Early indicators of MPA effects are detected by stereo-video

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ABSTRACT: Resource managers often outline discrete goals when implementing marine protected areas (MPAs), such as increases in organism abundance, biomass, or body size, to evaluate MPA success and thus inform future management decisions. Understanding which biological indicators are most sensitive to protection is essential for adaptive management, and while density is a commonly used metric to monitor MPAs, previous work has pointed to a lack of reliability of this metric to effectively evaluate MPAs, particularly during initial stages of protection. To determine which biological indicators of MPA success were evident 5 yr after protection began, we examined the differences in populations inside vs. outside MPAs for 3 fishes targeted by anglers — kelp bass *Paralabrax clathratus*, barred sand bass *P. nebulifer*, and California sheephead *Semicossyphus pulcher* — and 4 non-targeted species. We used stereo-video to determine the average body size, biomass, and density of each species in 7 MPAs in Southern California that were paired with nearby non-MPA sites. Responses of targeted species were detectable after 5 yr of protection in some MPAs. In most but not all MPAs, individuals were larger compared to outside MPAs for kelp bass and California sheephead. Biomass and density of targeted species appeared to be less sensitive to MPA effects. As expected, non-targeted species did not show evidence of MPA effects. Similar to past studies, our findings indicate that the choice of response variable and species studied may influence the perceived efficacy of MPAs, and we emphasize that increases in length may be a particularly sensitive indicator of effective protection.

KEY WORDS: Marine protected areas · MPAs · Kelp forest · *Semicossyphus pulcher* · *Paralabrax clathratus* · *P. nebulifer* · Rocky reef · Biomass · Size-based indicators · California

1. INTRODUCTION

In order to mitigate the impacts of overfishing on marine communities, there has been a shift towards ecosystem-based management, in which the entire ecosystem becomes the target for protection rather than individual species (Pikitch et al. 2004, Douvere 2008). The primary mitigation strategy for ecosystem-based management in marine systems is marine protected areas (MPAs), which are designated areas that are closed or partially closed to harvest and other activities. MPAs can act as insurance against overfishing by protecting a given area, which can serve as a refuge, ensuring that some members of the population will survive to reproduce (Bohnsack 1998,

Dayton et al. 2000). MPAs can also counteract the impacts of overfishing outside their boundaries through larval dispersal (Christie et al. 2010, Goñi et al. 2010) and spillover of adults to fished areas (da Silva et al. 2015). In these ways, MPAs can be effective tools in marine resource management by increasing abundance, diversity, egg production, and body size of organisms targeted by fishers (Jennings et al. 1995, Tetreault & Ambrose 2007, Babcock et al. 2010, Caselle et al. 2015).

Evaluation and monitoring are important components of successful implementation of MPAs. Three metrics are commonly used to evaluate responses of marine organisms to protection: density, biomass, and body size. Many studies have shown that MPAs

can increase these 3 metrics for targeted species (see meta-analyses by Lester et al. 2009, Giakoumi et al. 2017, Cresswell et al. 2019); however, less attention has been given to the differences in the detectability of these metrics and their biological implications. Biotic, anthropogenic, and abiotic factors can differentially affect density, body size, and biomass, and therefore these metrics may not be equally informative in assessing responses of marine organisms to protection (Paddack & Estes 2000, Kaplan et al. 2019).

As an increase in abundance of marine organisms is often a primary goal for MPAs, many studies report changes in density as a measure of MPA efficacy (e.g. Froeschke et al. 2006, Russ et al. 2015). The cessation of fishing creates the expectation that abundance of fished species will increase. Although increased density is an anticipated effect of MPAs (Lubchenco et al. 2003), studies have shown that it can be an inconsistent indicator of MPA effects (Soykan & Lewison 2015) and may take decades to be detectable (Nickols et al. 2019). Spatial variation in density can be more influenced by habitat than protection (Edgar et al. 2014, Russ et al. 2018), which can mask the effects of MPAs. Also, density can be strongly affected by life history traits, recruitment rates, and short-term environmental variability (Dayton et al. 2000, Caselle et al. 2015, Starr et al. 2015). For example, if periods of low recruitment follow MPA placement, then it may take more time to detect MPA effects than when high recruitment periods follow MPA placement (Nickols et al. 2019). Recruitment can be difficult to monitor and predict, and therefore changes in density may be an unreliable indicator of MPA effects since the effect size will be context dependent. Thus, without the ability to account for past recruitment and to predict future recruitment, changes or differences in abundance can be imprecise measures of recovery when evaluating MPAs (Nickols et al. 2019).

Population biomass is a metric that incorporates both density and body size. While biomass is also influenced by environmental and habitat variables, such as temperature, distance of the reef to a shelf break, and reef slope (Pondella et al. 2019), it has been suggested to be a more appropriate measure of population responses to protection than density alone (Soykan & Lewison 2015). For example, Kaplan et al. (2019) modeled recovery trajectories of organisms within MPAs and found that biomass should be used as an early indicator of MPA effects rather than abundance. By incorporating body size, measuring changes in biomass can abate potential environmen-

tal effects that can influence density more than body size (Vallès & Oxenford 2015).

Size-based indicators, without incorporating population density, can reveal the effects of fishing on population structure because of the size-selective nature of fishing (Shin et al. 2005). Average body sizes are affected by fishing in 2 ways: either because larger individuals are removed due to gear selectivity, size limits, or targeting of larger individuals to maximize profit; or because populations accumulate the effects of overfishing by the continuous removal of individuals over time, resulting in fewer old, large individuals (Shin et al. 2005). While somatic growth can be influenced by environmental variables, such as temperature and upwelling (Ong et al. 2017), as well as population density (i.e. density dependence; Vrtílek et al. 2019), increase in body size is likely to be a rapid and strong response to protection because it is expected that the largest, oldest individuals will benefit the most from protection in the early stages of an MPA (Kaplan et al. 2019). However, monitoring changes in the size structure of populations within MPAs can be imprecise or unrepresentative of actual size of a population when researchers use underwater visual census or fishery-dependent tools (Potts & Manooch 2002, Goetze et al. 2015).

With the potential for the commonly used indicators of MPA effects to change at different rates, as well as conflicting reports on which metric can be the most sensitive to protection, it can be difficult to predict MPA effects (Cresswell et al. 2019, Kaplan et al. 2019), and there is ambiguity on how quickly these indicators can be detected. A meta-analysis by Molloy et al. (2009) found that some MPAs showed strong effects of protection within 2 yr, but that others took decades to achieve similar impacts. If resource managers or the public expect MPAs to affect marine organisms within them more quickly than is possible, these unachievable targets may lead to a premature decision that an MPA is unsuccessful and needs adaptive management or removal. Knowing which biological changes will accrue in the early stages of a new MPA and how to detect them is important for resource managers who may need to make quick and adaptive decisions based on the status of current MPAs, which can inform the design of future MPAs.

The objectives of this study were to determine if MPA effects could be detected within young MPAs that had only been established for 5 yr and, if so, which indicator of recovery of fish populations, changes in density, biomass, or average body size, showed the strongest response to protection. To address these objectives, we quantified differences

in populations of fishes targeted by fishers as well as those not targeted by fishers between MPA and nearby non-MPA sites in 7 locations in Southern California. We tested 2 hypotheses: (1) biological differences between MPAs and nearby unprotected areas would be detectable within 5 yr of MPA implementation for targeted fishes and not for non-targeted fishes; and (2) size-based responses would be more sensitive indicators of MPA effects than density within young MPAs.

2. MATERIALS AND METHODS

2.1. Study sites

We selected 7 MPAs within the Southern California Bight: the Campus Point State Marine Conservation Area (SMCA), the Point Dume State Marine Reserve (SMR), the Point Vicente no take SMCA, the Laguna Beach SMR, the Swami's SMCA, the Long Point SMR, and the Blue Cavern Onshore SMCA. All of these MPAs were established in 2012 by the Marine Life Protection Act (MLPA) and protect ecological communities on nearshore, rocky reefs. These MPAs were designed using a bottom-up approach, allowing distinct groups to collaborate with managers to create both ecological and economic objectives (Saarman & Carr 2013). Zellmer et al. (2018) showed that fishing decreased significantly within the MPAs after they were established. While poaching is not completely absent from California MPAs, enforcement is explicitly mandated in the MLPA (Saarman &

Carr 2013). While conducting this study, we observed little or no fishing within the MPAs.

Using a match-paired design, each MPA was paired with a nearby, fished comparison area (non-MPA), resulting in 14 total areas surveyed (Fig. 1). Non-MPAs were selected based on having similar habitat characteristics and fish assemblages as the paired MPA. Each MPA and non-MPA pair was assigned a 'location' within the Southern California Bight: Santa Barbara (Campus Point SMCA), Malibu (Point Dume SMR), Palos Verdes (Point Vicente SMCA), Laguna (Laguna Beach SMR), San Diego (Swami's SMCA), West Catalina (Blue Cavern Onshore SMCA), and East Catalina (Long Point SMR). Each MPA and non-MPA was sampled between May and September of 2016 and 2017, except for West Catalina, which was only sampled in the summer of 2017. For more details on these study sites see Jaco & Steele (2020).

2.2. Sampling methods

We measured the size (total length) and density of fishes at each MPA and each non-MPA, as well as habitat characteristics. From size and density estimates, we calculated biomass using weight−length equations from Love (2011). Over the 2016−2017 study period, a total of nine 50 m transects was sampled at each MPA and each non-MPA. These were distributed throughout each MPA and non-MPA by sampling rocky reef in 3 zones (nearshore, mid-reef, and offshore) nearest to 3 random points selected with the Create Random Points tool in ArcGIS 10.4 (Environmental Systems Research Institute (ESRI) 2015). The distance between adjacent transects was typically greater than 100 m and the transects were spread throughout each MPA and non-MPA. On average, reef zones differed in depth, but there was considerable variation in depths among zones (means: 7.4, 11.0, and 15.2 m for nearshore, mid-reef, and offshore; with depth ranges of 5.0−14.4, 6.7−14.1, and 6.4−19.1 m, respectively).

Each transect consisted of a canopy (top 2 m of the water column), midwater, and benthic component. The transect tape for the canopy portion was reeled out first, and fish and giant kelp (*Macrocystis pyrifera*) canopy
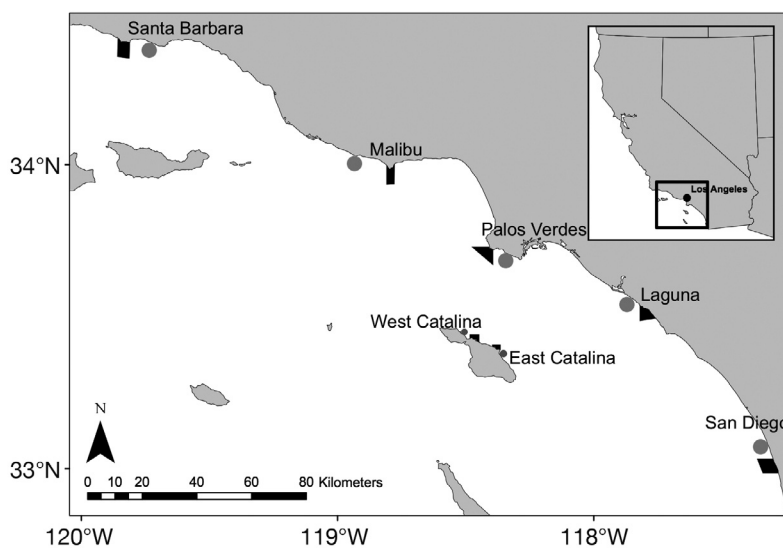

Fig. 1. The 7 locations used in this study showing the 7 MPAs (black polygons) and 7 non-MPA sites (grey circles)

cover were recorded within the top 2 m of the water column. The midwater portion was reeled out directly below the canopy portion, 6 m above the seafloor, except in the case of areas with a seafloor depth <9 m, in which the transect tape was reeled out 4 m above the seafloor. Finally the benthic portion of the transect was laid out along the seafloor.

Fish lengths and densities were determined using a SeaGIS diver-operated stereo-video camera system (www.seagis.com.au). Stereo-video is a technique that employs 2 video cameras in underwater housings that are mounted to a base bar and face the same direction. When the videos of the 2 cameras are analyzed with a specialized software program, an estimate of the 3-dimensional space within the video can be determined, allowing for measurements such as lengths of objects and the range of objects from the cameras. A diver swam the length of all three 50 m long components of each transect, keeping the stereo-video camera centered over the transect and facing forward. When a fish swims into the field of view of both cameras, it can be measured to the nearest millimeter with a less than 1% error under ideal conditions (e.g. as determined via measuring trials of a measuring stick in a controlled pool environment), though in more realistic field settings, typically within 1 cm of true length (Harvey et al. 2002). This technique allows for extremely accurate length measurements that are necessary for detecting small differences, which are what is expected for recently established MPAs. Our stereo-video system consisted of 2 GoPro HERO4 Silver cameras, with a base separation of 80 cm and an inward convergence of 4 degrees. Cameras were calibrated using the SeaGIS Calibration Cube and corresponding SeaGIS CAL software (www.seagis.com.au). For a complete review of the photogrammetry principles and stereo-camera system design see Harvey & Shortis (1995) and Goetze et al. (2019). All video processing was completed using the customized software SeaGIS EventMeasure (www.seagis.com.au).

The total lengths and density of species that are common and abundant within kelp forests throughout the Southern California Bight were recorded for each transect. We only focused on species that were abundant enough to have adequate statistical power across our study region. These species were categorized as either targeted by fishers or not targeted by fishers. The targeted species in this study were kelp bass *Paralabrax clathratus*, California sheephead *Semicossyphus pulcher*, and barred sand bass *P. nebulifer*. Because targeted species receive the direct benefits of protection from fishing within MPAs, they are expected to show strong responses to protection, provided their home range is smaller than the size of a typical MPA. Non-targeted species were used as controls for variation among sites not related to fishing because they were not expected to show any differences between MPAs and non-MPAs soon after protection, though time-lagged indirect effects can develop (Babcock et al. 2010). The non-targeted species were blacksmith *Chromis punctipinnis*, garibaldi *Hypsypops rubicundus*, señorita *Oxyjulis californica*, and rock wrasse *Halichoeres semicinctus*. These species are unlikely to be directly affected by protection from fishing. Señorita, rock wrasse, and blacksmith are relatively small fishes with small mouths making them difficult to catch on hook-and-line, as well as undesirable to fishers. While there are records of these 3 species being caught by fishers, the proportion of landings in Southern California compared to other targeted fishes is extremely low, and when caught, they are commonly released (RecFIN; www.recfin.org, accessed December 2019). It is illegal to fish for garibaldi in California, and though there may be a very small amount of illegal harvest of this species, there are no recorded landings (RecFIN). Because both California sheephead and rock wrasse are protogynous species in which males are the terminal phase and are generally larger than females, both of these wrasse species were separated into male and female categories for analyses.

We collected data on habitat characteristics of each site that could potentially influence fish populations, and therefore confound the results of this study. Data were collected by a diver who followed the diver recording fishes on each transect. Two types of data were recorded: macroalgal density and benthic data via random point contacts (RPCs), which categorized the substrate type, relief, biotic cover of the substrate, and kelp canopy presence. Densities of individual plants were recorded along 2 m wide belt transects, and categorized each into one of 4 height categories: canopy (6–18 m), midstory (4–6 m), high understory (1–2 m), and low understory (0.25–1 m). Due to logistical constraints, macroalgal species were not differentiated. RPCs were collected at a random point within each meter of the 50 m transect. All variables were recorded along the benthic portion of each transect except for giant kelp canopy presence, which was recorded along the canopy portion, as the number of random points directly beneath the kelp canopy. Substrate type was divided into 6 categories: bedrock (>2 m), large boulder (1–2 m), small boulder (0.1–1 m), cobble (1–10 cm), and sand (<1 cm). Substrate relief measured the absolute difference in height of the

highest and lowest points within a 0.25 × 0.5 m rectangle around each point, and was divided into 5 categories: >2 m, 1–2 m, 0.5–1 m, 10–50 cm, and 0–10 cm. At each point the surveyor also recorded the cover of benthic organisms or bare substratum.

2.3. Fish population metrics

2.3.1. Lengths

To determine fish lengths, we used the stereo measuring component of SeaGIS EventMeasure. This component uses trigonometric principles to calculate lengths derived from 3-dimensional estimates of space. Total lengths of all fishes were recorded regardless of distance from the cameras, provided the fish was identifiable and oriented in a way that could be measured (both snout and end of caudal fin visible in both videos, with little to no bend in the body or caudal fin).

2.3.2. Density

Density estimates included only individuals along transects if they were within 2 m of the stereo-camera, which was the lowest visibility encountered during our study. This 2 m range limit was used to avoid biases that are inherent to variable underwater visibility, which can affect density estimates (Bozec et al. 2011). The field of view at 2 m from the midpoint of the stereo-camera was 2.1 m wide × 1.4 m high. Thus, density was measured along a 50 × 2.1 × 1.4 m (147 m^3) belt transect for each of the 3 components of a transect. Density per transect (441 m^3) was calculated by summing the values of the canopy, midwater, and benthic portions of each transect.

2.3.3. Biomass

Population biomass density was estimated as the sum of the mass predicted for each fish along a transect. Mass was predicted from measured lengths using length-mass equations from Love (2011). The average population biomass of each species at a site was calculated by averaging the sum of the weights from each transect. Biomass estimates were constrained in the same way that density estimates were, using only individuals within 2 m of the stereo-camera (i.e. biomass of measurable fish along 50 × 2.1 × 1.4 m transects). Biomass (per 441 m^3) was calculated for each site and species by summing the values of the canopy, midwater, and benthic portions of each transect.

2.4. Statistical analyses

2.4.1. Lengths

We tested the hypothesis that fish would be larger in MPAs by comparing lengths of fish within MPAs with lengths in paired non-MPAs for each species. We only included fish that had reached the minimum size-at-maturity (values from Love 2011, M. S. Adreani & M. A. Steele unpubl. data, C. Williams unpubl. data) to avoid confounding MPA effects with natural variation in recruitment. All lengths were log (x + 1) transformed to meet the parametric assumptions of normality and homogeneity of variance. Normality was assessed by visual inspection of normal probability plots, and homogeneity of variance by visual inspection of residuals, as recommended by Quinn & Keough (2002).

To determine if fish were larger within MPAs and if this response to protection was consistent among MPAs, we used a general linear model (GLM) for each species, with MPA status (2 levels), location (7 levels, each with an MPA and non-MPA pair), and reef zone (3 levels: inner, middle, outer) as fixed categorical predictors, and depth as a covariate. Because we were interested in the constancy of any MPA effect among locations, we included the interaction between location and MPA status in the model, but to maximize test power, no other interactions were included. We used a GLM for each species, rather than a single model that included 'species' as a factor because not every species was found in each location. We treated individual fish as replicates in these analyses to avoid having to discard transects without fish on them, but analyses using transects as replicates (with mean lengths) produced qualitatively very similar results. All length analyses were conducted in the RStudio 1.1.419 software (RStudio Team 2015) using R version 3.3.3 (R Core Team 2017)

2.4.2. Density and biomass

Differences in density were tested in 2 ways: using a total density including all individuals, regardless of size; and by using only the density of mature individuals (i.e. including only individuals that had reached the minimum size-at-maturity). These 2 different measures of density were used because, during video processing,

some fish that entered the transect could not be measured due to their body positions. By using a total density, unmeasurable fish could be included, but it was not possible to determine if each fish had reached the minimum size-at-maturity. Total density was also the only response variable for which we combined the sexes for California sheephead and rock wrasse. For biomass, only mature individuals were included because relatively few fish that had not reached the minimum size-at-maturity were measured; thus, the results including immature individuals were very similar to the results of only including mature-sized individuals. Moreover, using only mature-sized individuals in estimating biomass allowed a more direct comparison of the metrics length and biomass.

To test if differences in fish density and biomass density between MPAs and non-MPAs could be detected as responses to protection, and if these responses varied among locations, we used univariate permutational analysis of covariance (PERMANCOVA) (Anderson 2001, 2006). A permutational approach was used because the density and biomass data were non-normal as there were many transects with density and biomass values of zero. The same predictor variables were included as in the previously described GLMs: MPA status (2 levels), location (7 levels), reef zone (3 levels) as fixed categorical factors, and depth as a covariate. Again, we only included the interaction for Location × MPA status in the model. A separate, univariate analysis was run for each response variable (total density, mature density, and biomass) for each of the study species. PERMANCOVA was performed on a Euclidean distance matrix. In the exploratory phase, we experimented with several different transformations of the data, which had little effect on the results and so we present the results from the raw, untransformed data. All density and biomass analyses were completed with the statistical software program PRIMER v7 (Clarke & Gorley 2015).

2.4.3. Habitat

To determine if there were any systematic differences between the habitat characteristics of the MPAs and non-MPAs that might confound tests of MPA effects on fishes, we ran a single PERMANCOVA on the habitat data we collected: algal density, relief, and RPC data. PERMANCOVA was used to test for any systematic differences between MPAs and non-MPAs as well as differences among the 7 locations or location-specific differences between MPA and non-MPA

pairs (the interaction term). Each algal height category was expressed as individuals per m². The RPC categories of kelp canopy presence, substrate type, and benthic cover, as well as relief counts, were converted into proportions for each transect because we were not always able to record 50 points on all transects. As a way to manage the lack of independence that is inherent to proportional data, a principal components analysis (PCA) was used for all habitat data to create principal component (PC) scores for each transect that were independent of one another. We generated PC scores separately for benthic RPC variables (substrate type, relief, and benthic cover) and algae data (both counts and kelp canopy cover) for each transect. Algae data were normalized before PCA to enable us to combine proportion and count data. Using a Euclidean distance matrix, the PC scores for each transect for both RPC and algae data were used as response variables in PERMANCOVA with the same design as above: MPA status (2 levels), location (7 levels), reef zone (3 levels) as fixed categorical factors, and depth as a covariate. Analyses were done in PRIMER v7 (Clarke & Gorley 2015).

3. RESULTS

3.1. Lengths

Targeted fishes tended to be larger inside MPAs than outside them; however, this was not the case at all locations, as indicated by significant interactions between MPA status and location (Fig. 2, Table 1). Kelp bass were significantly larger within MPAs at 5 of the 7 locations and male California sheephead were significantly larger within MPAs at 3 of the 7 locations. Laguna and East Catalina each showed relatively large differences inside vs. outside the MPA. In contrast, at locations such as Malibu and Palos Verdes, the differences between populations inside vs. outside the MPAs were negligible. Female California sheephead were marginally significantly larger within MPAs compared to non-MPAs (p = 0.054). A post-hoc Tukey test showed that in 1 particular MPA (Blue Cavern Onshore SMCA) female California sheephead were significantly larger, on average 3 cm longer, within the MPA than outside it (Fig. 2), but at all other sites, the difference in length was smaller and not statistically significant. Barred sand bass did not differ in length inside vs. outside MPAs.

As expected, non-targeted species did not appear to benefit from MPAs. Blacksmith were consistently larger outside MPAs than inside them (on average
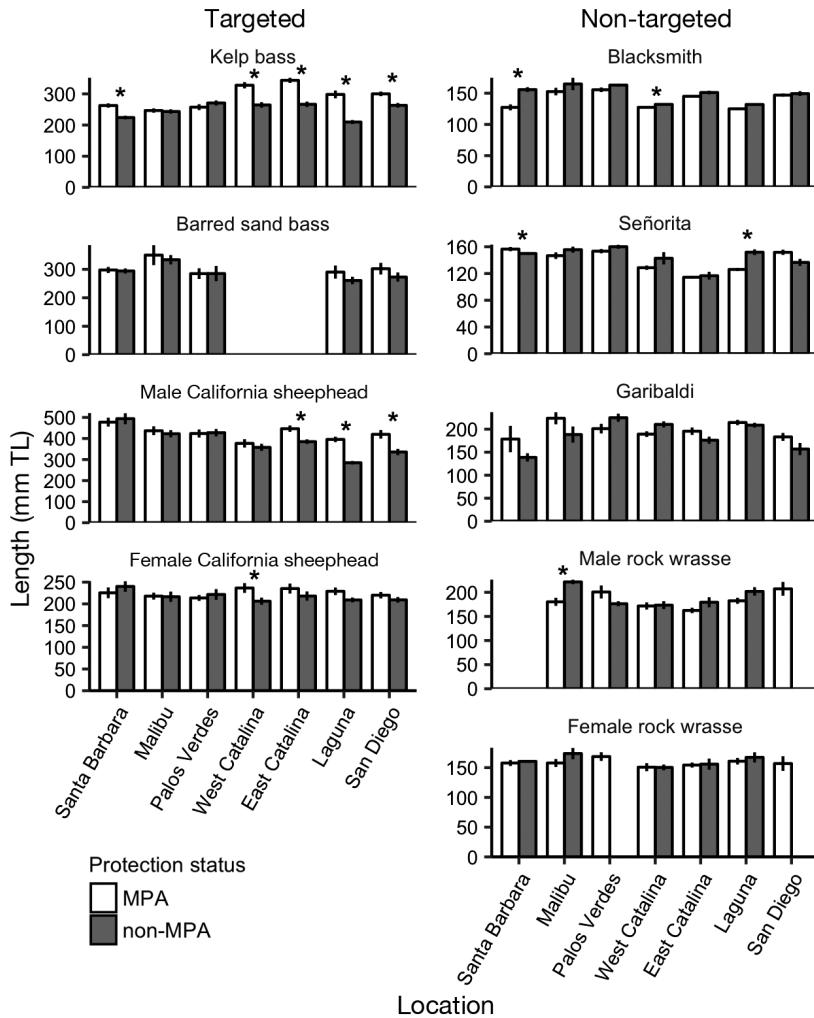
Fig. 2. Total lengths (TL) of fishes at 7 locations inside and outside MPAs. Means ±1 SE are shown. *p < 0.05; pairwise comparison test

0.3 cm larger outside vs. inside MPAs), and male rock wrasse also tended to be larger outside MPAs than inside them (on average 0.8 cm larger outside vs. inside MPAs) (Fig. 2, Table 1). Señorita had significantly different lengths inside vs. outside MPAs, but the direction of this difference (i.e. smaller or larger inside MPAs) varied significantly among locations (i.e. a significant MPA status × Location interaction; Table 1, Fig. 2). Female rock wrasse and garibaldi did not differ significantly in length inside vs. outside MPAs (Table 1).

3.2. Biomass

Biomass of only 1 of the targeted species/sexes differed between populations inside vs. outside MPAs: kelp bass had significantly higher biomass inside

MPAs (Table 2, Fig. 3), on average 288 g per transect (441 m^3) greater inside vs. outside MPAs. Male and female California sheephead and barred sand bass did not differ significantly in biomass between MPAs and non-MPAs (Table 2). Biomass of most of the non-targeted species/sexes also did not differ significantly inside vs. outside MPAs in any systematic manner (Table 2, Fig. 3). Blacksmith biomass was significantly different inside vs. outside MPAs, but this difference varied in direction and magnitude among the locations (i.e. a significant MPA status × Location interaction; Table 2, Fig. 3). This was exemplified by significantly higher biomass inside vs. outside the MPA at the East Catalina location but significantly lower biomass recorded inside vs. outside the MPA at the Santa Barbara location.

3.3. Density

3.3.1. Total density

For most species, both those targeted by fishers and those not targeted, density did not differ between sites inside vs. outside MPAs. The only targeted species that differed in density was kelp bass, which had significantly higher densities within MPAs than outside them (Table 3, Fig. 4), on average 1.7 more individuals per transect (441 m^3) inside vs. outside MPAs. The only non-targeted species that differed in density inside vs. outside MPAs were blacksmith and garibaldi. Averaged across all locations there were 3.7 more blacksmith per transect within MPAs compared to outside them (Table 3, Fig. 4). The difference in density for garibaldi was inconsistent in magnitude and direction among locations (Table 3, Fig. 4).

3.3.2. Mature density

Densities of mature individuals inside MPAs did not differ significantly compared to those outside them for targeted species/sexes (Table 4, Fig. 5).

Table 1. Results of general linear models (GLMs) comparing lengths of each species between MPAs and non-MPAs (MPA status) in different locations, including seafloor depth and reef zone (inner, middle, or outer) as predictors

Targeted	Kelp bass			Male California sheephead			Female California sheephead			Barred sand bass		
Factor	df	F	p	df	F	p	df	F	p	df	F	p
MPA status	1	74.47	<0.001	1	33.49	<0.001	1	3.72	0.054	1	1.6	0.20
Location	6	19.97	<0.001	6	14.68	<0.001	6	0.85	0.53	4	2.96	0.02
Depth	1	9.46	0.002	1	0.33	0.57	1	0.90	0.34	1	1.66	0.20
Reef zone	2	2.05	0.13	2	1.04	0.36	2	0.59	0.56	2	2.97	0.06
MPA status × Location	6	7.37	<0.001	6	4.57	<0.001	6	1.24	0.28	4	0.34	0.85
Error	1012			300			576			109		
Non-targeted	Blacksmith			Garibaldi			Male rock wrasse			Female rock wrasse		
Factor	df	F	p	df	F	p	df	F	p	df	F	p
MPA status	1	22.32	<0.001	1	1.09	0.30	1	5.90	0.02	1	0.70	0.41
Location	6	45.27	<0.001	6	6.46	<0.001	5	4.64	<0.001	6	1.09	0.37
Depth	1	12.96	<0.001	1	3.83	0.05	1	14.71	<0.001	1	0.09	0.76
Reef zone	2	23.71	<0.001	2	0.36	0.70	2	5.55	0.005	2	1.96	0.15
MPA status × Location	6	1.17	0.32	6	2.31	0.03	4	1.68	0.16	4	0.46	0.76
Error	1819			427			90			84		

	Señorita		
Factor	df	F	p
MPA status	1	6.79	0.009
Location	6	37.79	<0.001
Depth	1	0.16	0.69
Reef zone	2	40.90	<0.001
MPA status × Location	6	6.0	<0.001
Error	804		

Table 2. Results of GLMs comparing biomass density of each species between MPAs and non-MPAs (MPA status) in different locations, including seafloor depth and reef zone (inner, middle, or outer) as predictors

Targeted	Kelp bass			Male California sheephead			Female California sheephead			Barred sand bass		
Factor	df	F	p	df	F	p	df	F	p	df	F	p
MPA status	1	6.15	0.01	1	0.65	0.44	1	0.19	0.67	1	0.01	0.92
Location	6	2.08	0.055	6	1.91	0.06	6	1.65	0.14	4	1.94	0.10
Depth	1	2.87	0.10	1	0.67	0.42	1	0.73	0.43	1	0.07	0.80
Reef zone	2	0.69	0.51	2	1.12	0.31	2	1.58	0.21	2	0.54	0.60
MPA status × Location	6	1.10	0.28	6	0.41	0.90	6	1.74	0.12	4	0.61	0.67
Error	109			109			109			77		
Non-targeted	Blacksmith			Garibaldi			Male rock wrasse			Female rock wrasse		
Factor	df	F	p	df	F	p	df	F	p	df	F	p
MPA status	1	3.23	0.08	1	2.03	0.16	1	0.26	0.64	1	<0.01	0.99
Location	6	9.32	0.001	6	4.50	0.002	5	3.99	0.005	6	4.39	0.002
Depth	1	8.35	0.004	1	2.78	0.10	1	0.68	0.39	1	2.76	0.10
Reef zone	2	0.60	0.54	2	0.70	0.52	2	2.09	0.11	2	2.54	0.11
MPA status × Location	6	4.12	0.001	6	1.45	0.20	5	0.26	0.95	6	1.41	0.23
Error	109			109			93			109		

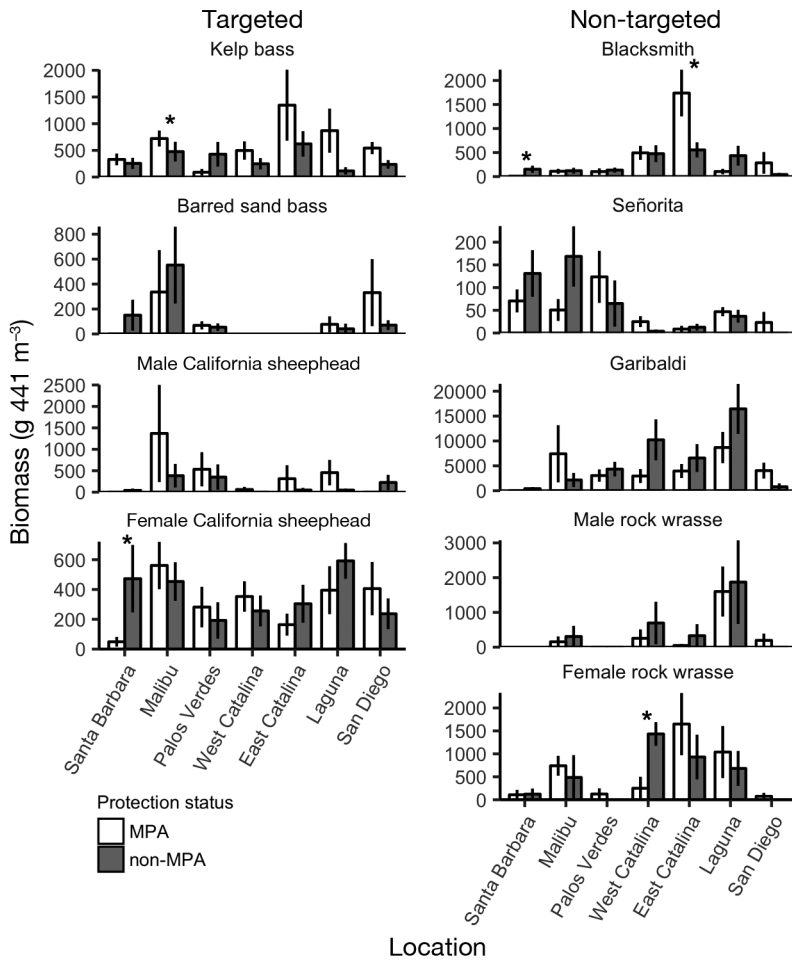|	Señorita		
Factor	df	F	p
MPA status	1	0.16	0.67
Location	6	3.76	0.002
Depth	1	0.21	0.63
Reef zone	2	0.57	0.55
MPA status × Location	6	1.64	0.14
Error	109		

Fig. 3. Biomass of mature individuals in each of 7 locations inside and outside MPAs. Means ±1 SE are shown. *p < 0.05; pairwise comparison test

Among non-targeted species, only blacksmith and female rock wrasse differed significantly in densities of mature individuals between MPAs and non-MPAs, but this difference was inconsistent among locations (Table 4, Fig. 5).

3.3.3. Habitat

There were no systematic differences in habitat between MPA and non-MPA sites that would have confounded tests for effects of MPAs on the fishes studied. A PCA summarized the RPC substratum categories and relief into 3 PCs, explaining 66.9% of the total variation (PC1: 41.5%; PC2: 16.1%; PC3: 9.3%), and the algae categories into 3 PCs, explaining 83.7% of the total variation (PC1: 38.5%; PC2: 31%; PC3: 14.2%) (see Table A1 in the Appendix). Using these 6 components, PERMANCOVA detected no main effect of MPA status ($F_{1,112} = 1.78$, p = 0.18),

indicating that on average, MPAs did not contain better or worse habitat than non-MPA sites. There was a significant interaction between MPA status and location suggesting that habitat differed between some MPA and non-MPA pairs, but in an inconsistent manner ($F_{2,112} = 4.04$, p = 0.001). While habitat differed between MPA and non-MPA pairs in some locations, primarily West Catalina, Malibu, and Santa Barbara, such differences were not present in all locations. Thus, habitat differences are unlikely to be responsible for differences in fish responses between MPAs and non-MPAs detected across the 7 locations (Fig. 6).

4. DISCUSSION

Despite considerable variability among locations, we were able to detect some evidence of effects of MPAs on fishes after only 5 yr of protection. Differences in length, i.e. larger fish inside MPAs than outside them, were more evident than differences in density or biomass. Also, indicators of MPA effects were not all equally detected among species or sexes that are targeted by fishers. Thus, our study shows that the biological measurement chosen by researchers or resource managers, as well as the species examined, may influence the interpretation of MPA success or failure.

Our study lacked the before portion of a before–after control–impact (BACI) design, which would have allowed us to distinguish MPA effects from inherent differences between paired MPA and non-MPA sites (e.g. due to better habitat in MPAs). Lacking before-protection data, we instead measured and compared the habitat between MPAs and non-MPAs; and we studied species not targeted by fishers as controls in which one would not expect rapid MPA effects. Both approaches supported the hypothesis that differences we attribute to MPA effects were indeed the results of protection from fishing rather than other inherent differences between MPAs and non-MPAs. Although certain MPA and non-MPA pairs had different habitat, these differences were inconsistent among pairs and thus were unlikely to

Table 3. Results of GLMs comparing total density of each species between MPAs and non-MPAs (MPA status) in different locations, including seafloor depth and reef zone (inner, middle, or outer) as predictors

Targeted		Kelp bass			California sheephead			Barred sand bass	
Factor	df	F	p	df	F	p	df	F	p
MPA status	1	5.49	0.02	1	<0.01	0.99	1	0.36	0.58
Location	6	5.20	0.001	6	9.26	0.001	4	1.46	0.20
Depth	1	0.73	0.40	1	6.86	0.01	1	1.88	0.17
Reef zone	2	1.84	0.16	2	0.23	0.81	2	1.38	0.27
MPA status × Location	6	1.29	0.28	6	1.42	0.22	4	1.32	0.25
Error	109			109			77		
Non-targeted		Blacksmith			Garibaldi			Rock wrasse	
Factor	df	F	p	df	F	p	df	F	p
MPA status	1	5.49	0.02	1	<0.01	0.99	1	0.36	0.58
Location	6	5.20	0.001	6	9.26	0.001	4	1.46	0.20
Depth	1	3.67	0.06	1	5.63	0.02	1	2.39	0.11
Reef zone	2	0.03	0.97	2	0.42	0.62	2	3.95	0.02
MPA status × Location	6	0.49	0.83	6	4.19	0.002	6	1.18	0.34
Error	109			109			109		
		Señorita							
Factor	df	F	p						
MPA status	1	0.66	0.42						
Location	6	1.96	0.08						
Depth	1	1.83	0.19						
Reef zone	2	1.18	0.33						
MPA status × Location	6	1.08	0.38						
Error	109								

drive the patterns we attribute to MPA effects. Because habitat in MPAs was not consistently better than in non-MPAs, any effects of habitat on fish assemblages would likely cause more variation in the indicators we measured of the studied fishes, thus reducing the ability to detect MPA effects rather than being a confounding factor.

Additionally, few of the control species, i.e. those not targeted by fishers, were consistently larger, more dense, or had higher biomass density across all MPA and non-MPA pairs (i.e. no 'main effects' of protection), supporting our hypothesis that differences inside MPAs vs. outside them in species targeted by fishers were caused by protection. Two non-targeted species/sexes tended to be larger outside MPAs than inside them: blacksmith and male rock wrasse. This pattern of smaller, prey species being larger outside MPAs than inside MPAs is consistent with the hypothesis that a buildup of predator biomass inside MPAs increased mortality rates of prey, reducing their average size, as has been noted in other studies (e.g. Selden et al. 2017). However, given that we did not detect much buildup of predator biomass, it is difficult for us to argue that this is the reason we found larger sizes of some prey species outside MPAs than

inside. Biomass and density (total and mature individuals only) did not differ consistently inside vs. outside MPAs for most of the non-targeted species/sexes, though there were some differences between specific MPA and non-MPA pairs (i.e. MPA status × Location interactions). The only non-targeted species that differed in biomass or density inside vs. outside MPAs across locations was blacksmith, and that difference was only evident for total density, i.e. only when including immature individuals. Two probable reasons why biomass and density were generally similar inside vs. outside MPAs for non-targeted species are that (1) fishing has little effect on these species and (2) indirect effects due to increased predation on these small prey species had not yet developed in the young MPAs we studied (Babcock et al. 2010). The differences in density and biomass we found were likely caused by natural variation in recruitment and mortality rates, which may have been influenced by differences in habitat among sites.

Many studies on the recovery of exploited fish populations within MPAs lump species together (e.g. Côté et al. 2001, Barrett et al. 2007, Babcock et al. 2010). Our results, however, provide evidence that
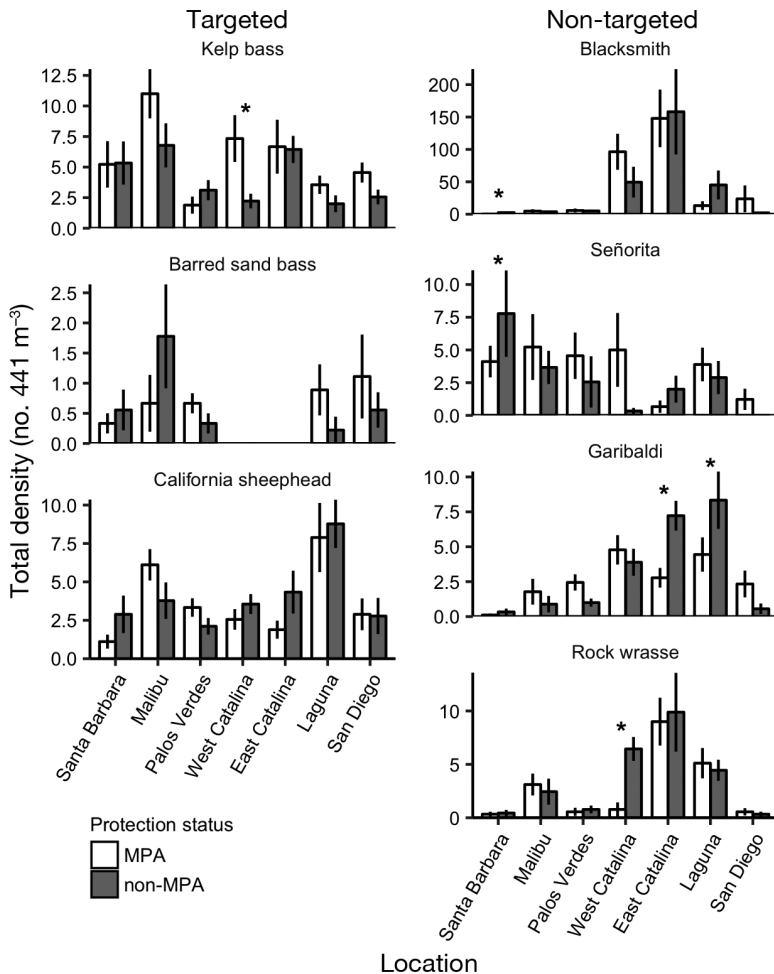
Fig. 4. Total density (mature + immature individuals) in each of 7 locations inside and outside MPAs. Means ±1 SE are shown. *p < 0.05; pairwise comparison test

typical of many in that they do not extend far offshore, may provide little protection for barred sand bass during the period when they suffer the most fishing mortality. Additionally, in 2012, the same year that the MPAs in this study were implemented, the California Department of Fish and Wildlife increased the minimum size limit of barred sand bass and kelp bass from 12 to 14 inches (30.5 to 35.6 cm), effectively protecting some of the fish in the non-MPA sites that had not been protected prior to 2012. This change of size limit would mask MPA effects on size, making our test for MPA effects on these 2 species conservative. Nevertheless, we still found clear evidence of MPA effects on length of kelp bass. Length of female California sheephead did not appear to respond to protection in MPAs as strongly as length of males of this species. This difference is likely because females are not as subject to size-selective harvesting as males. Male California sheephead are larger than females and are targeted more by recreational fishers (Cowen 1990). Because of this weaker size-selection on females, protection is less likely to change the size structure of females in the population.

While there were larger kelp bass and male California sheephead within some MPAs, the magnitude of this difference in size inside vs. outside MPAs varied among locations, indicating that MPAs vary in efficacy. In some MPAs, these 2 species were significantly larger than in nearby areas outside them, but in other MPAs, there was no difference in size from fish outside them. Elsewhere, we have shown that spatial variation in fishing pressure prior to MPA implementation is a good predictor of variation in the magnitude of MPA effects, with larger effects accruing in areas with high fishing pressure (Jaco & Steele 2020). Other factors can also affect MPA success, such as the size of the area protected, connectivity to other habitats, community buy-in, and enforcement (DeLeo & Micheli 2015, Giakoumi et al. 2017, Gill et al. 2017). The present study, along with many others, supports the view that MPAs are not a 'one size fits all' strategy, and highlights the extent to which effects of protection can vary among them.

recovery often varies among fish species, and highlights the importance of species-specific data, as has been found in other studies (e.g. Caselle et al. 2015, Di Franco et al. 2018). Not all of the fishes targeted by fishers were larger inside MPAs. Two of the 4 species/sexes targeted by fishers were larger within some MPAs, kelp bass and male California sheephead (though the magnitude of this difference varied among locations), and a third was nearly statistically significantly (p = 0.054) larger in MPAs, female California sheephead. Barred sand bass, however, were not larger inside MPAs. The lack of MPA effects on this species may be the result of its migratory spawning behavior. A large portion of the barred sand bass population migrates offshore during the summer to spawn in areas that are outside nearshore MPAs (McKinzie et al. 2014), and most of the catch of this species is made on their spawning grounds (Erisman et al. 2011). Therefore, the MPAs studied, which are

Table 4. Results of GLMs comparing density of mature fish of each species between MPAs and non-MPAs (MPA status) in different locations, including seafloor depth and reef zone (inner, middle, or outer) as predictors

Targeted	Kelp bass			Male California sheephead			Female California sheephead			Barred sand bass		
Factor	df	*F*	p	df	*F*	p	df	*F*	p	df	*F*	p
MPA status	1	1.17	0.27	1	0.26	0.63	1	0.18	0.69	1	0.09	0.75
Location	6	2.62	0.02	6	3.22	0.007	6	3.75	0.001	4	1.28	0.28
Depth	1	0.26	0.6	1	0.41	0.53	1	2.10	0.15	1	0.06	0.83
Reef zone	2	4.39	0.02	2	0.76	0.49	2	0.37	0.68	2	0.03	0.98
MPA status × Location	6	0.43	0.84	6	0.39	0.90	6	2.17	0.055	4	1.17	0.33
Error	109			109			109			77		

Non-targeted	Blacksmith			Garibaldi			Male rock wrasse			Female rock wrasse		
Factor	df	*F*	p	df	*F*	p	df	*F*	p	df	*F*	p
MPA status	1	2.29	0.11	1	1.42	0.26	1	0.19	0.64	1	<0.01	0.99
Location	6	9.25	0.001	6	4.77	0.001	5	5.68	0.001	6	5.75	0.001
Depth	1	7.45	0.01	1	2.71	0.11	1	1.32	0.23	1	5.14	0.03
Reef zone	2	0.04	0.97	2	0.58	0.53	2	1.48	0.24	2	2.42	0.1
MPA status × Location	6	4.14	0.001	6	1.47	0.2	5	1.68	0.15	6	2.47	0.02
Error	109			109			93			109		

	Señorita		
Factor	df	*F*	p
MPA status	1	0.34	0.58
Location	6	3.26	0.003
Depth	1	0.16	0.67
Reef zone	2	0.46	0.65
MPA status × Location	6	1.32	0.25
Error	109		

Total density, density of mature individuals, and population biomass appeared to be less sensitive metrics of impacts of protection within MPAs than fish length. The lack of sensitivity could be a statistical power problem, or differences in density and biomass density may just take longer to develop. Estimates of density and biomass density (due to its incorporation of density) were more variable than estimates of lengths (note error bars in Figs. 2–5), revealing lower test power caused by high variation in numbers of fishes from transect to transect. This power problem can potentially be overcome by sampling more transects or making the transects larger, which would require more time and effort. But the lower sensitivity to MPA effects was not simply a power problem. Whereas the magnitude of the difference in lengths between MPA and non-MPA pairs varied among locations (from no difference in length to considerably larger in MPAs), differences in density and biomass were of magnitude and direction (i.e. both significantly higher and significantly lower densities and biomass were found inside MPAs). This spatial variation in density and biomass may reflect differences in habitat quality, larval supply and recruitment, or other factors at our study sites rather than the cessation of fishing. It has also been shown that changes in density, and therefore biomass, can occur slowly, and can be subject to single-generation oscillations (White et al. 2013).

In the present study, stereo-video was a valuable tool that enabled detection of modest differences in the size of fishes inside vs. outside relatively young MPAs (e.g. on average, 4.7 cm for male California sheephead and 4.2 cm for kelp bass). The strength of this fishery-independent tool is both its accuracy in measuring length and the fact that it is not subject to observer bias. Under ideal conditions (e.g. pool trials), the length errors made by the stereo-video system we used were typically <1%, although accuracy in the field is more likely somewhat less, with estimates typically within 1 cm of true length (Harvey et al. 2003). In contrast, visual estimates of fish size by SCUBA divers are less accurate. For example, Bower et al. (2011) found that even very experienced divers, trained in estimating fish size, made errors greater than 10%. This 10% error rate may be large enough
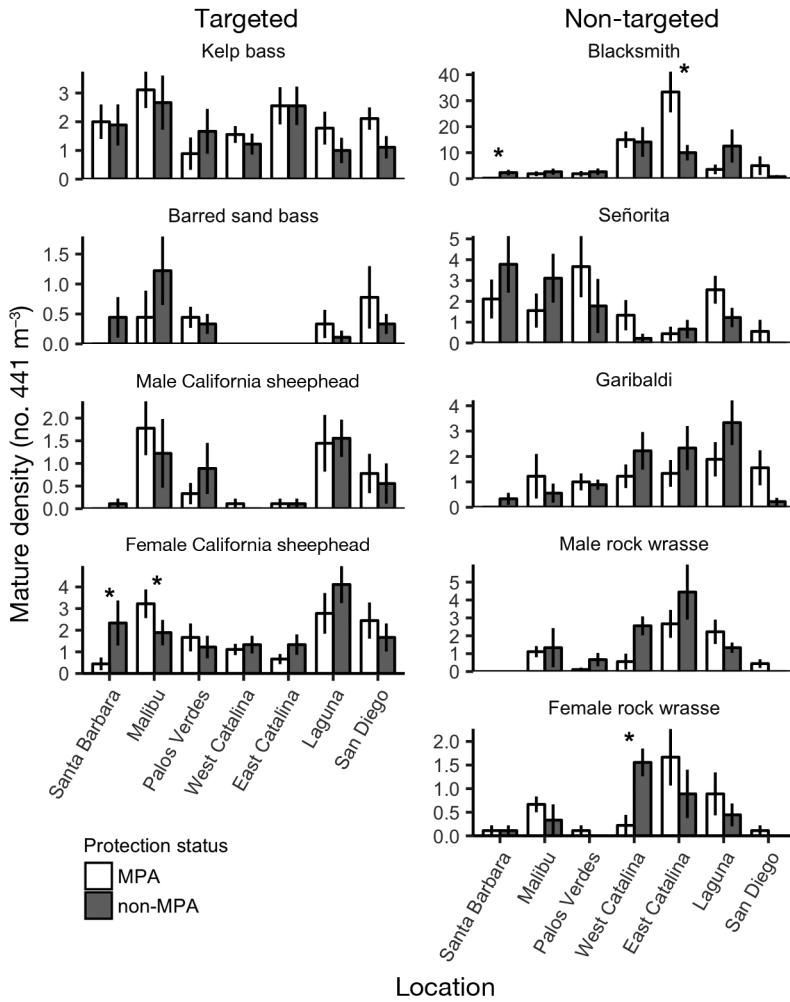
Fig. 5. Density of mature individuals in each of 7 locations inside and outside MPAs. Means ±1 SE are shown. *p < 0.05; pairwise comparison test
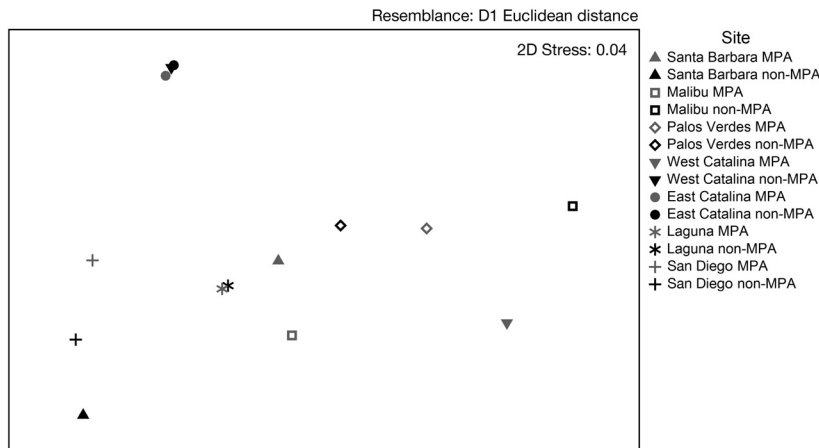

Fig. 6. nMDS plot illustrating differences in habitat characteristics averaged for all transects for each MPA and non-MPA

to mask MPA effects, particularly during the early stages of protection. Moreover, and very importantly, stereo-video should be less prone to subconscious bias of observers, who know when they are diving in an MPA.

However, while more accurate and less subconsciously biased than underwater visual census done by divers, using stereo-video introduces other complications. While the cost of stereo-video has decreased, it is nevertheless an expensive tool, which may limit who has access to it. This method also requires considerable time for processing the video. Additionally, not all fishes recorded can be measured. In total (not constrained to transect dimensions), we were only able to measure 34% of the individuals recorded, a percentage that was widely variable among species. Schooling species had lower percentages measurable (e.g. 23% of blacksmith), whereas species with larger, solitary individuals were more consistently measurable (e.g. 65% of male California sheephead).

Our study highlights the value of size-based indicators for evaluating fishing and MPA effects, a point also made by other studies (see examples in Paddack & Estes 2000, Shin et al. 2005, Kaplan et al. 2019). Because the body size of an organism is correlated with many life-history traits, such as growth rates, reproduction, and survival (Shin et al. 2005), and because body size of both predators and prey can affect trophic interactions (De-Long et al. 2015, Selden et al. 2017), this metric can be useful in assessing the state of an ecosystem. Also, our study shows that change in body sizes is a detectable and rapid response to the cessation of fishing, while changes in density or biomass are probably slower to accrue. Vallès & Oxenford (2015) investigated the influence of fishing on fish assemblages across the Caribbean and also found that density may not always be

appropriate for examining differences in fishing impacts among sites because, in their study, density was primarily explained by environmental variables. While enhancing and protecting the abundance of targeted assemblages is a primary goal for MPAs, MPA effects may be over- or underestimated when only considering this metric due to strong or weak recruitment years. Monitoring changes in size structure should also be prioritized when quantifying the efficacy of MPAs, particularly young ones, to capture effects that are not as susceptible to stochastic year-to-year variation, such as recruitment.

MPAs provide unique opportunities to study responses to changes in fishing pressure. Many studies focus on long-term effects of MPAs on targeted populations. However, the initial responses of organisms to protection may be important to understand the dynamic process of recovery of exploited fishes, and measuring changes in size-based indicators may be one of the best ways to evaluate initial responses. Ecosystem-based management using MPAs may play a vital role in the future health of marine ecosystems and it is important to understand how to best evaluate and monitor this strategy.

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Appendix 1

Table A1. Results of Principal Components Analysis of (a) Random Point Contact data and (b) Algae density

(a) Random Point Contact

Eigenvalues

PC	Eigenvalues	% Variation	Cum. % Variation
1	0.2460	41.5	41.5
2	0.0954	16.1	57.6
3	0.0555	9.3	66.9
4	0.0398	6.7	73.6
5	0.0323	5.4	79.1

Eigenvectors. (Coefficients in the linear combinations of variables making up PC's)

Variable	PC1	PC2	PC3	PC4	PC5
Substrate: Bedrock	−0.539	0.624	−0.233	0.008	−0.005
Substrate: Large Boulder	0.256	0.086	0.038	−0.141	0.223
Substrate: Small Boulder	0.275	−0.037	0.171	−0.122	0.220
Substrate: Cobble	0.097	−0.119	0.162	−0.141	−0.602
Substrate: Sand	−0.088	−0.554	−0.138	0.396	0.163
Relief: 0-10cm	−0.545	−0.399	0.120	−0.417	−0.034
Relief: 10cm-50cm	0.005	0.200	0.632	0.543	−0.137
Relief: 50cm-1m	0.299	0.026	−0.623	0.231	−0.288
Relief: 1m-2m	0.179	0.092	−0.128	−0.190	0.249
Relief: >2m	0.062	0.081	−0.001	−0.166	0.210
Bare Rock	−0.035	0.013	0.019	−0.170	−0.228
Bare sand	−0.085	−0.199	−0.135	0.141	−0.035
Shell Debris	0.004	−0.012	0.007	0.017	−0.061
Sediment/mud	−0.004	0.000	0.000	−0.005	0.004
Dead giant kelp holdfast	−0.004	−0.011	0.001	0.000	0.005
Erect red algae	−0.193	0.027	−0.029	0.304	0.363
Encrusting red algae	−0.004	0.003	0.003	−0.026	0.009
Turf	−0.001	0.001	0.039	0.044	−0.009
Crustose coralline algae	0.147	0.112	0.043	−0.102	−0.216
Articulated coralline algae	−0.032	0.021	0.006	0.029	0.019
Sargassum spp.	0.219	0.073	0.146	−0.192	0.149
Live kelp holdfast	−0.028	−0.020	0.000	0.012	−0.014
Other brown	0.086	−0.006	0.060	−0.080	0.175
Solitary tubeworm	−0.012	−0.011	−0.024	0.002	−0.012
Colonial tubeworm	−0.002	0.007	−0.006	0.025	−0.004
Cup coral	0.004	−0.001	−0.039	0.000	−0.024
Anemone	−0.003	−0.002	−0.017	−0.007	−0.010
Hydroids	0.000	−0.001	0.002	0.001	−0.002
Gorgonian	−0.001	−0.032	−0.018	0.016	0.020
Colonial tunicate	−0.003	−0.003	−0.023	0.002	−0.029
Solitary tunicate	−0.004	−0.005	−0.010	−0.008	−0.012
Embedded cucumber	−0.005	−0.001	−0.003	−0.015	−0.003
Barnacle	0.020	0.002	0.013	−0.024	0.012
Bryozoan	−0.054	0.069	−0.020	0.039	−0.114
Sponge	−0.003	−0.010	−0.015	−0.002	0.009
Green algae	−0.001	−0.003	0.002	0.000	−0.001
Surf grass	−0.002	−0.010	0.001	0.004	0.007
Vermetid Gastropod	0.000	0.003	−0.002	0.001	0.001
Clam	−0.005	−0.004	−0.001	−0.008	0.000
Mussel	0.000	−0.001	0.000	0.000	0.001

Table A1 (continued)

(b) Algae density and giant kelp canopy cover

Eigenvalues

PC	Eigenvalues	% Variation	Cum. % Variation
1	1.98	38.5	38.5
2	1.60	31.0	69.5
3	0.73	14.2	83.7

Eigenvectors. (Coefficients in the linear combinations of variables making up PC's)

Variable	PC1	PC2	PC3
Giant kelp canopy % cover	0.585	−0.253	−0.398
Canopy density (6-18 m tall)	0.533	−0.318	−0.243
Midstory density (4-6 m tall)	0.277	−0.433	0.836
High understory density (1-2 m tall)	−0.373	−0.589	−0.049
Short understory density (0.25-1m tall)	−0.396	−0.548	−0.284