Conservation benefits of marine protected areas accrue across a large ecologically connected network

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Abstract

Marine protected areas (MPAs) are widely implemented tools for long-term ocean conservation and resource management. Assessments of MPA performance are increasingly needed to inform whether conservation and management targets are achieved. In coordinated networks of MPAs, which are often designed to protect multiple ecosystems and benefit multiple stakeholder groups, single-ecosystem assessments of MPA performance risk mischaracterizing network-level effects that may span multiple ecosystems and geographic regions. Here, we evaluated the conservation performance of 59 MPAs in California’s MPA network, encompassing four primary ecosystems (surf zone, kelp forest, shallow reef, deep reef) and four bioregions, and identified MPA attributes that best explain performance. Using a meta-analytic framework, we evaluated the ability of MPAs to conserve fish biomass, richness, and diversity. Across the entire network of MPAs, biomass of species targeted by fishing was positively associated with the level of regulatory protection (no-take, partial-take, take-allowed) and was significantly greater inside no-take MPAs, while species not targeted by fishing had similar biomass in MPAs and areas open to fishing. In contrast, species richness and diversity were not as strongly enhanced by MPA protection. Conservation performance increased with MPA age, pre-implementation fisheries landings, and habitat diversity. Our results show that important drivers of single MPA effectiveness also stand at the network scale and highlight key features of conservation effectiveness.

Significance Statement

This study explored the performance of marine protected areas (MPAs) across a large scientifically designed and functionally coherent network, and found that conservation benefits accrue across multiple coastal ecosystems. Biomass of fish species targeted by fisheries was elevated in individual MPAs relative to areas that allow fishing, but the overall network-level performance was greater than its individual parts. MPA performance was best explained by MPA age, pre-implementation fisheries landings, and habitat diversity. These findings highlight opportunities for strategic planning and assessment frameworks that maximize conservation impact. With international targets aimed at protecting 30 percent of the world’s oceans by 2030, MPA design and assessment frameworks should consider conservation performance at multiple ecologically relevant scales, spanning individual MPAs to coordinated networks.

1. Introduction

Marine protected areas (MPAs) are an area-based management strategy primarily focused on long-term ocean biodiversity conservation. There is global interest in protecting 30% of the ocean by 2030 (30 x 30) (1, 2). However, only 8% of the world's oceans are presently covered by MPAs (3, 4). Although MPAs are increasingly implemented to provide climate mitigation and resilience (5, 6), and fisheries benefits (7), many were originally envisioned primarily as tools to stimulate the recovery of populations from harvesting, while protecting biodiversity and ecosystem functions (8). Whether MPAs promote climate resilience (9–11) or fisheries benefits (12, 13) is still a matter of debate (14). By contrast, the conservation performance of MPAs — their ability to maintain higher biomass of harvested species, biodiversity, and/or ecosystem functioning relative to fished locations (15) — is widely documented (16–21) and remains the central objective of most MPA management plans (22).

Globally, many MPAs are implemented as a single spatially discrete unit (23–25). However, there are increasing calls for coordinated networks of MPAs that effectively protect biodiversity within and across ecosystems at multiple geographic scales (26–30). Networks typically include multiple MPAs connected through propagule dispersal and/or adult movement, and these networks can encompass many types of ecosystems under various forms of regulatory protection (25, 31). We define 'ecosystem' as encompassing both the biotic and abiotic components of a particular portion of nearshore coastal environments (i.e., sandy surf zones, kelp forests, shallow rock reefs, deep reefs). Many existing MPA networks aim to protect multiple physical habitats (e.g., hard and soft substrata, etc.) across depth strata and ecosystems (e.g., coral reefs, rock reefs, kelp forests, seagrasses, mangroves, etc.), and expansions in global MPA coverage are envisioned to be "ecologically representative" and to "efficiently and effectively" protect diverse habitats (1).

Studies of MPA performance have largely focused on specific ecosystems individually (e.g., coral reef, mangrove, rocky reef, kelp forest, and open ocean) and have rarely evaluated performance across multiple ecosystems either within an individual MPA or across an MPA network (see Fig. 2C of Gill et al. 2017 for a rare exception, though sample size is limited). Single-ecosystem and site assessments of MPA performance risk mischaracterizing network-level effects, which may span multiple ecosystems and geographic regions. MPA performance is likely to vary among ecosystems given differences in community composition, history of fisheries and resource exploitation, vulnerability to anthropogenic stressors, level of protection and compliance, and sensitivity to environmental variation and physical disturbance. Moreover, not including multiple ecosystems in assessments impedes our understanding of their interactions and the synergistic effects of protection. As such, there is a need to holistically evaluate the performance of regional MPA networks containing diverse ecosystems within a common framework.

The design and management of MPA networks requires understanding the features (e.g., age, size, historic fishing intensity, habitat representation, etc.) that promote their efficacy, which could vary in relative importance by ecosystem. Many large-scale syntheses have revealed features associated with MPA conservation performance, but most have either focused on a single type of ecosystem (17, 32) or on pooled data across ecosystems (16, 18, 20, 21). As such, synthetic evaluations are needed to test whether features that confer conservation benefits at the individual MPA scale are also key determinants at the network level, and whether coordinated networks of MPAs result in conservation benefits that are greater than the sum of their individual parts (25).

California's large MPA network presents a unique opportunity to elucidate the impacts of MPAs across diverse fish assemblages inhabiting a variety of ecosystems across multiple habitats and coastal geographies, and to identify the MPA features that determine conservation performance. The network contains 124 MPAs that protect 16% of state waters across 17,700 km of coastline, spanning approximately 10 degrees of latitude. It was scientifically designed with size and spacing guidelines to ensure ecological connectivity (that is, the dispersal and delivery of propagules which we hereafter refer to as 'settlement magnitude') and network functionality (33). Among other goals, the network was explicitly designed to protect "representative and unique marine life habitats in California waters for their intrinsic values" (34). It encompasses hard- and soft-bottom habitats ranging from sandy beaches and the rocky intertidal to depths of 1,000 m. For most locations, coordinated long-term monitoring was initiated in 2007 (the year in which the network expansion began) for the surf zone, kelp forests, shallow rocky reefs, and deep rocky reefs on the continental shelf. This provides a long and rich time series, in some cases pre-dating MPA establishment, for evaluating the impact of different levels of regulatory protection (e.g., no-take, partial-take, or take-allowed) and MPA features on biomass and biodiversity across multiple habitats and ecosystems.

In this study, we draw on multiple years of long-term monitoring data inside and outside of MPAs distributed throughout California's large MPA network to examine the impact of regulatory protection on fish biomass, species richness, and biodiversity across surf zone, kelp forest, shallow reef, and deep reef ecosystems. Specifically, we tested the following hypotheses: (1) regulatory protection that limits or prohibits fishing confers positive conservation benefits (fish biomass, richness, and diversity) that vary by protection level (partial-take vs. no-take) across coastal ecosystems; (2) the benefits conferred by regulatory protection are strongest in MPAs that were intensively harvested prior to implementation and for species that are targeted by fisheries; (3) a network of MPAs confers conservation benefits that accrue across ecosystems; and (4) the relative outcomes of regulatory protection on conservation performance is explained by MPA features such as age, size, local pre-implementation fishing pressure, larval settlement magnitude, habitat richness, and habitat diversity. We evaluated these features as correlates of MPA conservation performance to inform regulations that could be leveraged when implementing, assessing, or adaptively managing MPA networks around the world (1, 35, 36).

2. Results

2.1. MPA network performance

Across the entire statewide network of MPAs (i.e., results pooled across ecosystems, regions, and MPAs, **Figure 1**), targeted (i.e., fished) fish biomass was positively associated with regulatory protection and was significantly greater inside no-take MPAs compared to areas that allowed take (**Figure 2A,** Effect size (E.S.) = 0.491, p-value < 0.001, SI Appendix **Table S6**). Non-targeted fish species biomass was not greater inside no-take or partial-take MPAs relative to reference sites (areas that allow fishing). For partial-take MPAs, fish biomass was not significantly different between targeted and non-targeted species; however, targeted species biomass was elevated inside MPAs compared to reference sites (**Figure 2A**). Fish species diversity and richness did not respond to any protection level in any ecosystem (*Supplementary Information*, **Figure S1**).

2.2. Regional performance

MPA-level conservation performance differed geographically by region. Three out of four regions exhibited significantly higher targeted fish biomass inside no-take MPAs when pooled across ecosystems (**Figure 2B;** SI Appendix, **Table S7**). These three regions (North Central Coast, Central Coast, South Coast) also had slightly higher non-targeted fish biomass in no-take MPAs, although this result was not significant (SI Appendix, **Table S7**). The South Coast, the region with the largest human population size and fishing pressure, showed the strongest overall positive effect of regulatory protection in no-take MPAs for targeted species (E.S. = 0.627, p-value < 0.001, SI Appendix, **Table S7**). Interestingly, the only regionally significant effect size for partial-take MPAs was for targeted species in the North Coast (E.S. = 1.901, p-value = 0.037, SI Appendix **Table S7**). The other three regions (North Central, Central, South) had similar effect sizes for targeted and non-targeted species in partial-take MPAs.

2.3. Ecosystem-specific performance

In the surf zone, MPA conservation performance was generally positive but varied by region and MPA type with no regional gradient (**Figure 2C** ‘Surf zone’, SI Appendix, **Table S9**). Across all MPAs for the surf zone ecosystem, the pooled response ratios were higher inside of both no-take and partial-take MPAs, but this result was non-significant (SI Appendix, **Table S8**). The North Coast exhibited strongly positive and significant response ratios for both targeted and non-targeted species for the single no-take MPA surveyed (E.S. = 0.613, p-value < 0.001, SI Appendix, **Table S8**). Targeted fish biomass was also significantly higher inside the no-take MPA in the North Central Coast region (E.S. = 1.053, p-value = 0.02), while non-targeted species biomass was higher outside (E.S. = -0.525, p-value = 0.015). Both targeted and non-targeted fish biomass for the Central Coast showed slightly negative, though non-significant, effects of no-take MPAs. For South Coast no-take MPAs, response ratios were higher inside MPAs but this result was not significant.

The kelp forest ecosystem exhibited significantly higher fish biomass inside no-take MPAs for targeted species when pooled across all regions (**Figure 2C** ‘Kelp forest’; E.S. = 0.461, p-value= 0.005, SI Appendix, **Table S8**). A strong regional gradient in MPA performance was also apparent for kelp forest fishes, with the South Coast and Central Coast regions showing strong and significant positive effects inside no-take MPAs, the North Central Coast exhibiting a positive but non-significant effect, and the North Coast exhibiting a negative, though non-significant, effect (**Figure 2C** ‘Kelp forest’). In partial-take MPAs, targeted fish biomass was significantly higher in the North Coast (E.S. = 1.199, p-value < 0.001, SI Appendix, **Table S9**), but non-significant for all other regions and overall.

Among the four ecosystems included in our analyses, positive biomass response ratios were most pronounced in the shallow reef ecosystem (**Figure 2C** ‘Shallow reef’, SI Appendix, **Table S8**). Targeted fish biomass was significantly higher in no-take MPAs in all four regions (SI Appendix, **Table S9**), and when pooled across regions (E.S. = 0.853, p-value < 0.001, SI Appendix, **Table S8**). Because of the gear type (hook-and-line) used to sample shallow reef fishes, non-targeted species were rarely caught and thus not included. The shallow reef ecosystem also selectively sampled only no-take MPAs, and therefore partial-take MPAs were not included in the analysis.

Finally, in the deep reef ecosystem, the overall effect size was significantly positive for non-targeted fish biomass in no-take MPAs when pooled across regions (**Figure 2C**, E.S. = 0.284, p-value = 0.019, SI Appendix, **Table S8**). However, this result is likely influenced by the South Coast region, which showed a very positive and strong effect size for non-targeted fish biomass in no-take MPAs (E.S. = 0.506, p-value = 0.005, SI Appendix, **Table S9**). Among the four ecosystems, the deep reef had the strongest positive effect size in partial-take MPAs for both targeted and non-targeted species (SI Appendix, **Table S9**).

2.4. MPA-level performance

Across the network of 59 sampled MPAs, the effect of regulatory protection was positive for the majority of MPAs when pooled across ecosystems (**Figure 3**). Targeted fish species biomass was significantly higher in 21 out of 59 MPAs (36% of MPAs), although 45 (76% of MPAs) showed positive effect sizes for targeted fish biomass. Non-targeted fish species biomass was also elevated inside MPAs (**Figure 3;** SI Appendix, **Table S10**). 21 out of 56 MPAs (37%) had significantly higher biomass in the MPAs, and 32 had elevated (57%, though non-significant) biomass. However, there were proportional differences between targeted and non-targeted species within individual regions. In the North Coast, 6 out of 8 (75%) MPAs had higher biomass for targeted species, whereas non-targeted species had greater biomass in only 3 out of 7 MPAs (42%) with higher biomass. In the North Central region, 9 out of 10 MPAs had higher targeted biomass (90%) and 6 out of 8 (75%) MPAs had higher non-targeted biomass. In the Central Coast region, 11 of 15 MPAs (73%) had higher targeted species biomass, whereas 10 out of 15 (66%) had higher non-targeted biomass. Finally, in the South Coast region 19 out of 26 MPAs (73%) had higher targeted biomass, whereas the number of MPAs with higher or lower non-targeted biomass was equally distributed (13 out of 26, 50%).

2.5. Network-level predictors of conservation performance

The meta-generalized additive model captured a moderate amount of variation in the data (GCV: 0.0739, n = 292, adjusted-r^2= 0.157, $p < 0.001$) and revealed highly influential MPA features that explained performance (response ratio effect size) across ecosystems (**Figure 4**). Results of the model indicated that MPA age ($p = 0.001$, EDF: 1.85), local pre-implementation landings ($p < 0.001$, EDF: 1.57), and habitat diversity ($p < 0.001$, EDF: 1) were the strongest significant correlates of conservation performance (SI Appendix, **Table S11**). Conservation performance (i.e., the difference in fish biomass between MPA and reference sites) significantly increased with increasing MPA age and habitat diversity. However, pre-implementation fisheries landings were slightly inversely related to performance ($p < 0.001$, EDF: 1.57). The impacts of proportion rock and MPA size, while statistically significant, were highly non-linear, but larger MPAs and those with greater proportion of rock generally had stronger positive responses, especially at the upper value range.

3. Discussion

This study explored the performance of marine protected areas across a scientifically designed and functionally coherent network and found that conservation benefits accrue across multiple coastal ecosystems. While many studies have evaluated MPA performance within individual protected areas or across single ecosystems, few have explored the conservation outcomes of entire networks of MPAs across multiple biological ecosystems (but see (37)). Our findings highlight opportunities for strategic planning and assessment frameworks that maximize conservation impact.

Our analyses indicated that among all MPA features, MPA age and habitat diversity were the strongest overall predictors of performance, where older MPAs with more representative habitats tended to hold relatively more fish biomass than their associated reference sites. The California network was designed with specific attention to ensuring habitat representation and replication within MPAs and in each region (31), using increasingly sophisticated spatial mapping tools throughout the design process. Incorporating a diversity of habitats within MPAs and networks not only serves to increase the magnitude of biodiversity protection, but can provide resilience to disturbances including future climate impacts (38). However, despite widespread discussion and theoretical treatment of this MPA trait, to our knowledge, this is the first quantitative test of the importance of habitat diversity to MPA performance.

Another critical and widely discussed design principle for MPA networks is connectivity (29, 37). In an effective network, organisms must be able to travel or disperse through larval connectivity among protected areas. Indeed, the California network design phase incorporated perhaps one of the most detailed sets of MPA size and spacing guidelines to date, taking into account generalized larval dispersal distances and patterns of ocean circulation (31). By using different size and spacing of protected areas, a network can protect species with different life histories and behavioral characteristics and may offer better conservation performance than single large protected areas (39, 40). Yet, here, using realistic, estimated settlement magnitude from larval dispersal modeling, we did not find a significant effect of connectivity on MPA performance for fishes when synthesized across ecosystems. However, estimated settlement magnitude was important on an individual-ecosystem level. These two contrasting results likely reflect that organismal-level estimates of larval durations are needed to accurately assess the relative importance of connectivity for individual ecosystems to entire MPAs.

Our finding of higher fish species biomass inside of no-take MPAs is likely the result of regulatory protection (i.e., an emergent effect) and not a placement effect. Emergent effects are expected to increase in magnitude inside of the MPA relative to the outside location over time as a result of regulatory protection (i.e., continued fishing outside the MPA restricts increases in biomass), until spillover replenishes neighboring unprotected areas (41–43). However, placement effects occur when an MPA is implemented in an area with higher pre-existing biomass (or more suitable habitat) than the reference area (7, 44, 45). Our analyses suggest that higher targeted species biomass observed in MPAs is the result of an emergent effect of regulatory protection because MPA age was the strongest determinant of biomass response ratios in the majority of ecosystems studied. If this was the result of a placement effect, MPA age would not be a strong determinant of performance, as high pre-existing biomass would remain stable through time. It is important to note, however, that placement effects may provide other positive enabling conditions (such as more suitable habitat) that may be important in the design phase of networks. Furthermore, our finding of a positive, but non-significant, increase in the biomass of non-targeted fish species supports an ‘MPA effect,’ since non-targeted species should not have a direct response to protection and therefore serve as a type of control measure (12, 46, 47).

Regional differences in MPA performance may be the result of a combination of sampling limitations, variation in species life history traits, or environmental perturbations (32). Disentangling these effects becomes even more challenging when evaluating large MPA networks that span biogeographic regions. For example, ecosystems in the North Coast region were comparatively less sampled than the South Coast, potentially limiting the power to detect an MPA effect. MPAs along the North Coast are also the youngest in the network, further limiting the effect size for these MPAs given our finding that effect sizes increase with age. However, the North Coast is also characteristically dominated by species that are long-lived, late to mature, and have more episodic year-class recruitment success (48), which could contribute to a slower response in this region. Additionally, during the study period, a marine heatwave spanning the years 2014-2016 occurred only two years after full implementation of the MPA network (11). Environmental perturbations, such as marine heatwaves, can reduce the ability to detect MPA effects (49), especially in locations where MPAs were not originally designed to provide climate resilience (11, 50). In our study system, the impacts of the marine heatwave event on fish biomass remain unclear, but trends in biomass and biodiversity over time inside and outside of MPAs were likely impacted by this environmental perturbation (9, 51, 52).

Across the four ecosystems included in our analyses, we hypothesized that MPA responses would be strongest in MPAs where pre-implementation fishing was greatest. While historic fishing intensity explained a moderate amount of variation in biomass across the MPA network, observed differences in performance between ecosystems could be the result of sampling gear types or other regulatory protection measures. For example, our analyses showed that conservation performance was strongest for shallow reef fishes. The shallow reef monitoring group used hook and line sampling, which disproportionately selects older, larger individuals and may reflect higher sampling of size ranges that are typically targeted by fisheries. Conversely, visual sampling conducted by the kelp forest and deep reef ecosystems as well as surf zone seine sampling is non-selective and results in high proportions of smaller individuals, which do not receive the same fishing pressure as larger individuals of the same species. Interestingly, the deep reef ecosystem showed comparatively lower responses in targeted fish biomass relative to the other ecosystems. Many of the locations sampled in the deep reef ecosystem were within a Rockfish Conservation Areas (RCAs), which restricted fishing since 2002 across large swaths of the West Coast of the U.S. to depths less than 36-

100m to reduce the incidental catch of overfished species (53). These depth closures likely created additional protection for fishes outside of the state's network of MPAs (54), which could explain the less pronounced difference in the effect size for the deep reef ecosystem.

Our finding of no differences in taxonomic diversity and richness inside and outside MPAs is consistent with other studies that explored these metrics of MPA performance (55, 56). The primary regulation associated with the California MPA network, and many global MPAs, involves a restriction or reduction of fishing activities, which generally affects fish assemblages through the total number of individuals, size structure, and their relative abundance (proportional representation of each species). Therefore, the fishes most impacted by fishing pre-implementation are likely to see the greatest biomass response (46, 47). However, since diversity considers the number of species and their evenness, the taxonomic diversity of fishes may not change as a result of regulatory implementation, or there may be more nuanced increases in evenness without changes in the absolute number (richness) of species. Other taxonomic diversity indices such as functional or trait-based evaluations could provide additional pathways to evaluate MPA performance (52, 57, 58). This effect should be considered when proposing new MPAs or networks with goals of increasing biodiversity, especially in locations with other ecosystem management tools in place (e.g., water quality, traditional fisheries management, tribal or indigenous management).

Ultimately, our findings suggest that an ecologically connected network of MPAs can have positive conservation benefits that accrue across multiple ecosystems. We found that MPA features such as age, habitat diversity, and local pre-implementation landings are highly influential on conservation performance. Although the conservation performance of MPAs can vary across individual MPAs, coastal geographies, and ecosystems, a scientifically designed and functionally coherent network can provide net positive benefits that are greater than its individual components. With international targets aimed at protecting 30 percent of the world's oceans by 2030 (1, 2), MPA design and assessment frameworks should consider performance at multiple ecologically relevant scales, spanning individual MPAs to multiple ecosystems and coordinated networks.

4. Materials and methods

4.1. Study area and long-term monitoring

Several ecosystem-specific research groups conduct annual monitoring within California's MPA network. We focused our analyses on four ecosystems that have extensive spatial and temporal monitoring coverage of fishes across the MPA network: surf zone, kelp forest (depths less than 20 m), shallow reef (depths less than 40 m, but outside of kelp), and deep reef (depths 30-100 m, **Figure 1A**). Each monitoring program uses a paired sampling design where surveys are conducted inside a given MPA and at a neighboring reference area where fishing is allowed. The ecosystem-specific sampling methods are described in *SI Appendix, Methods*.

California's MPA network consists of 124 MPAs that vary in protection level, including 49 no-take State Marine Reserves (SMR), 10 no-take State Marine Conservation Areas (SMCA), 60 SMCAs that allow limited-take of specific organisms (with different regulations for each SMCA), and five State Marine Recreational Management Areas that allow the take of waterfowl (31). All protection levels are hereafter referred to as 'MPAs.' MPAs were implemented across four regions (North, North Central, Central, and South) at different times between 2007-2012, although the network contains some older pre-existing MPAs (**Figure 1B;** (59)). For our analyses, we consider two types of regulatory protection: no-take MPAs and partial-take MPAs. An MPA was designated as a *de facto* no-take MPA for a particular ecosystem if any allowed partial-take was unlikely to directly or indirectly affect the species that reside in that particular ecosystem (e.g., take of salmon in an MPA is unlikely to affect any of our four focal ecosystems; see *SI Appendix* **Table S4** and Smith et al. 2023).

4.2. Conservation performance across the MPA network

We evaluated the conservation performance of the MPA network in terms of targeted and non-targeted fish species biomass, richness, and diversity across four ecosystems and two levels of protection (no-take vs. partial-take). Biomass was estimated for the surf zone, kelp forest, shallow reef, and deep reef ecosystems using habitat-specific estimates of fish abundance and body size. Fish length was converted to weight using a standardized biomass parameter table for each species following an extensive literature search. We identified the parameters for other missing species by taking the median conversion parameters for that species reported in FishBase (60). We then calculated biomass across all targeted and non-targeted fish species at the smallest replicable unit (e.g., seine, transect, or fishing cell inside or outside an MPA; *SI Appendix, Methods*).

We assessed the conservation performance of the MPA network by evaluating the relative distribution and predictors of fish species biomass, richness (number of species), and diversity (Shannon index) inside and outside MPAs distributed throughout the network. Among the 124 MPAs in the network, 59 were sampled by at least one ecosystem monitoring group over the study period. These MPAs each had a single paired reference area where fishing was allowed. We used a log-response ratio approach to quantify the relative strength of MPA effects between each pair of protected and fished sites (Hamilton et al., 2010; Ziegler et al., 2022). This yielded a unitless scaled metric of MPA performance that permitted us to compare responses of fish assemblages across multiple monitoring groups in different ecosystems, all sampled using different methods and metrics. The log response ratio for MPA *j* in year *i* ($Y_{j,i}$) was calculated as:

$$Y_{j,i} = log \frac{\bar{X}_{Inside_{j,i}}}{\bar{X}_{Outside_{j,i}}} \qquad \text{Eq. 1}$$

where $\bar{X}_{Inside_{j,i}}$ and $\bar{X}_{Outside_{j,i}}$ represent the mean performance metric (biomass, diversity, or richness) across replicate units inside or outside an MPA *j*, respectively, in a given year *i*. Taking the log of the response ratio reduces the variance and scales the response around zero, such that a value above zero indicates a positive effect of the MPA on a given conservation performance metric, while a negative value indicates lower MPA performance (i.e., fish biomass, diversity, or richness was greater outside the MPA). To account for sites where zeros occasionally occurred outside the MPA (precluding inclusion of those MPAs due to an undefined log response ratio), we added a small constant calculated as 10% of the mean of all values for a given ecosystem, year, MPA type (no-take or partial-take), and site type (inside or outside an MPA). We calculated a fractional constant to account for interannual variability, and because adding a random constant (e.g., 0.01) could inadvertently skew the response distribution in favor of either the inside or outside locations.

4.3. Synthesis and inference framework

We used two statistical approaches to assess three metrics (biomass, richness, and diversity) of MPA conservation performance. First, for biomass, we compared the log response ratio of total biomass for targeted and non-targeted fish species using a meta-analytic framework. We classified the target status for each species *a priori* to our analyses using a combination of fisheries data from California and expert opinion for each ecosystem (*Supplementary Information* **Table S1**); we did not use body size to inform this classification since size selectivity varies by gear type. The null assumption is that non-targeted fish species should not respond (either positively or negatively) to MPA implementation as a direct result of fishing activities; instead, they act as a type of 'control' for variation in environmental conditions that may affect all species similarly. We infer that a stronger positive response of targeted species relative to non-targeted species signifies the predicted effects of MPA protection. Second, for species richness and diversity, we compared the distribution of the log response ratios for each ecosystem and evaluated significance using a two-tailed t-test on the log response ratio. This was the most appropriate form of analysis since richness and diversity were each calculated across replicates within an MPA, since sampling was often depth-stratified and many species are associated with particular depths; therefore, it would be inappropriate to calculate these two performance metrics at a smaller scale (e.g., seine, transect, or fishing cell).

We used a meta-analytic framework to evaluate the effect of regulatory protection on fish biomass across the evaluated MPAs and ecosystems. This analysis used biomass as the focal performance metric because it contained both an effect size and associated unit variance for each ecosystem and MPA. However, the shallow reef ecosystem used hook-and-line sampling, the same gear used to target nearshore recreational fish species, meaning that non-targeted fish species were not sufficiently sampled for inclusion in the meta-analysis. The biomass effect size for each ecosystem at a given MPA was modeled as the log-ratio described in section 4.2 (Eq. 1). When data were collected within an individual MPA over time, we retained only the most recent results to reflect the longest duration of protection for a given ecosystem (21). The within-study variance of each unique ecosystem-MPA combination was calculated as:

$$v_{E_j} = \frac{\sigma^2_{Inside_{E_j}}}{n_{Inside_{E_j}} * \bar{X}_{Inside_{E,i}}} + \frac{\sigma^2_{Outside_{E_j}}}{n_{Outside_{E_j}} * \bar{X}_{Outside_{E,i}}} \quad \text{Eq. 2}$$

where $\bar{X}_{Inside_{E,i}}$ and $\bar{X}_{Outside_{E,i}}$ are the mean biomass estimates (targeted or non-targeted, separately) for a given ecosystem E (surf zone, kelp forest, shallow reef, deep reef) inside and outside of MPA j in the most recent year; σ is the standard deviation associated with each mean at E_j; and n is the number of replicates (seines, transects, or fishing cells) used to estimate the mean for E_j.

The conservation performance of an individual MPA (*n* = 59), region (*n* = 4), or ecosystem (*n* = 4) (**Figure 1B**) was calculated as a weighted average of the effect size as a function of target status (targeted or non-targeted) as:

$$\bar{R} = \frac{\sum_{i=1}^{n_i}(w_i Y_j)}{\sum_{i=1}^{n_i} w_i Y_j} \quad \text{Eq. 3}$$

where Y_j is defined above (Eq. 1), and w_i is the inverse of the within $v_{E,i}$ and between $\hat{\tau}^2$ study variance defined as:

$$w_i = \frac{1}{v_{E_j} + \hat{\tau}^2} \quad \text{Eq. 4}$$

and

$$\hat{\tau}^2 = \frac{Q-(k-1)}{c} \quad \text{Eq. 5}$$

k is the number of ecosystems, *c* is a constant equal to $k-1$, and Q is the overall heterogeneity given by:

$$Q = \sum_{i=1}^{n_i} w_i (Y_j - \bar{R})^2 \quad \text{Eq. 6}$$

4.4. MPA features and conservation performance

To evaluate the network-level predictors of MPA conservation performance across all ecosystems and sampled MPAs, we constructed a meta-generalized additive model (meta-GAM) using the *mgcv* package in R (61). We evaluated the impact of eight MPA features on conservation performance (log ratio effect size): MPA age (year), MPA size (km^2), habitat diversity (number of habitats and their relative area), habitat richness (number of distinct habitats), proportion of MPA with rocky bottom, local pre-MPA fisheries landings, ecosystem-specific estimated larval settlement, and total estimated larval settlement to an MPA; the last two estimated from ROMS (Regional Ocean Modeling System) larval dispersal and models. We restricted the analysis to no-take MPAs and targeted fish species to parse the overall relationship between performance and each predictor variable while holding the most restricted level of protection (no-take) constant. To further explore the ecosystem-level predictors of conservation performance, we used a series of random forest models on individual ecosystems. See the *SI Appendix Methods* and *Results* for details on the random forest models, and **Tables S2 and S3** for details on how each MPA feature was defined and derived.

To construct the meta-GAM, MPA features were added as smoothing terms and year was included as a cyclic cubic regression spline to account for periodic trends over time in the data. The model included all sampled no-take MPAs and ecosystems weighted using w_i (Eq. 4). We used a Gaussian link function and cubic spline to determine the optimal level of smoothing for each predictor. Model selection was conducted using generalized cross-validation (GCV) with a forward selection procedure (62).

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Data accessibility

The data that support the findings of this study are openly available in DataONE from the following resources: surf zone (63), kelp forest (64), shallow reef (65), deep reef (66). Additional metadata are provided in SI Appendix **Table S2**. All source code is available in GitHub at https://github.com/NCEAS/ca-mpa

Conflicts of interest

The authors declare no conflicts of interest.

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702 **Figures**

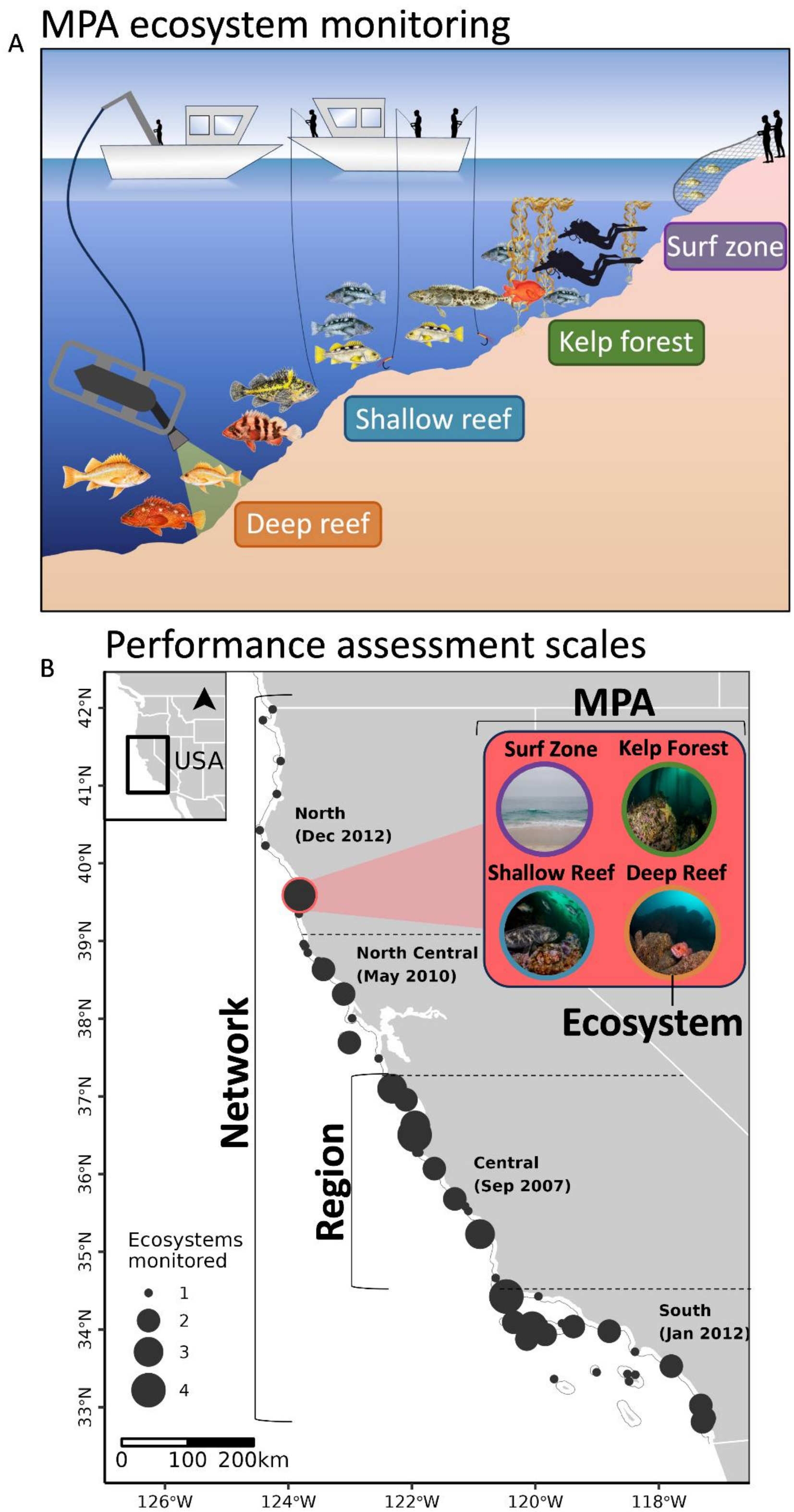

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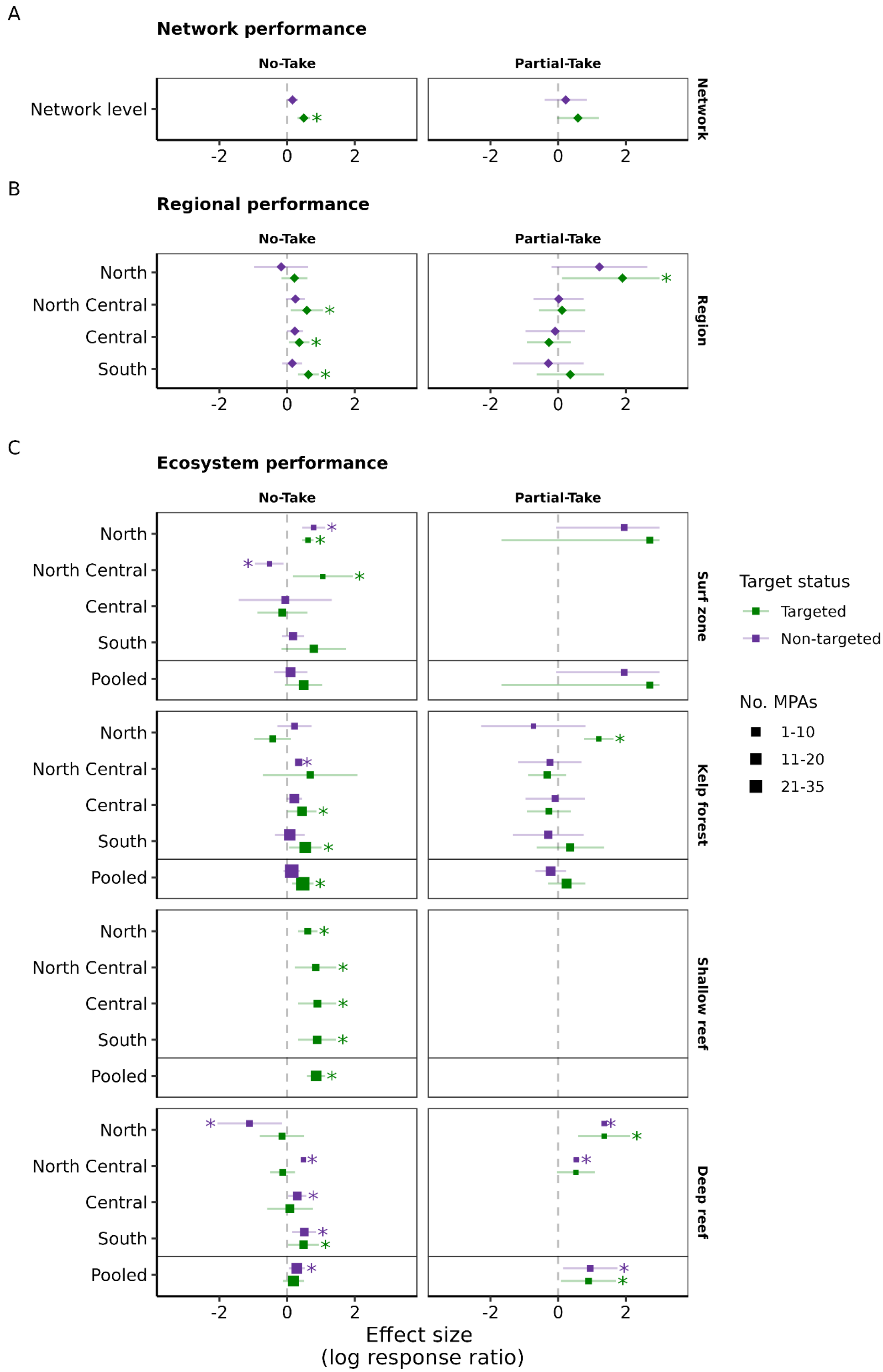
Figure 1. Ecosystem sampling methods and monitoring sites in California's network of marine protected areas (MPAs). In **(A)**, the general sampling methods are shown for the surf zone (seine; purple), kelp forest (scuba surveys; green), shallow reef (hook-and-line; blue), and deep reef (remotely operated vehicle; orange) ecosystems. In **(B)**, MPAs sampled (*n* = 59) by any ecosystem are shown as black circles, and the circle size corresponds to the number of ecosystems that sampled a given MPA. Four scales of assessing MPA performance are conceptually depicted: network (across all ecosystems and MPAs for the network), regional (across MPAs and ecosystems within a region, implemented in a given month and year), ecosystem (analysis for a single ecosystem across sampled MPAs), and MPA (performance assessment within individual MPAs across ecosystems).


A
Network performance
No-Take
Partial-Take
Network level
Network
B
Regional performance
North
North Central
Central
South
Region
C
Ecosystem performance
Pooled
Surf zone
Kelp forest
Shallow reef
Deep reef
Target status
Targeted
Non-targeted
No. MPAs
1-10
11-20
21-35
-2
0
2
Effect size
(log response ratio)

714

Figure 2. Biomass log response ratios for targeted (green) and non-targeted (purple) fish species by protection level (no-take vs. partial-take), across **(A)** the entire network and by **(B)** region and **(C)** ecosystem. Each square represents the mean effect size across MPAs for a given region with 95% confidence intervals (upper bounds greater than 3 were truncated to ease visualization), and asterisks denote significance ($p < 0.05$). Square size represents the relative number of MPAs included in the effect size. The vertical dotted line at 0 represents the line of no effect. Positive values indicate higher biomass in MPAs, and negative values indicate higher biomass outside of MPAs. The pooled statistic represents the meta-analytic effect size across all regions for a given ecosystem. Finally, data gaps indicate that MPAs or species assemblages were not sampled within a region for a given ecosystem (e.g., non-target species in the shallow reef due to hook and line sampling).

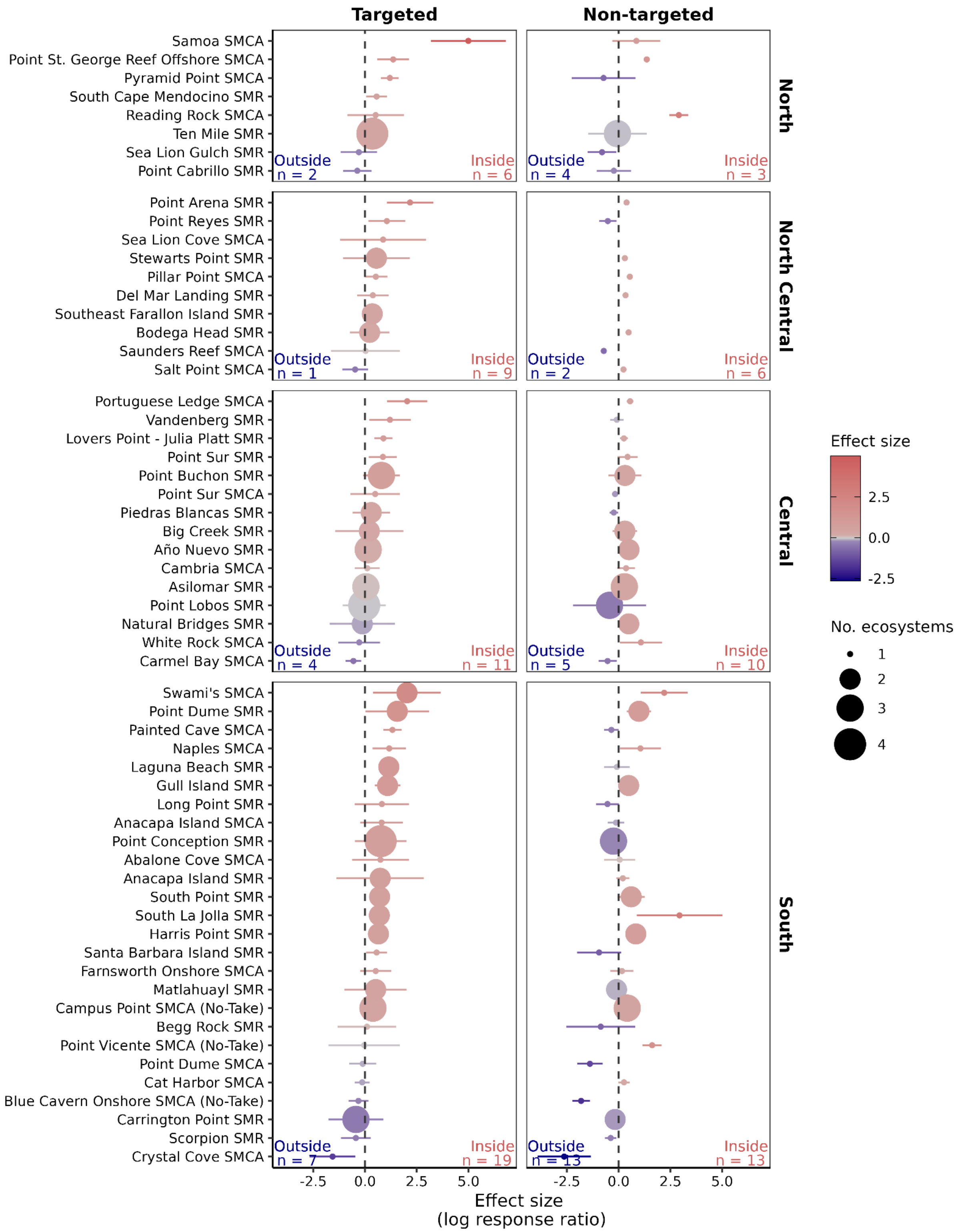


Figure 3. Biomass log response ratios for targeted (left) and non-targeted (right) fish species for 59 MPAs by region. Each point represents the weighted mean effect size (log response ratio)

for a given MPA across all ecosystems (weighted by the inverse of the variance), and point size depicts the number of ecosystems included in the effect size. Each effect size was calculated for the most recent year of data to reflect the longest duration of protection for a given ecosystem. Error bars depict 95% confidence intervals. The vertical dashed line at 0 represents the null assumption of comparable biomass estimates inside (red) and outside (blue) of MPAs. Therefore, positive values (red) indicate greater biomass inside the MPAs, and negative values (blue) indicate greater biomass outside of MPAs. MPA sample sizes (n) are indicated in the lower corners of each panel.

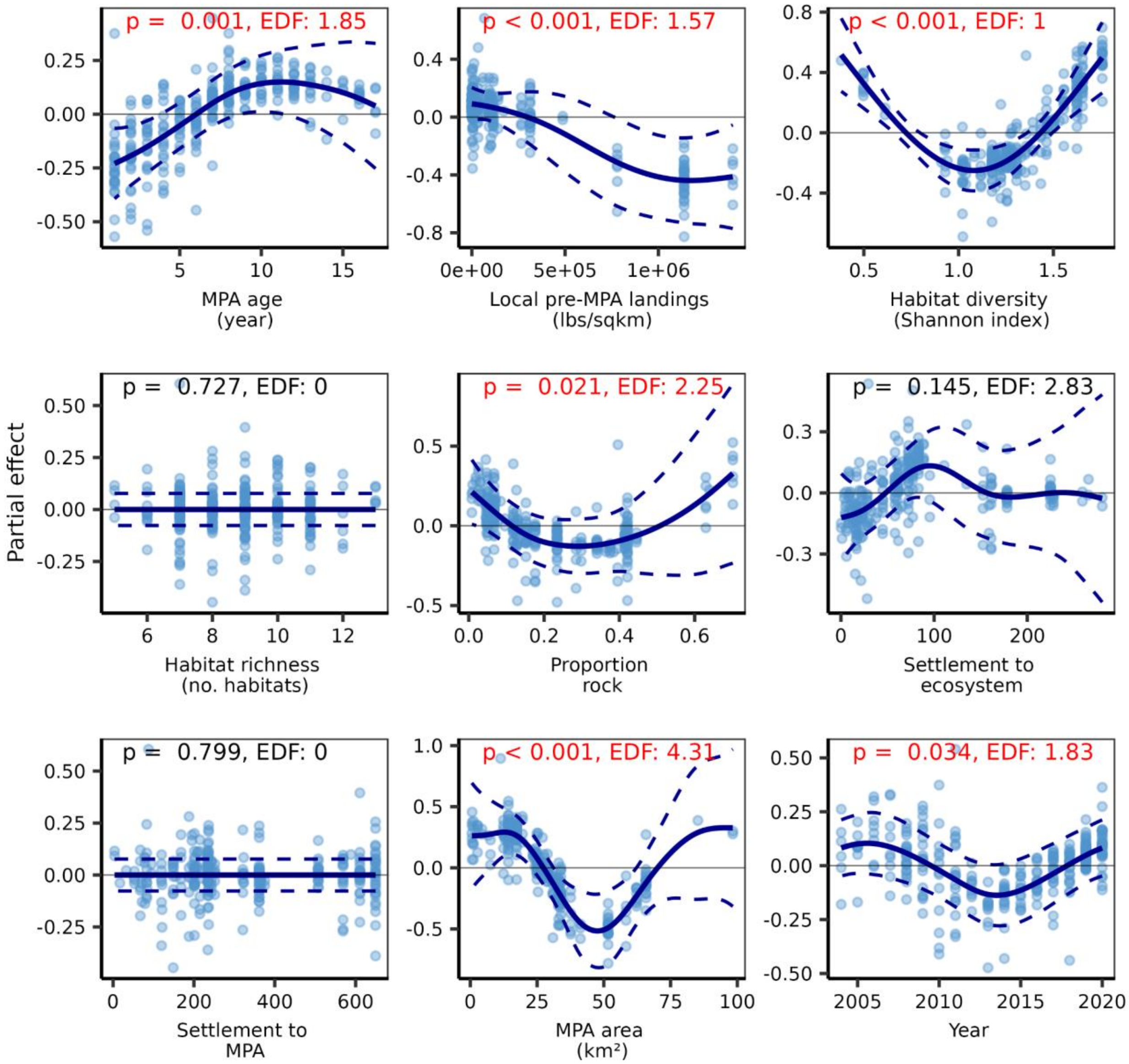


Figure 4. Partial effects of MPA features on performance from a meta-generalized additive model (meta-GAM). Partial effects represent the smoothing term while holding all other variables constant. Solid blue lines depict the shape of the relationship between each MPA feature and performance (response ratio effect size), and dashed lines represent 95% confidence intervals. Residuals are shown as blue points. The p-values (p) for each relationship and the effective degrees of freedom (EDF), a measure of flexibility, are shown at the top of each plot; red text indicates statistically significant relationships. See Supplementary Methods Tables S2 and S3 for details on how each feature was defined and derived.

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Supplementary Information Appendix

“Conservation benefits of marine protected areas accrue across a large ecologically connected network”

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Supplementary Methods

Monitoring sampling design

Surf zone: Surveys of surf zone fish at each MPA and reference site were conducted three times a year (June - November) during standardized tide windows (less than equal to 1 m) and safe ocean conditions. On each survey date, six beach seine hauls (net dimensions: 15.25 m long x 1.8 m high, 1 cm mesh with two poles attached on each end and central a 1.8 m x 1.8 m x 1.8 m bag) were conducted in the shallow surf zone (<1.5 m). Fish from each haul were identified, counted, and measured (standard and/or total length for the first 30 individuals of each species per haul) before being released at the capture site. For biomass estimates, we resampled from the size-frequency distribution of the 30 subsampled individuals to estimate the total length-frequency distribution of all individuals for a given haul.

Kelp forest: Replicate sampling sites are distributed within each MPA and at nearby “reference” sites of comparable habitat characteristics to those inside the MPA. Each survey site typically consists of a rectangular area, extending 150 m parallel with the shore. The onshore-offshore dimension varies depending on the width of the reef and the offshore distance of the 20 m isobath (depth). Typically, two to four sites inside and two to four sites outside each MPA were surveyed with the number and shape of sites varying depending on habitat (e.g., onshore-offshore steepness of the reef) and longshore width of the MPA. To characterize the ecological community throughout each sampling site, belt transects (30 m x 2 m) were distributed across a depth gradient from the 5 m to the 20 m isobath at each site. Surveys were generally conducted in 1-2 visits to a site per year from June/July through October/November each year. Diver surveys were conducted to estimate the density and size distribution of all conspicuous fishes along replicate transects at three levels (bottom, midwater, canopy) in the water column. More details for each of the methods are described in (46, 67, 68). For our analyses, we excluded canopy surveys because of temporal inconsistencies and combined the midwater and benthic surveys to estimate total fish density along replicate transects inside and outside of MPAs.

Shallow reef: Within the boundaries of each sampled MPA and reference area, 500 m by 500 m fixed grid cells were delineated in rocky habitats shallower than 40 m depth (to limit fishing mortality associated with barotrauma). Surveys were conducted annually along the Central Coast from 2007–2020 and expanded to the North and South Coasts in 2017. Volunteer anglers were recruited from various fishing clubs, online fishing websites, and from previous collaborative studies. Before each day of fishing, four grid cells in a given MPA or reference site were randomly chosen for sampling. Captains were instructed to locate three suitable fishing locations within each grid cell to complete fishing drifts with a goal of 15 minutes each. For each drift, information on the number of anglers, time spent fishing (minutes), location (GPS coordinates), depth (ft), habitat relief, and other environmental variables were recorded. Anglers used a standardized set of fishing gear across the entire state (shrimp flies with squid bait) and within regions to capture a variety of species and cover the spectrum of typical hook-and-line fishing gear used by anglers (69–71). Captured fishes were identified to species, measured to the nearest cm, and released. Lengths reported are total length, defined as the distance from the tip of the snout to the most posterior part of the caudal fin without compressing the tail.

Deep reef: Remotely Operated Vehicle (ROV) survey sites were initially identified using bathymetric bottom maps and then confirmed during exploratory ROV surveys. Sampling blocks that were 500 m wide and up to 3 km long were then created using GIS maps. Reference sites were selected based on map-based estimations of similarity in the types and amounts of rocky substrate present, proximity to one another, and depth. A stratified-random design of transects was used and the ROV recorded video while moving along a fixed transect path along the seafloor. Thus, videos collected from 500 m long transect lines were used as sampling units. Video imagery collected was analyzed to characterize substrate types present and to identify and count all demersal and epibenthic finfish and macro-invertebrates. Using a series of non-overlapping video quadrats, the distribution, relative abundance, and density of species were estimated along each transect, as described in (72) and (73). All organisms were identified, enumerated, and recorded with UTC timecode and linked to ROV position and sensor files. Forward digital still photographs were used to verify species identifications where high resolution of species characteristics was required. Estimates of fish lengths were made using paired lasers mounted on the ROV.

Estimated larval settlement magnitude

We estimated larval settlement magnitude across the MPA network as the total summed settlement of propagules (spores, eggs, larvae) entering each MPA. We used a Regional Ocean Model System (ROMS) particle tracking which simulates dispersal in three spatial dimensions (through the movement of X, Y, Z vectors) and one temporal dimension. This simulated dispersal is based on an average solution across 15 years (1999-2013) and the range spans from 100km south of CA into Baja California, Mexico, and north up through Oregon, although for this project we focused on only California's range. Approximately 88000 "propagule" particles are released across 557 ROMS cells (365 cells in California). Larvae move hourly, but with daily averaged currents (i.e., every hour we interpolate the daily average currents from the ROMS model in space and time to find the current at each particle location, and then we move each particle with its appropriate current velocity). Landward of the 500 m depth isobath, larvae are also given a random pulse simulating tidal currents of 5 cm/s. This pulse is also given every hour in addition to the daily-averaged motion. Settlement only occurs within 10% of PLD (e.g., for PLD of 30 days: 27-33 days).

ROMS solutions were run at three "lengths of time" to simulate differing PLDs of common species' life history: 30, 60, and 90 days. We then took an elemental average of the corresponding three PLD matrices to represent an average dispersal across common species inhabiting Rocky intertidal, Shallow Rocky Reef, 30-100m Rock, and 100-200m Rock habitats. The ROMS output can be considered a measure of connectivity among cells (locations) but should not be considered – on its own – an estimate of one cell's contribution of propagules to other cells. This is because cells in ROMS grids are only characterized by oceanographic forcing and spatial dimensions (and vertical layers), and we simulated the release of the same number of particles from each cell. To estimate the actual settlement of a species, propagule production for donor cells and the amount of suitable habitat for receiving cells was incorporated based on the idea that propagules will scale with the amount of available habitat a species occupies in both donor and settlement locations. Specifically, across each habitat type we took the product of the donor-to-recipient cell propagule connectivity with the area of habitat in the donor cell and the area of habitat in the recipient cell. We then summed all propagule contributions coming from every donor cell (both MPAs and areas of fishing) into a recipient cell (MPAs only) to quantify the total summed settlement across all MPAs within the network.

Habitat estimates

We examined the habitat richness, habitat diversity, and total proportion of rock within MPAs using estimates of the area extent of major habitats present within the boundaries of each MPA (**Table S3**). Major habitats include both nearshore/offshore (0-3000 m depth) and onshore (shoreline) characteristics identified as important during the MLPA planning process. Habitat richness was calculated as the number of unique habitat types within each MPA. Habitat diversity was calculated as Shannon diversity using the area of each habitat type within the MPA. Proportion rock was calculated as the total area of hard substrate (across all depths) divided by the total size of the MPA.

Evaluating ecosystem-level performance drivers using random forests

We used the *randomForest* package in R (74) to fit and evaluate ecosystem-specific random forest models that predict conservation performance based on the eight evaluated MPA features. We evaluated feature importance as the mean decrease in node impurity resulting from splitting the tree on each feature and we evaluated the marginal effects of each feature on conservation performance by measuring its impact when holding the other features at their ecosystem-specific averages. Importantly, the random forest models used the most recent year of sampling for each MPA to reflect the longest duration of protection. The model was constructed using 500 trees with one third of the variables sampled at each split.

Supplementary Results

Ecosystem-level predictors of conservation performance

The ecosystem-specific random forest models explained a large proportion of the variation in conservation performance (log ratio effect size) across MPAs (r^2=0.65-0.77; *SI* **Figure S2**). However, the importance of each MPA feature varied by ecosystem. MPA age and size (area) were generally strong predictors of ecosystem-specific performance, which the surf zone and deep reef ecosystems responding particularly positively to MPA size. Local pre-implementation fisheries landings were positively correlated with conservation performance in the deep reef ecosystem, such that fish biomass responded more strongly and positively to regulatory protection. Habitat diversity and richness were also generally positively correlated with conservation performance. Interestingly, estimated settlement magnitude was important on an individual-ecosystem level, especially for the surf zone and shallow reef ecosystems, where higher settlement magnitude was correlated with greater targeted fish biomass.

Supplementary Tables

Table S1. Observed species by ecosystem (surf zone, kelp forest, shallow reef, and deep reef) and their target status.

Scientific name	Target status	Surf zone	Kelp forest	Shallow reef	Deep reef
Agonidae spp	Non-targeted				X
Alopias vulpinus	Targeted		X	X	
Ammodytes hexapterus	Targeted				X
Amphistichus argenteus	Targeted	X	X		X
Amphistichus koelzi	Targeted	X			
Amphistichus rhodoterus	Targeted	X			
Anarrhichthys ocellatus	Non-targeted		X	X	X
Anisotremus davidsonii	Targeted		X	X	
Anoplagonus inermis	Non-targeted		X		
Anoplopoma fimbria	Targeted				X
Apodichthys flavidus	Non-targeted		X		
Apogon guadalupensis	Non-targeted		X		
Apristurus brunneus	Non-targeted				X
Artedius harringtoni	Non-targeted			X	
Atherinidae spp	Targeted	X			
Atherinops affinis	Targeted	X		X	
Atherinopsidae spp	Non-targeted		X	X	
Atherinopsis californiensis	Targeted			X	
Atractoscion nobilis	Targeted	X	X	X	
Aulorhynchus flavidus	Non-targeted	X	X	X	X
Balistes polylepis	Non-targeted		X		
Bathymasteridae spp	Non-targeted		X		
Beringraja binoculata	Targeted		X		X

Beringraja rhina	Targeted				X
Beringraja stellulata	Targeted		X	X	X
Bothidae spp	Targeted		X		
Brachygenys californiensis	Targeted		X	X	
Brachyistius frenatus	Non-targeted	X	X		X
Caliraja spp	Targeted				X
Carcharhinus obscurus	Targeted		X		
Caulolatilus princeps	Targeted		X	X	X
Cebidichthys violaceus	Targeted		X		
Cephaloscyllium ventriosum	Non-targeted		X		X
Cheilotrema saturnum	Targeted	X	X		
Chromis punctipinnis	Non-targeted		X	X	X
Citharichthys sordidus	Targeted		X	X	X
Citharichthys spp	Targeted		X	X	
Citharichthys stigmaeus	Targeted	X	X	X	
Citharichthys xanthostigma	Targeted			X	
Clinidae spp	Non-targeted	X			
Clupea pallasii	Targeted	X			
Cottidae spp	Non-targeted				X
Cryptacanthodes giganteus	Non-targeted		X		
Cymatogaster aggregata	Targeted	X	X		X
Decapterus macarellus	Targeted		X		
Embiotoca jacksoni	Targeted	X	X		X
Embiotoca lateralis	Targeted	X	X	X	X
Embiotocidae spp	Targeted		X		X
Engraulis mordax	Targeted	X	X	X	
Enophrys bison	Non-targeted		X	X	X
Enophrys taurina	Non-targeted			X	
Entosphenus tridentatus	Non-targeted				X
Eopsetta jordani	Targeted			X	X
Eptatretus stoutii	Targeted				X
Ernogrammus walkeri	Non-targeted		X		
Fundulus parvipinnis	Non-targeted	X			
Gadidae spp	Non-targeted				X
Galeorhinus galeus	Targeted		X	X	
Genyonemus lineatus	Targeted	X		X	
Gibbonsia metzi	Non-targeted	X			X
Gibbonsia montereyensis	Non-targeted	X			
Gibbonsia spp	Non-targeted	X			
Girella nigricans	Targeted	X	X	X	X
Glyptocephalus zachirus	Targeted				X
Gobiesox maeandricus	Non-targeted		X		
Gobiidae spp	Non-targeted				X
Gymnothorax mordax	Non-targeted		X		X
Halichoeres semicinctus	Non-targeted		X	X	X
Hemilepidotus hemilepidotus	Non-targeted		X		

Hemilepidotus spinosus	Non-targeted		X		
Heterodontus francisci	Non-targeted		X		X
Heterostichus rostratus	Non-targeted	X	X		
Hexagrammidae spp	Targeted				X
Hexagrammos decagrammus	Targeted		X	X	X
Hexagrammos lagocephalus	Targeted		X	X	X
Hexagrammos spp	Targeted		X		
Hexanchus griseus	Targeted		X		X
Hippoglossina stomata	Targeted			X	
Hippoglossus stenolepis	Targeted			X	X
Hydrolagus colliei	Non-targeted				X
Hyperprosopon anale	Targeted	X	X		
Hyperprosopon argenteum	Targeted	X	X		
Hyperprosopon ellipticum	Targeted	X	X		
Hypomesus pretiosus	Targeted	X			
Hypsurus caryi	Targeted	X	X		X
Hypsypops rubicundus	Non-targeted		X	X	X
Kyphosus azureus	Targeted	X	X		
Leiocottus hirundo	Non-targeted		X		
Lepidopsetta bilineata	Targeted			X	X
Leptocottus armatus	Non-targeted	X	X		X
Lethops connectens	Non-targeted		X		
Lycodes pacificus	Targeted				X
Lyopsetta exilis	Targeted				X
Lythrypnus dalli	Non-targeted				X
Macrouridae spp	Non-targeted				X
Medialuna californiensis	Targeted	X	X	X	X
Menticirrhus undulatus	Targeted	X			
Merluccius productus	Targeted				X
Micrometrus aurora	Non-targeted	X			
Micrometrus minimus	Non-targeted	X	X		
Microstomus pacificus	Targeted				X
Mola mola	Non-targeted		X		X
Morone saxatilis	Targeted	X			
Mugil cephalus	Targeted	X			
Myliobatis californica	Targeted	X	X	X	X
Neoclinus blanchardi	Non-targeted		X	X	
Notorynchus cepedianus	Targeted		X		
Oncorhynchus tshawytscha	Targeted			X	
Ophiodon elongatus	Targeted		X	X	X
Osmeridae spp	Targeted				X
Oxyjulis californica	Non-targeted		X	X	X
Oxylebius pictus	Non-targeted		X	X	X
Paralabrax clathratus	Targeted	X	X	X	X
Paralabrax maculatofasciatus	Targeted		X		
Paralabrax nebulifer	Targeted		X	X	

Paralichthyidae spp	Targeted	X			X
Paralichthys californicus	Targeted	X	X	X	X
Parophrys vetulus	Targeted				X
Pegusa lascaris	Targeted				X
Phanerodon atripes	Non-targeted		X	X	X
Phanerodon furcatus	Targeted	X	X		X
Phanerodon vacca	Targeted	X	X	X	X
Pholidae spp	Non-targeted	X	X		
Platichthys stellatus	Targeted	X			X
Platyrhinoidis triseriata	Non-targeted	X	X		
Pleuronectidae spp	Targeted		X		X
Pleuronichthys coenosus	Non-targeted		X		
Pleuronichthys ritteri	Non-targeted				X
Porichthys notatus	Non-targeted		X		X
Prionace glauca	Targeted		X		
Prognathodes falcifer	Non-targeted		X		
Psettichthys melanostictus	Targeted	X		X	
Pseudobatos productus	Targeted	X	X		
Rajidae spp	Targeted				X
Rathbunella alleni	Non-targeted		X		
Rathbunella hypoplecta	Non-targeted		X		X
Rhacochilus toxotes	Targeted		X	X	X
Rhamphocottus richardsonii	Non-targeted		X		
Rhinogobiops nicholsii	Non-targeted		X		X
Roncador stearnsii	Targeted	X			
Ronquilus jordani	Non-targeted		X		
Sarda chiliensis	Targeted		X	X	
Sardinops sagax	Targeted	X	X	X	
Sciaenidae spp	Targeted				X
Scomber japonicus	Targeted		X	X	
Scombridae spp	Targeted			X	
Scorpaena guttata	Targeted		X	X	X
Scorpaenichthys marmoratus	Targeted	X	X	X	X
Scorpaenidae spp	Targeted				X
Scorpaenodes xyris	Non-targeted		X		
Sebastes atrovirens	Targeted		X	X	X
Sebastes auriculatus	Targeted		X	X	X
Sebastes aurora	Targeted				X
Sebastes babcocki	Non-targeted				X
Sebastes borealis	Targeted				X
Sebastes carnatus	Targeted		X	X	X
Sebastes caurinus	Targeted		X	X	X
Sebastes chlorostictus	Targeted				X
Sebastes chrysomelas	Targeted		X	X	X
Sebastes constellatus	Targeted			X	X
Sebastes crameri	Targeted				X

Sebastes dallii	Targeted		X	X	X
Sebastes diaconus	Targeted			X	
Sebastes diploproa	Targeted		X		X
Sebastes elongatus	Targeted				X
Sebastes ensifer	Targeted				X
Sebastes entomelas	Targeted		X	X	X
Sebastes flavidus	Targeted			X	X
Sebastes goodei	Targeted				X
Sebastes helvomaculatus	Non-targeted				X
Sebastes hopkinsi	Targeted		X	X	X
Sebastes jordani	Targeted				X
Sebastes lentiginosus	Targeted			X	X
Sebastes levis	Targeted				X
Sebastes maliger	Targeted		X	X	X
Sebastes melanops	Targeted		X	X	X
Sebastes melanostomus	Targeted				X
Sebastes miniatus	Targeted		X	X	X
Sebastes mystinus	Targeted		X	X	X
Sebastes nebulosus	Targeted		X	X	X
Sebastes nigrocinctus	Targeted			X	X
Sebastes ovalis	Targeted				X
Sebastes paucispinis	Targeted	X	X	X	X
Sebastes pinniger	Targeted		X	X	X
Sebastes rastrelliger	Targeted	X	X	X	
Sebastes rosaceus	Targeted		X	X	X
Sebastes rosenblatti	Targeted				X
Sebastes ruberrimus	Targeted			X	X
Sebastes rubrivinctus	Targeted		X		X
Sebastes rufus	Targeted				X
Sebastes saxicola	Targeted		X		X
Sebastes semicinctus	Targeted		X		X
Sebastes serranoides	Targeted			X	X
Sebastes serriceps	Targeted		X	X	X
Sebastes simulator	Targeted				X
Sebastes spp	Targeted	X	X	X	X
Sebastes umbrosus	Targeted		X	X	X
Sebastes wilsoni	Non-targeted				X
Sebastidae spp	Targeted				X
Sebastolobus alascanus	Targeted				X
Semicossyphus pulcher	Targeted		X	X	X
Seriola lalandi	Targeted		X	X	X
Seriphus politus	Targeted	X			
Sphyraena argentea	Targeted		X	X	
Squalus acanthias	Targeted		X	X	
Squatina californica	Targeted		X		X
Stellerina xyosterna	Non-targeted	X			

Stereolepis gigas	Non-targeted		X	X	X
Stichaeidae spp	Non-targeted		X		
Syngnathus californiensis	Non-targeted	X			
Syngnathus leptorhynchus	Non-targeted	X			
Syngnathus spp	Non-targeted	X	X		
Synodus lucioceps	Non-targeted		X	X	X
Tetronarce californica	Non-targeted		X		X
Thaleichthys pacificus	Targeted		X		
Trachurus symmetricus	Targeted		X	X	
Triakis semifasciata	Targeted	X	X		
Ulvicola sanctaerosae	Non-targeted		X		
Umbrina roncador	Targeted	X		X	
Urobatis halleri	Targeted	X	X		
Xystreurys liolepis	Targeted			X	
Zalembius rosaceus	Non-targeted		X		X
Zaniolepis frenata	Non-targeted				X
Zaniolepis latipinnis	Non-targeted				X
Zaniolepis spp	Non-targeted				X
Zapteryx exasperata	Targeted		X		
Zoarcidae spp	Non-targeted	X			X

Table S2. MPA features used to predict conservation performance. California Department of Fish and Wildlife (CDFW); Regional Ocean Modeling System (ROMS); Environmental Sensitivity Index (ESI).

Category	**Feature**	**Source**	**Details**
MPA feature	MPA age (yr)	CDFW MPA GIS file	
MPA feature	MPA size (km^2)	CDFW MPA GIS file	
MPA feature	Regulatory status	CDFW MPA GIS file	
Habitat	Settlement magnitude		Simulated using ROMS (see supplementary *Methods*)
Habitat	Habitat richness	CDFW bottom substrate and ESI shoreline	Number of unique habitat types
Habitat	Habitat diversity	CDFW bottom substrate and ESI shoreline	Shannon diversity using area of each habitat type
Habitat	Proportion of rock bottom	CDFW bottom substrate	Total hard substrate divided by MPA size
Human	Pre-MPA fishing pressure	CDFW fish tickets	Calculated at the block-level using 10 years of landings data preceding the oldest MPA in the block.
Biological	Species traits	Kelp forest + FishBase	

Table S3. Habitat types and data sources used to estimate habitat diversity, habitat richness, and proportion of rock within each MPA.

Habitat Type	Data Information
Hard substrate (0-30m)	High resolution (2m to 10m) multibeam mapping, mostly from the California Seafloor Mapping Project. Area totals calculated from a vector file. Depth information from the high resolution bathymetry data where available. Small mapping gaps filled in through interpolation and added to the total.
Hard substrate (30-100m)	
Hard substrate (100-200m)	
Hard substrate (200-3000m)	
Soft substrate (0-30m)	
Soft substrate (30-100m)	
Soft substrate (100-200m)	
Soft substrate (200-3000m)	
Kelp canopy (0-30m)	Data from CDFW kelp overflights (14 years; '89, '99, '02-'06, '08-'10, '13-'16), composite of all available data for maximum canopy extent.(Saarman 2020, unpublished). Captures both giant and bull kelp and covers the whole coast of California.
Coastal marsh	Data from NOAA ESI shoreline data, using the 2010 update for southern California. Source data has up to 3 classifications for each coastal segment (landward, seaward1, seaward2), length totals reflect all of these classifications, but do not double-count (for example landward is gravel beach, seaward1 is fine-grained beach, this segment counted just once as beach). Linear estimates were converted to area using median beach widths.
Tidal flats	
Hardened/armored shoreline	
Sandy beach	
Rocky intertidal	

Table S4. List of *de facto* MPAs for each ecosystem. MPA type is the state-designated status of the MPA, and the *de facto* status is indicated for each ecosystem. An MPA was designated as a *de facto* no-take MPA for a particular ecosystem if any allowed partial-take was unlikely to affect the species that reside in that particular ecosystem (e.g., take of salmon in an MPA is unlikely to affect any of our four focal ecosystems; Smith et al. 2023). Empty cells indicate that particular MPA was not sampled within a given ecosystem.

MPA name	MPA type	Surf zone	Kelp forest	Shallow reef	Deep reef
Campus Point SMCA	SMCA	SMR	SMR		SMR
White Rock SMCA	SMCA		SMR		
Point Vicente SMCA	SMCA		SMR		
Blue Cavern Onshore SMCA	SMCA		SMR		
Abalone Cove SMCA	SMCA		SMR		
Farnsworth Onshore SMCA	SMCA		SMR		
Point Dume SMCA	SMCA		SMR		
Swami's SMCA	SMCA		SMR	SMR	
Piedras Blancas SMCA	SMCA				SMR
Point Sur SMCA	SMCA				SMR
Southeast Farallon Island SMCA	SMCA				SMR
Point Arena SMCA	SMCA				SMR
Portuguese Ledge SMCA	SMCA				SMR
Big Creek SMCA	SMCA				SMR

Table S5. Sampling years by ecosystem for MPAs with paired reference sites. Empty cells indicate that particular MPA was not sampled within a given ecosystem.

MPA name	Surf zone	Kelp forest	Shallow reef	Deep reef
Abalone Cove SMCA		2011, 2013, 2015, 2016, 2017, 2018, 2019, 2020		
Anacapa Island SMCA		2004, 2005, 2006, 2007, 2008, 2009		
Anacapa Island SMR		2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2014, 2015, 2016, 2017, 2018, 2019, 2020	2017, 2018, 2019, 2020	
Asilomar SMR	2019, 2020	2007, 2008, 2011		2007, 2008
Año Nuevo SMR	2019, 2020		2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020	2015, 2019
Begg Rock SMR		2009, 2013		
Big Creek SMR		2001, 2002, 2003, 2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2015		2016
Blue Cavern Onshore SMCA		2004, 2011, 2012, 2019, 2020		
Bodega Head SMR			2017, 2018, 2019, 2020	2015, 2019
Cambria SMCA		2003, 2004, 2005, 2007, 2008		
Campus Point SMCA	2019, 2020	2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020		2014, 2019
Carmel Bay SMCA		2001, 2002, 2003, 2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020		
Carrington Point SMR		2003, 2004, 2005, 2007, 2008	2017, 2018, 2019, 2020	2005, 2006, 2007, 2009, 2014, 2019
Cat Harbor SMCA		2004, 2005, 2011, 2012, 2019, 2020		
Crystal Cove SMCA		2011, 2012, 2019, 2020		
Del Mar Landing SMR		2010, 2011		
Farnsworth Onshore SMCA		2011, 2012, 2019		
Gull Island SMR		2003, 2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2014, 2015, 2016, 2017, 2018, 2019, 2020		2014, 2019

Harris Point SMR		2003, 2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2014, 2016, 2018, 2019, 2020		2005, 2006, 2007, 2009, 2014, 2019
Laguna Beach SMR	2019, 2020		2017	
Long Point SMR		2011, 2012, 2019, 2020		
Lovers Point - Julia Platt SMR		2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007, 2008, 2009, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020		
Matlahuayl SMR	2019, 2020	2011, 2012, 2019, 2020		
Naples SMCA		2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020		
Natural Bridges SMR	2019, 2020	2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011		
Painted Cave SMCA		2003, 2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2014, 2015, 2016, 2017, 2018, 2019, 2020		
Piedras Blancas SMR		2003, 2004, 2005, 2006, 2007, 2008	2008, 2009, 2010, 2011, 2012, 2013, 2014, 2016, 2017, 2018, 2019, 2020	
Pillar Point SMCA				2015
Point Arena SMR		2011		
Point Buchon SMR		2007, 2008, 2009, 2010, 2011, 2016, 2017, 2018, 2019, 2020	2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020	2008, 2009, 2016, 2019
Point Cabrillo SMR		2014, 2015, 2017, 2018, 2019		
Point Conception SMR	2019, 2020	2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007, 2009, 2010, 2011, 2012	2018	2014, 2019
Point Dume SMCA		2010, 2011, 2012, 2013, 2019, 2020		
Point Dume SMR	2019, 2020	2008, 2019, 2020		
Point Lobos SMR	2019, 2020	2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020	2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020	2008, 2009, 2016, 2019
Point Reyes SMR	2019, 2020			
Point St. George Reef				2014

Offshore SMCA				
Point Sur SMCA				2008
Point Sur SMR		2005, 2006, 2007, 2008, 2010, 2011, 2017, 2019, 2020		
Point Vicente SMCA		2004, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020		
Portuguese Ledge SMCA				2016, 2019
Pyramid Point SMCA		2018		
Reading Rock SMCA	2019, 2020			
Salt Point SMCA		2010, 2011		
Samoa SMCA	2019, 2020			
Santa Barbara Island SMR		2004, 2005, 2006, 2007, 2008, 2011, 2013, 2019		
Saunders Reef SMCA		2010, 2011, 2016, 2017, 2018, 2019, 2020		
Scorpion SMR		2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020		
Sea Lion Cove SMCA		2010, 2011		
Sea Lion Gulch SMR				2014
South Cape Mendocino SMR			2017, 2018, 2019, 2020	
South La Jolla SMR		2011, 2012, 2019, 2020	2017, 2018, 2019, 2020	
South Point SMR		2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020		2005, 2006, 2007, 2009, 2014, 2019
Southeast Farallon Island SMR			2017, 2018	2011
Stewarts Point SMR		2010, 2011, 2017, 2018, 2019	2017, 2018, 2019, 2020	
Swami's SMCA		2011, 2012, 2019	2017, 2018, 2019, 2020	
Ten Mile SMR	2019, 2020	2014, 2015, 2018, 2019, 2020	2017, 2018, 2019, 2020	2014
Vandenberg SMR		2000, 2001, 2002, 2003, 2004, 2005, 2006, 2008		
White Rock SMCA		2003, 2004, 2005, 2006, 2007, 2008, 2009, 2011		

Table S6. Network-level meta analysis results pooled across the entire network of MPAs, ecosystems, and regions. The p-values (p) in red text indicates statistically significant relationships.

MPA type	Allowed take	Target status	Effect size	Standard error	P-value	95% lower	95% upper	No. MPA-Ecosystem pairs	Tau-2	Q
SMCA	Partial-take	Targeted	0.587	0.314	0.062	-0.029	1.203	15	1.237	119.856
SMR	No-take	Targeted	0.491	0.096	*<0.001*	0.304	0.679	78	0.561	984.041
SMCA	Partial-take	Nontargeted	0.224	0.319	0.482	-0.4	0.849	14	1.307	5843.407
SMR	No-take	Nontargeted	0.159	0.087	0.069	-0.012	0.33	62	0.382	639.999

Table S7. Regional-level meta analysis results from meta analyses pooled across MPAs and ecosystems within a region. The p-values (p) in red text indicates statistically significant relationships.

Region	MPA type	Allowed take	Target status	Effect size	Standard error	P-val	95% lower	95% upper	No. MPA-Ecosystem pairs	Tau-2	Q
North Coast	SMCA	Partial-take	Targeted	1.901	0.912	*0.037*	0.115	3.688	4	2.967	17.48
North Coast	SMR	No-take	Targeted	0.215	0.194	0.268	-0.165	0.596	7	0.165	17.738
North Coast	SMCA	Partial-take	Nontargeted	1.22	0.721	0.09	-0.192	2.633	4	1.849	50.963
North Coast	SMR	No-take	Nontargeted	-0.176	0.407	0.666	-0.973	0.621	5	0.681	27.055
North Central Coast	SMCA	Partial-take	Targeted	0.114	0.349	0.744	-0.57	0.798	4	0.223	6.086
North Central Coast	SMR	No-take	Targeted	0.582	0.244	*0.017*	0.104	1.061	9	0.428	86.266
North Central Coast	SMCA	Partial-take	Nontargeted	0.017	0.378	0.965	-0.725	0.758	3	0.428	548.886
North Central Coast	SMR	No-take	Nontargeted	0.243	0.142	0.087	-0.035	0.522	5	0.094	36.958
Central Coast	SMCA	Partial-take	Targeted	-0.271	0.331	0.414	-0.92	0.379	2	0.158	3.432
Central Coast	SMR	No-take	Targeted	0.358	0.154	*0.02*	0.056	0.661	25	0.452	168.822
Central Coast	SMCA	Partial-take	Nontargeted	-0.088	0.447	0.844	-0.964	0.788	2	0.351	8.165
Central Coast	SMR	No-take	Nontargeted	0.228	0.123	0.064	-0.013	0.468	21	0.254	227.005
South Coast	SMCA	Partial-take	Targeted	0.359	0.508	0.48	-0.637	1.355	5	1.132	41.364
South Coast	SMR	No-take	Targeted	0.627	0.156	*<0.001*	0.321	0.932	37	0.724	599.105
South Coast	SMCA	Partial-take	Nontargeted	-0.289	0.534	0.588	-1.337	0.758	5	1.289	27.991
South Coast	SMR	No-take	Nontargeted	0.15	0.148	0.311	-0.14	0.439	31	0.554	308.952

Table S8. Ecosystem-level meta analysis results from meta analyses pooled across MPAs within an ecosystem and target status. The p-values (p) in red text indicates statistically significant relationships.

Ecosystem	MPA type	Allowed take	Target status	Effect size	Standard error	P-value	95% lower	95% upper	No. MPAs	Tau-2	Q
Deep reef	SMCA	Partial-take	Targeted	0.898	0.415	*0.031*	0.084	1.712	2	0.232	2.985
Deep reef	SMR	No-take	Targeted	0.185	0.163	0.254	-0.133	0.504	17	0.296	54.662
Deep reef	SMCA	Partial-take	Nontargeted	0.948	0.409	*0.021*	0.146	1.749	2	0.333	282.304
Deep reef	SMR	No-take	Nontargeted	0.284	0.121	*0.019*	0.046	0.522	16	0.164	173.862
Kelp forest	SMCA	Partial-take	Targeted	0.251	0.28	0.371	-0.299	0.8	11	0.672	86.105
Kelp forest	SMR	No-take	Targeted	0.461	0.163	*0.005*	0.141	0.781	35	0.743	659.659
Kelp forest	SMCA	Partial-take	Nontargeted	-0.222	0.232	0.34	-0.677	0.234	10	0.439	482.223
Kelp forest	SMR	No-take	Nontargeted	0.135	0.122	0.266	-0.103	0.374	35	0.42	374.409
Shallow reef	SMR	No-take	Targeted	0.853	0.136	*<0.001*	0.587	1.12	15	0.236	123.596
Surf zone	SMCA	Partial-take	Targeted	2.709	2.238	0.226	-1.677	7.095	2	9.352	14.995
Surf zone	SMR	No-take	Targeted	0.486	0.282	0.085	-0.066	1.038	11	0.653	61.019
Surf zone	SMCA	Partial-take	Nontargeted	1.951	1.022	0.056	-0.052	3.954	2	1.896	10.332
Surf zone	SMR	No-take	Nontargeted	0.104	0.251	0.678	-0.388	0.596	11	0.628	88.295

Table S9. Ecosystem-level meta analysis results by region. The p-values (p) in red text indicates statistically significant relationships.

Ecosystem	Region	MPA type	Allowed take	Target status	Effect size	Standard error	P-value	95% lower	95% upper	No. MPAs	Tau-2	Q
Deep reef	North	SMCA	Partial-take	Targeted	1.359	0.392	*0.001*	0.592	2.127	1	0	0
Deep reef	North	SMR	No-take	Targeted	-0.153	0.334	0.646	-0.808	0.501	2	0	0.233
Deep reef	North	SMCA	Partial-take	Nontargeted	1.355	0.003	*<0.001*	1.349	1.362	1	0	0
Deep reef	North	SMR	No-take	Nontargeted	-1.109	0.487	*0.023*	-2.064	-0.155	2	0.208	1.557
Deep reef	North Central	SMCA	Partial-take	Targeted	0.524	0.283	0.064	-0.031	1.079	1	0	0
Deep reef	North Central	SMR	No-take	Targeted	-0.133	0.186	0.477	-0.498	0.233	2	0	0.989
Deep reef	North Central	SMCA	Partial-take	Nontargeted	0.537	0.049	*<0.001*	0.442	0.632	1	0	0
Deep reef	North Central	SMR	No-take	Nontargeted	0.478	0.033	*<0.001*	0.414	0.542	1	0	0
Deep reef	Central	SMR	No-take	Targeted	0.083	0.344	0.81	-0.592	0.757	7	0.632	26.222
Deep reef	Central	SMR	No-take	Nontargeted	0.302	0.136	*0.027*	0.035	0.569	7	0.097	110.697
Deep reef	South	SMR	No-take	Targeted	0.484	0.23	*0.035*	0.035	0.934	6	0.197	14.132
Deep reef	South	SMR	No-take	Nontargeted	0.506	0.179	*0.005*	0.154	0.857	6	0.108	17.21
Kelp forest	North	SMCA	Partial-take	Targeted	1.199	0.22	*<0.001*	0.768	1.631	1	0	0
Kelp forest	North	SMR	No-take	Targeted	-0.428	0.276	0.121	-0.968	0.113	2	0	0.062
Kelp forest	North	SMCA	Partial-take	Nontargeted	-0.731	0.788	0.354	-2.275	0.813	1	0	0
Kelp forest	North	SMR	No-take	Nontargeted	0.218	0.259	0.4	-0.29	0.727	2	0.089	1.981
Kelp forest	North Central	SMCA	Partial-take	Targeted	-0.321	0.286	0.262	-0.881	0.24	3	0	1.682
Kelp forest	North Central	SMR	No-take	Targeted	0.682	0.711	0.338	-0.712	2.077	3	1.341	15.21
Kelp forest	North Central	SMCA	Partial-take	Nontargeted	-0.243	0.476	0.61	-1.176	0.69	2	0.452	444.855
Kelp forest	North Central	SMR	No-take	Nontargeted	0.343	0.025	*<0.001*	0.294	0.391	3	0.001	8.748
Kelp forest	Central	SMCA	Partial-take	Targeted	-0.271	0.331	0.414	-0.92	0.379	2	0.158	3.432
Kelp forest	Central	SMR	No-take	Targeted	0.438	0.219	*0.045*	0.009	0.866	10	0.358	55.822
Kelp forest	Central	SMCA	Partial-take	Nontargeted	-0.088	0.447	0.844	-0.964	0.788	2	0.351	8.165
Kelp forest	Central	SMR	No-take	Nontargeted	0.212	0.117	0.069	-0.017	0.441	10	0.086	59.421
Kelp forest	South	SMCA	Partial-take	Targeted	0.359	0.508	0.48	-0.637	1.355	5	1.132	41.364
Kelp forest	South	SMR	No-take	Targeted	0.539	0.246	*0.028*	0.057	1.02	20	0.969	450.915
Kelp forest	South	SMCA	Partial-take	Nontargeted	-0.289	0.534	0.588	-1.337	0.758	5	1.289	27.991
Kelp forest	South	SMR	No-take	Nontargeted	0.078	0.223	0.725	-0.359	0.516	20	0.843	205.663

Shallow reef	North	SMR	No-take	Targeted	0.609	0.147	*<0.001*	0.322	0.897	2	0	0.056
Shallow reef	North Central	SMR	No-take	Targeted	0.841	0.313	*0.007*	0.228	1.455	3	0.251	26.794
Shallow reef	Central	SMR	No-take	Targeted	0.892	0.287	*0.002*	0.329	1.454	4	0.3	38.549
Shallow reef	South	SMR	No-take	Targeted	0.887	0.284	*0.002*	0.33	1.444	6	0.437	48.364
Surf zone	North	SMCA	Partial-take	Targeted	2.709	2.238	0.226	-1.677	7.095	2	9.352	14.995
Surf zone	North	SMR	No-take	Targeted	0.613	0.087	*<0.001*	0.443	0.782	1	0	0
Surf zone	North	SMCA	Partial-take	Nontargeted	1.951	1.022	0.056	-0.052	3.954	2	1.896	10.332
Surf zone	North	SMR	No-take	Nontargeted	0.785	0.171	*<0.001*	0.449	1.121	1	0	0
Surf zone	North Central	SMR	No-take	Targeted	1.053	0.454	*0.02*	0.162	1.944	1	0	0
Surf zone	North Central	SMR	No-take	Nontargeted	-0.525	0.216	*0.015*	-0.949	-0.101	1	0	0
Surf zone	Central	SMR	No-take	Targeted	-0.143	0.377	0.704	-0.883	0.596	4	0.295	6.943
Surf zone	Central	SMR	No-take	Nontargeted	-0.057	0.703	0.935	-1.435	1.32	4	1.897	52.276
Surf zone	South	SMR	No-take	Targeted	0.789	0.486	0.104	-0.163	1.742	5	0.958	36.967
Surf zone	South	SMR	No-take	Nontargeted	0.173	0.167	0.3	-0.155	0.502	5	0.082	10.228

Table S10. MPA-level meta analysis results from meta analyses pooled across MPAs within an ecosystem, region, and target status. The p-values (p) in red text indicates statistically significant relationships.

	Region	MPA name	Target status	Effect size	Standard error	P-value	95% lower	95% upper	Tau-2	Q	Ecosystem (latest year)
1	North	Point Cabrillo SMR	Targeted	-0.374	0.35	0.285	-1.06	0.311	0	0	Kelp forest (2019)
1	North	Point Cabrillo SMR	Non-targeted	-0.232	0.426	0.585	-1.067	0.602	0	0	Kelp forest (2019)
2	North	Sea Lion Gulch SMR	Targeted	-0.297	0.447	0.506	-1.173	0.579	0	0	Deep reef (2014)
2	North	Sea Lion Gulch SMR	Non-targeted	-0.802	0.352	*0.023*	-1.492	-0.111	0	0	Deep reef (2014)
3	North	Ten Mile SMR	Targeted	0.352	0.237	0.137	-0.111	0.816	0.142	7.409	Surf zone (2019), Kelp forest (2020), Shallow reef (2020), Deep reef (2014)
3	North	Ten Mile SMR	Non-targeted	-0.061	0.723	0.933	-1.477	1.355	1.395	14	Surf zone (2020), Kelp forest (2020), Deep reef (2014)
4	North	Reading Rock SMCA	Targeted	0.511	0.698	0.463	-0.856	1.879	0	0	Surf zone (2020)
4	North	Reading Rock SMCA	Non-targeted	2.903	0.235	*<0.001*	2.442	3.365	0	0	Surf zone (2020)
5	North	South Cape Mendocino SMR	Targeted	0.559	0.26	*0.032*	0.049	1.068	0	0	Shallow reef (2020)
6	North	Pyramid Point SMCA	Targeted	1.199	0.22	*<0.001*	0.768	1.631	0	0	Kelp forest (2018)
6	North	Pyramid Point SMCA	Non-targeted	-0.731	0.788	0.354	-2.275	0.813	0	0	Kelp forest (2018)
7	North	Point St. George Reef Offshore SMCA	Targeted	1.359	0.392	0.001	0.592	2.127	0	0	Deep reef (2014)
7	North	Point St. George Reef Offshore SMCA	Non-targeted	1.355	0.003	*<0.001*	1.349	1.362	0	0	Deep reef (2014)
8	North	Samoa SMCA	Targeted	4.988	0.922	*<0.001*	3.181	6.795	0	0	Surf zone (2020)
8	North	Samoa SMCA	Non-targeted	0.854	0.592	0.149	-0.307	2.015	0	0	Surf zone (2020)
9	North Central	Salt Point SMCA	Targeted	-0.476	0.317	0.133	-1.098	0.145	0	0	Kelp forest (2011)
9	North Central	Salt Point SMCA	Non-targeted	0.232	0.022	*<0.001*	0.189	0.276	0	0	Kelp forest (2011)
10	North Central	Saunders Reef SMCA	Targeted	0.026	0.848	0.976	-1.637	1.689	0	0	Kelp forest (2020)
10	North Central	Saunders Reef SMCA	Non-targeted	-0.719	0.039	*<0.001*	-0.797	-0.642	0	0	Kelp forest (2020)

11	North Central	Bodega Head SMR	Targeted	0.222	0.484	0.647	-0.727	1.171	0.396	6.253	Shallow reef (2020), Deep reef (2019)
11	North Central	Bodega Head SMR	Non-targeted	0.478	0.033	*<0.001*	0.414	0.542	0	0	Deep reef (2019)
12	North Central	Southeast Farallon Island SMR	Targeted	0.35	0.153	*0.022*	0.05	0.649	0	0.14	Shallow reef (2018), Deep reef (2011)
13	North Central	Del Mar Landing SMR	Targeted	0.379	0.387	0.328	-0.38	1.138	0	0	Kelp forest (2011)
13	North Central	Del Mar Landing SMR	Non-targeted	0.333	0.026	*<0.001*	0.281	0.384	0	0	Kelp forest (2011)
14	North Central	Pillar Point SMCA	Targeted	0.524	0.283	0.064	-0.031	1.079	0	0	Deep reef (2015)
14	North Central	Pillar Point SMCA	Non-targeted	0.537	0.049	*<0.001*	0.442	0.632	0	0	Deep reef (2015)
15	North Central	Stewarts Point SMR	Targeted	0.55	0.825	0.505	-1.066	2.166	1.317	31.137	Kelp forest (2019), Shallow reef (2020)
15	North Central	Stewarts Point SMR	Non-targeted	0.299	0.029	*<0.001*	0.242	0.355	0	0	Kelp forest (2019)
16	North Central	Sea Lion Cove SMCA	Targeted	0.874	1.058	0.409	-1.201	2.948	0	0	Kelp forest (2011)
17	North Central	Point Reyes SMR	Targeted	1.053	0.454	*0.02*	0.162	1.944	0	0	Surf zone (2020)
17	North Central	Point Reyes SMR	Non-targeted	-0.525	0.216	*0.015*	-0.949	-0.101	0	0	Surf zone (2020)
18	North Central	Point Arena SMR	Targeted	2.172	0.573	*<0.001*	1.05	3.294	0	0	Kelp forest (2011)
18	North Central	Point Arena SMR	Non-targeted	0.379	0.01	*<0.001*	0.359	0.399	0	0	Kelp forest (2011)
19	Central	Carmel Bay SMCA	Targeted	-0.562	0.19	*0.003*	-0.935	-0.189	0	0	Kelp forest (2020)
19	Central	Carmel Bay SMCA	Non-targeted	-0.536	0.224	*0.017*	-0.976	-0.097	0	0	Kelp forest (2020)
20	Central	White Rock SMCA	Targeted	-0.281	0.512	0.583	-1.284	0.723	0	0	Kelp forest (2011)
20	Central	White Rock SMCA	Non-targeted	1.072	0.518	*0.039*	0.057	2.088	0	0	Kelp forest (2011)
21	Central	Natural Bridges SMR	Targeted	-0.132	0.806	0.87	-1.711	1.447	1.085	6.054	Surf zone (2020), Kelp forest (2011)

21	Central	Natural Bridges SMR	Non-targeted	0.488	0.042	*<0.001*	0.406	0.57	0	0.042	Surf zone (2020), Kelp forest (2011)
22	Central	Point Lobos SMR	Targeted	-0.041	0.529	0.939	-1.078	0.996	0.955	69.556	Surf zone (2020), Kelp forest (2020), Shallow reef (2020), Deep reef (2019)
22	Central	Point Lobos SMR	Non-targeted	-0.439	0.898	0.625	-2.199	1.321	2.305	40.281	Surf zone (2020), Kelp forest (2020), Deep reef (2019)
23	Central	Asilomar SMR	Targeted	0.041	0.266	0.878	-0.481	0.562	0	0.483	Surf zone (2020), Kelp forest (2011), Deep reef (2008)
23	Central	Asilomar SMR	Non-targeted	0.275	0.29	0.342	-0.293	0.843	0.223	19.348	Surf zone (2019), Kelp forest (2011), Deep reef (2008)
24	Central	Cambria SMCA	Targeted	0.107	0.307	0.728	-0.494	0.708	0	0	Kelp forest (2008)
24	Central	Cambria SMCA	Non-targeted	0.358	0.218	0.101	-0.07	0.786	0	0	Kelp forest (2008)
25	Central	Año Nuevo SMR	Targeted	0.154	0.124	0.214	-0.089	0.397	0	1.741	Surf zone (2020), Shallow reef (2020), Deep reef (2019)
25	Central	Año Nuevo SMR	Non-targeted	0.497	0.051	*<0.001*	0.397	0.597	0	0	Surf zone (2020), Deep reef (2019)
26	Central	Big Creek SMR	Targeted	0.206	0.839	0.806	-1.438	1.851	1.228	7.349	Kelp forest (2015), Deep reef (2016)
26	Central	Big Creek SMR	Non-targeted	0.298	0.304	0.328	-0.299	0.894	0.025	1.074	Kelp forest (2015), Deep reef (2016)
27	Central	Piedras Blancas SMR	Targeted	0.298	0.46	0.516	-0.603	1.2	0.388	12.28	Kelp forest (2008), Shallow reef (2020)
27	Central	Piedras Blancas SMR	Non-targeted	-0.237	0.106	*0.025*	-0.443	-0.03	0	0	Kelp forest (2008)
28	Central	Point Sur SMCA	Targeted	0.492	0.609	0.419	-0.701	1.686	0	0	Deep reef (2008)
28	Central	Point Sur SMCA	Non-targeted	-0.173	0.055	*0.002*	-0.281	-0.066	0	0	Deep reef (2008)
29	Central	Point Buchon SMR	Targeted	0.791	0.454	0.081	-0.099	1.68	0.535	14.303	Kelp forest (2020), Shallow reef (2020), Deep reef (2019)
29	Central	Point Buchon SMR	Non-targeted	0.304	0.408	0.456	-0.496	1.103	0.217	1.993	Kelp forest (2020), Deep reef (2019)
30	Central	Point Sur SMR	Targeted	0.863	0.346	*0.013*	0.184	1.541	0	0	Kelp forest (2020)
30	Central	Point Sur SMR	Non-targeted	0.429	0.248	0.084	-0.057	0.916	0	0	Kelp forest (2020)
31	Central	Lovers Point - Julia Platt SMR	Targeted	0.887	0.223	*<0.001*	0.451	1.324	0	0	Kelp forest (2020)
31	Central	Lovers Point - Julia Platt SMR	Non-targeted	0.252	0.096	*0.009*	0.064	0.44	0	0	Kelp forest (2020)
32	Central	Vandenberg SMR	Targeted	1.203	0.512	*0.019*	0.2	2.206	0	0	Kelp forest (2008)
32	Central	Vandenberg SMR	Non-targeted	-0.092	0.164	0.573	-0.415	0.23	0	0	Kelp forest (2008)
33	Central	Portuguese Ledge SMCA	Targeted	2.034	0.499	*<0.001*	1.057	3.011	0	0	Deep reef (2019)
33	Central	Portuguese Ledge SMCA	Non-targeted	0.554	0.083	*<0.001*	0.391	0.717	0	0	Deep reef (2019)

34	South	Crystal Cove SMCA	Targeted	-1.566	0.565	*0.006*	-2.672	-0.459	0	0	Kelp forest (2020)
34	South	Crystal Cove SMCA	Non-targeted	-2.631	0.659	*<0.001*	-3.922	-1.339	0	0	Kelp forest (2020)
35	South	Scorpion SMR	Targeted	-0.442	0.367	0.229	-1.161	0.278	0	0	Kelp forest (2020)
35	South	Scorpion SMR	Non-targeted	-0.386	0.141	*0.006*	-0.663	-0.109	0	0	Kelp forest (2020)
36	South	Carrington Point SMR	Targeted	-0.438	0.672	0.514	-1.755	0.879	1.278	47.933	Kelp forest (2008), Shallow reef (2020), Deep reef (2019)
36	South	Carrington Point SMR	Non-targeted	-0.17	0.065	*0.009*	-0.297	-0.043	0	0.009	Kelp forest (2008), Deep reef (2019)
37	South	Blue Cavern Onshore SMCA (No-Take)	Targeted	-0.319	0.247	0.196	-0.802	0.165	0	0	Kelp forest (2020)
37	South	Blue Cavern Onshore SMCA (No-Take)	Non-targeted	-1.814	0.215	*<0.001*	-2.234	-1.393	0	0	Kelp forest (2020)
38	South	Cat Harbor SMCA	Targeted	-0.138	0.183	0.451	-0.497	0.221	0	0	Kelp forest (2020)
38	South	Cat Harbor SMCA	Non-targeted	0.258	0.139	0.063	-0.014	0.529	0	0	Kelp forest (2020)
39	South	Point Dume SMCA	Targeted	-0.112	0.335	0.738	-0.768	0.544	0	0	Kelp forest (2020)
39	South	Point Dume SMCA	Non-targeted	-1.388	0.313	*<0.001*	-2	-0.775	0	0	Kelp forest (2020)
40	South	Point Vicente SMCA (No-Take)	Targeted	-0.04	0.88	0.964	-1.765	1.685	0	0	Kelp forest (2020)
40	South	Point Vicente SMCA (No-Take)	Non-targeted	1.615	0.235	*<0.001*	1.154	2.076	0	0	Kelp forest (2020)
41	South	Begg Rock SMR	Targeted	0.094	0.719	0.896	-1.315	1.504	0	0	Kelp forest (2013)
41	South	Begg Rock SMR	Non-targeted	-0.866	0.848	0.308	-2.528	0.797	0	0	Kelp forest (2013)
42	South	Campus Point SMCA (No-Take)	Targeted	0.382	0.229	0.095	-0.067	0.831	0	1.583	Surf zone (2020), Kelp forest (2020), Deep reef (2019)
42	South	Campus Point SMCA (No-Take)	Non-targeted	0.412	0.046	*<0.001*	0.322	0.502	0	0.597	Surf zone (2020), Kelp forest (2020), Deep reef (2019)
43	South	Matlahuayl SMR	Targeted	0.512	0.767	0.504	-0.991	2.015	0.94	4.978	Surf zone (2020), Kelp forest (2020)
43	South	Matlahuayl SMR	Non-targeted	-0.102	0.212	0.632	-0.518	0.314	0.031	1.47	Surf zone (2020), Kelp forest (2020)
44	South	Farnsworth Onshore SMCA	Targeted	0.515	0.383	0.179	-0.236	1.267	0	0	Kelp forest (2019)
44	South	Farnsworth Onshore SMCA	Non-targeted	0.159	0.286	0.579	-0.402	0.721	0	0	Kelp forest (2019)
45	South	Santa Barbara Island SMR	Targeted	0.558	0.26	*0.032*	0.048	1.068	0	0	Kelp forest (2019)
45	South	Santa Barbara Island SMR	Non-targeted	-0.947	0.543	0.081	-2.012	0.117	0	0	Kelp forest (2019)

46	South	Harris Point SMR	Targeted	0.647	0.262	*0.013*	0.135	1.16	0	0.405	Kelp forest (2020), Deep reef (2019)
46	South	Harris Point SMR	Non-targeted	0.827	0.121	*<0.001*	0.59	1.065	0	0.466	Kelp forest (2020), Deep reef (2019)
47	South	South La Jolla SMR	Targeted	0.689	0.15	*<0.001*	0.396	0.982	0	0.105	Kelp forest (2020), Shallow reef (2020)
47	South	South La Jolla SMR	Non-targeted	2.938	1.054	*0.005*	0.872	5.003	0	0	Kelp forest (2020)
48	South	South Point SMR	Targeted	0.703	0.203	*0.001*	0.306	1.101	0	0.656	Kelp forest (2020), Deep reef (2019)
48	South	South Point SMR	Non-targeted	0.605	0.334	0.07	-0.049	1.259	0.163	3.649	Kelp forest (2020), Deep reef (2019)
49	South	Anacapa Island SMR	Targeted	0.73	1.077	0.498	-1.38	2.841	2.257	36.451	Kelp forest (2020), Shallow reef (2020)
49	South	Anacapa Island SMR	Non-targeted	0.202	0.16	0.206	-0.112	0.516	0	0	Kelp forest (2020)
50	South	Abalone Cove SMCA	Targeted	0.744	0.7	0.288	-0.628	2.116	0	0	Kelp forest (2020)
50	South	Abalone Cove SMCA	Non-targeted	0.051	0.381	0.894	-0.697	0.798	0	0	Kelp forest (2020)
51	South	Point Conception SMR	Targeted	0.755	0.633	0.233	-0.486	1.996	1.432	37.845	Surf zone (2020), Kelp forest (2012), Shallow reef (2018), Deep reef (2019)
51	South	Point Conception SMR	Non-targeted	-0.249	0.173	0.15	-0.589	0.091	0	0.27	Surf zone (2020), Kelp forest (2012), Deep reef (2019)
52	South	Anacapa Island SMCA	Targeted	0.802	0.525	0.127	-0.227	1.831	0	0	Kelp forest (2009)
52	South	Anacapa Island SMCA	Non-targeted	-0.129	0.204	0.528	-0.528	0.271	0	0	Kelp forest (2009)
53	South	Long Point SMR	Targeted	0.815	0.668	0.222	-0.493	2.124	0	0	Kelp forest (2020)
53	South	Long Point SMR	Non-targeted	-0.539	0.284	0.057	-1.096	0.017	0	0	Kelp forest (2020)
54	South	Gull Island SMR	Targeted	1.087	0.316	*0.001*	0.468	1.706	0	0.175	Kelp forest (2020), Deep reef (2019)
54	South	Gull Island SMR	Non-targeted	0.483	0.192	*0.012*	0.107	0.859	0	0.019	Kelp forest (2020), Deep reef (2019)
55	South	Laguna Beach SMR	Targeted	1.147	0.173	*<0.001*	0.807	1.487	0	0.616	Surf zone (2020), Shallow reef (2017)
55	South	Laguna Beach SMR	Non-targeted	-0.087	0.317	0.785	-0.708	0.535	0	0	Surf zone (2020)
56	South	Naples SMCA	Targeted	1.17	0.409	*0.004*	0.367	1.972	0	0	Kelp forest (2020)
56	South	Naples SMCA	Non-targeted	1.053	0.506	*0.037*	0.061	2.045	0	0	Kelp forest (2020)
57	South	Painted Cave SMCA	Targeted	1.322	0.227	*<0.001*	0.878	1.766	0	0	Kelp forest (2020)
57	South	Painted Cave SMCA	Non-targeted	-0.354	0.178	*0.047*	-0.704	-0.005	0	0	Kelp forest (2020)
58	South	Point Dume SMR	Targeted	1.555	0.784	*0.047*	0.018	3.092	0.995	5.175	Surf zone (2020), Kelp forest (2020)
58	South	Point Dume SMR	Non-targeted	0.98	0.299	*0.001*	0.394	1.566	0	0.324	Surf zone (2020), Kelp forest (2020)
59	South	Swami's SMCA	Targeted	2.024	0.835	*0.015*	0.387	3.662	1.374	64.785	Kelp forest (2019), Shallow reef (2020)
59	South	Swami's SMCA	Non-targeted	2.199	0.579	*<0.001*	1.064	3.335	0	0	Kelp forest (2019)

Table S11. Results from a meta-generalized additive model exploring features of MPA performance.

meta-GAM model						
Component	**Term**	**Estimate**	**Std Error**	**t-value**	**p-value**	
A. parametric coefficients	(Intercept)	0.386	0.039	9.808	0.0000	***
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth terms	s(size)	4.309	9.000	2.151	0.0002	***
	s(habitat_richness)	0.000	2.000	0.000	0.7272	
	s(habitat_diversity)	1.000	2.000	9.742	0.0000	***
	s(prop_rock)	2.247	9.000	0.688	0.0214	*
	s(fishing_pressure)	1.571	9.000	1.055	0.0009	***
	s(age_at_survey)	1.845	9.000	1.137	0.0012	**
	s(settlement_habitat)	2.832	8.000	0.559	0.1447	
	s(settlement_mpa_total)	0.000	9.000	0.000	0.7994	
	s(year)	1.828	8.000	0.632	0.0340	*

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05

Adjusted R-squared: 0.157, Deviance explained 0.203

GCV : 0.0739, Scale est: 0.0697, N: 292

Supplementary Figures

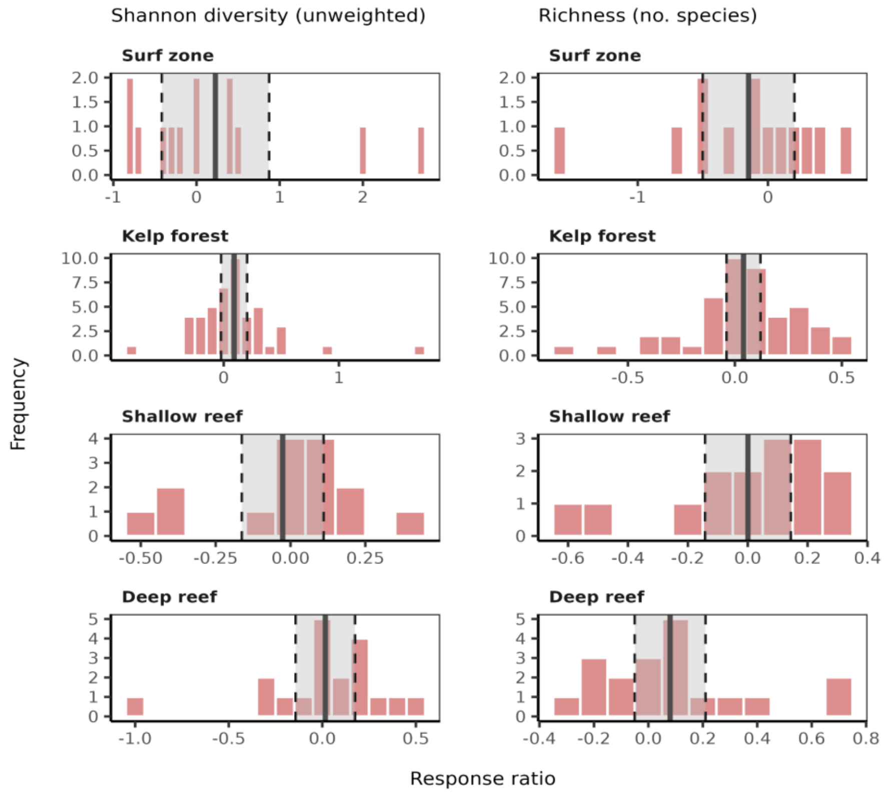

Figure S1. Shannon diversity (left) and richness (right) response ratios for four ecosystems (surf zone, kelp forest, shallow reef, deep reef). Each bar represents the response ratio frequency for the most recent year of sampling for each MPA. Solid vertical lines represent the mean response ratio, and the shaded areas indicate the 95% confidence interval. Confidence regions for all ecosystems overlap with 0, indicating that species diversity and richness are not significantly distinguishable between MPAs and areas that allow fishing.

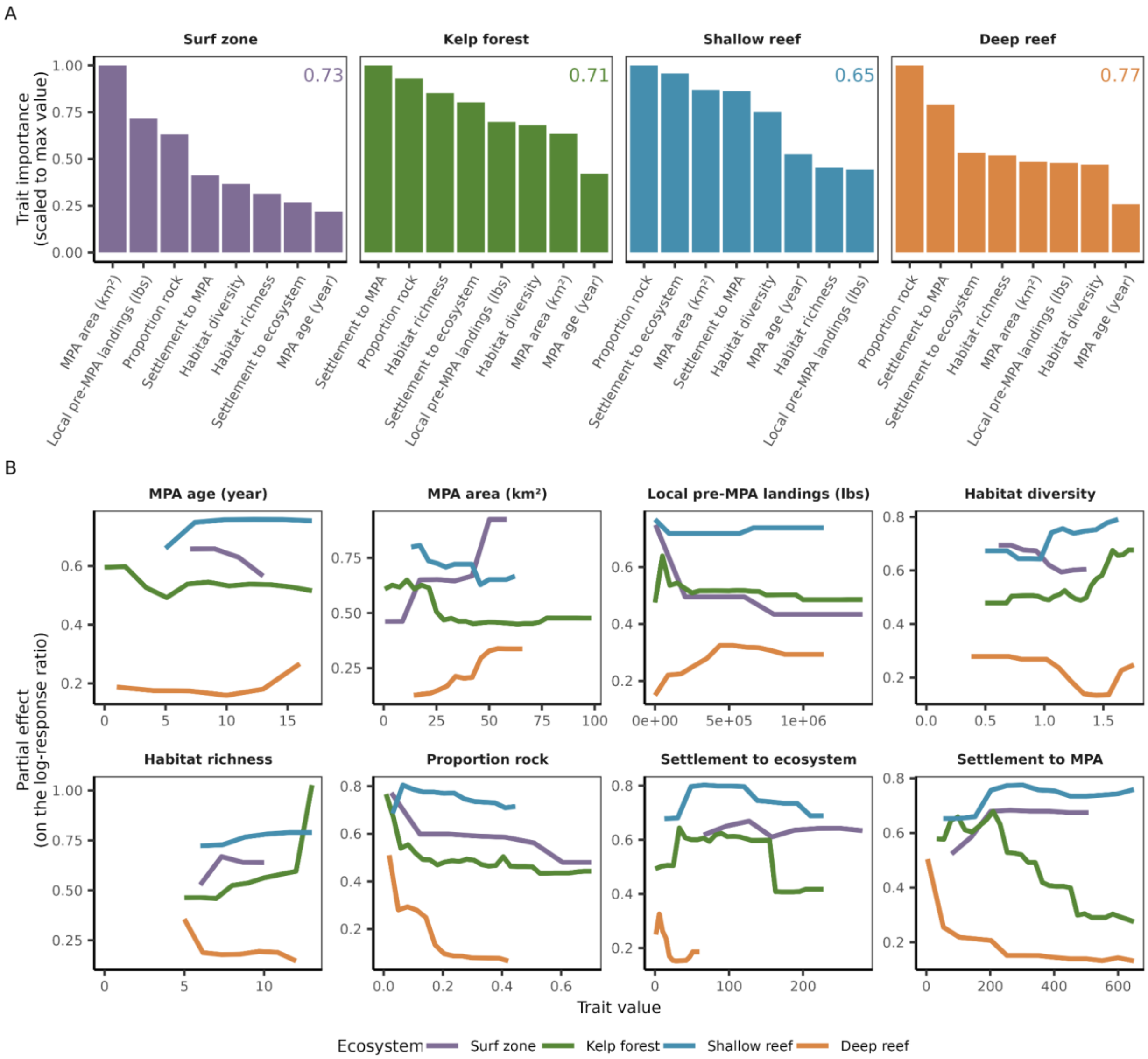

Figure S2. The **(A)** importance and **(B)** partial effects of MPA features on surf zone (purple), kelp forest (green), shallow reef (blue), and deep reef (orange) ecosystem-specific conservation performance (log-response ratio) for targeted species estimated by the random forest models. In **(A)**, feature importance is measured as the mean decrease in node impurity resulting from splitting on each feature scaled to the maximum value. MPA features are sorted in order of decreasing importance. The r^2 of each model fit is printed in the top-right corner of each plot. In **(B)**, lines indicate the ecosystem-specific impact of varying each MPA feature on conservation performance (log-response ratio) holding other features at their means. Panels are arranged in descending rank-order (MPA age = highest, settlement to MPA = lowest) based on the average impurity score across ecosystems.