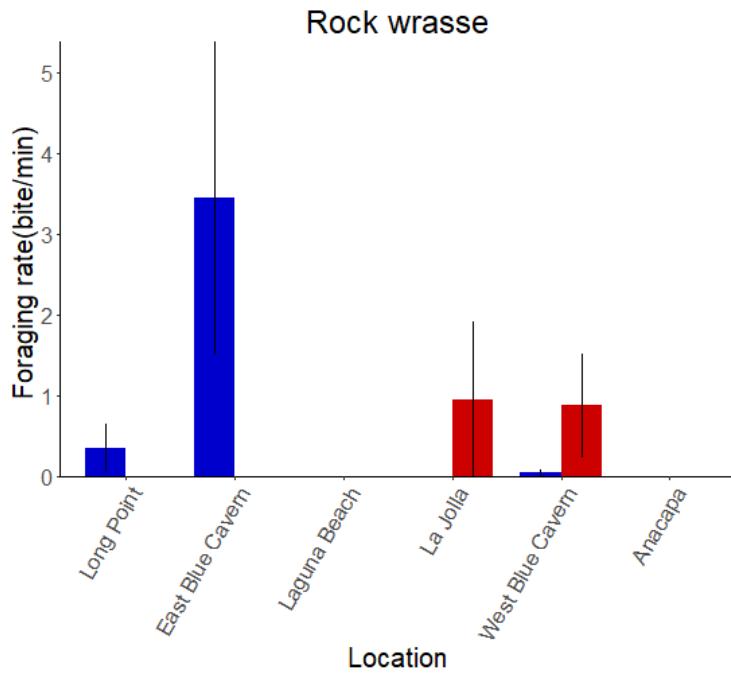
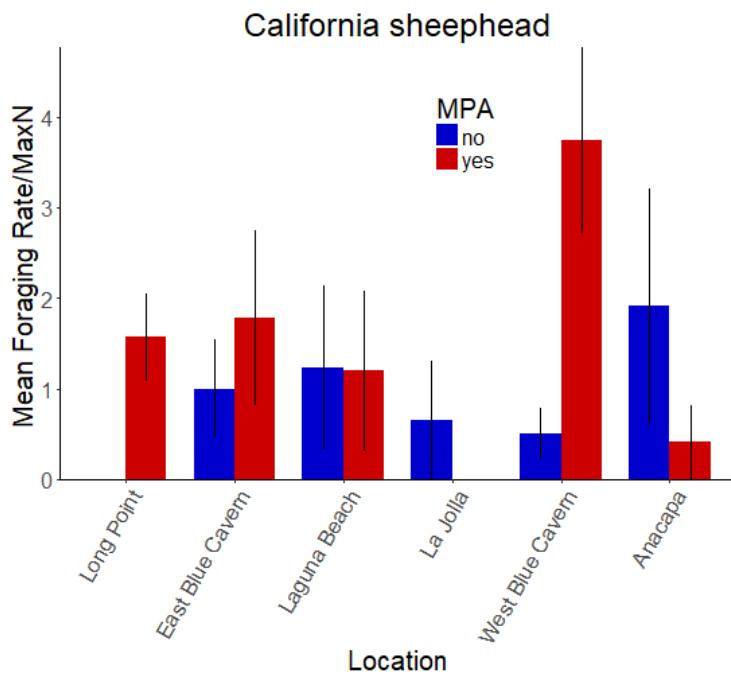


Figure 13. Foraging rate on bait of two fishes inside (red) and outside (blue) of 6 MPAs in the Southern California Bight: (A) California sheephead (targeted by fishing); and (B) rock wrasse (not targeted by fishing). Means \pm 1 SE are shown; $n = 35$ for each mean.

A.



B.

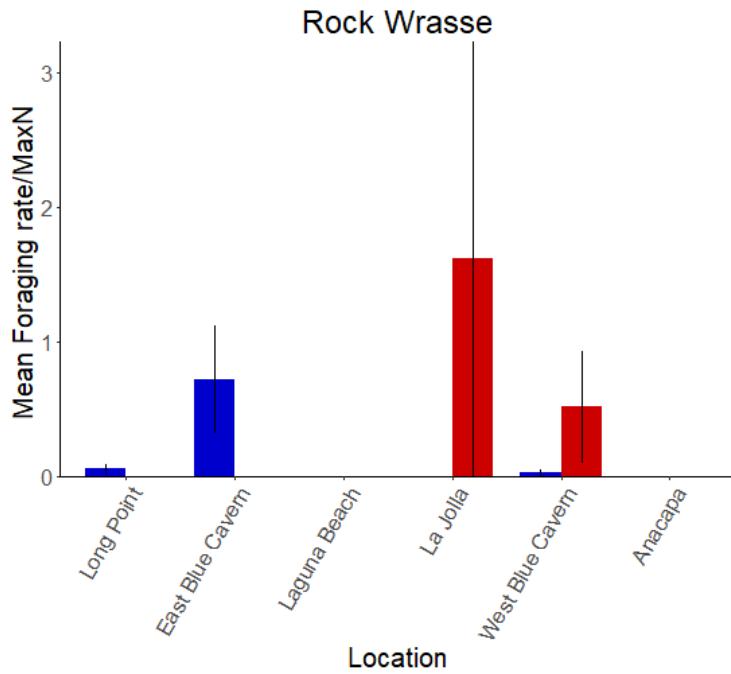


Figure 14. Foraging rate on bait divided by MaxN of two fishes inside (red) and outside (blue) of 6 MPAs in the Southern California Bight: (A) California sheephead (targeted by fishing); and (B) rock wrasse (not targeted by fishing). Means \pm 1 SE are shown; $n = 35$ for each mean.

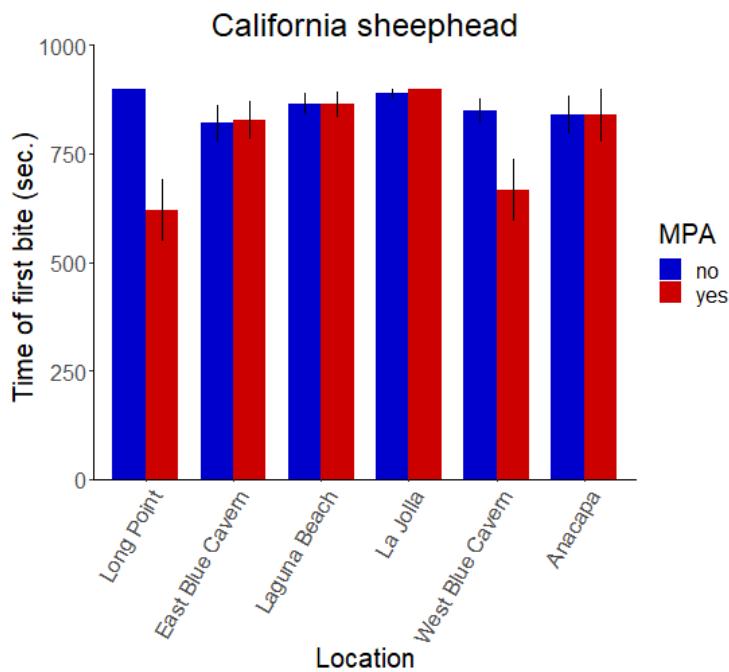


Figure 15. Time of first bite (sec.) of California sheephead, inside (red) and outside (blue) of 6 MPAs in the Southern California Bight. Individuals that did not feed during the BRUV deployment had a total time of 900 sec. (Long Point (non-MPA) and La Jolla (MPA)). Means \pm 1 SE are shown; $n = 35$ for each mean.