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Tentative Title: Restoration of trophic cascades within kelp forests following the establishment of a network of marine protected areas

Short Title: MPA network restores trophic cascades

Authors: Emily Donham^{1*}, Tom Bell², Jennifer E. Caselle³, Bartholomew DiFiore^{1,4}, Scott Gabara⁵, Scott Hamilton⁶, Li Kui³, Robert Miller³, Dan Pondella⁷, Peter Raimondi⁸, Daniel Reed³, and Adrian Stier¹

Affiliations:

¹Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, CA 93106, USA

²Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

³Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA 93106, USA

⁴NOAA

⁵National Parks Service

⁶Moss Landing Marine Laboratories, San Jose State University, Moss Landing, CA 95039, USA

⁷Occidental College, Los Angeles, CA 90041, USA

⁸Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA 95060, USA

***Corresponding author:** edonham@ucsb.edu

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ABSTRACT

Protected areas have potential to preserve and/or restore ecosystem structure and function by reducing or eliminating human impacts. Yet, few studies have assessed how changes in structure as a consequence of protection scale up to alter ecosystem function (i.e., primary production). Yet, protection often disproportionately increases the abundance and size of species high on the food chain and could therefore have widespread ramifications for ecosystem function through trophic cascades. Here we test the hypothesis that marine protected area (MPA) implementation induces trophic cascades in kelp forest ecosystems, by increasing the abundance and/or biomass of formerly harvested sea urchin predators, reducing the abundance of herbivorous sea urchins, and allowing primary production to increase. In this study, we synthesize nearly 40 years of satellite-derived estimates of kelp biomass in the Southern California Bight with long-term SCUBA diver surveys of fish and invertebrate abundances in kelp forests encompassing a large network of MPAs. While we did not detect effects of MPA implementation on predator density and biomass sea urchin densities declined and giant kelp biomass increased inside MPAs compared to adjacent reference sites.

INTRODUCTION

Human activities (e.g., overharvesting, pollution, climate change) are dramatically reshaping ecosystems worldwide often resulting in habitat degradation and the decline or loss of species. One tool that has been heavily utilized to mitigate these impacts is the establishment of protected areas that exclude or limit the activities permitted within protected area boundaries. Most studies that have evaluated the effectiveness of protection have focused on measuring how targeted species change over time and often show increased biomass, size, and abundance within protected areas (Halpern 2003). Fewer studies have linked these changes in structure to changes in function even though community level processes are often more indicative of the overall health and resilience of an ecosystem (REF) and are therefore crucial metrics of success. Furthermore, protection often disproportionately increases the abundance and size of species high on the food chain, which is known to have widespread ramifications for ecosystem function through trophic cascades (Estes et al. 2011). Trophic cascades occur where large predators eat or scare herbivores such that consumption is reduced, thus allowing primary producers to thrive. This indirect positive effect of large predators on primary production has been well-documented in both mesocosm studies and in natural systems (Pinnegar et al. 2000). However, whether protected areas induce trophic cascades and restore lost ecosystem function remains an active area of research (Cheng et al. 2019, Heineke et al. 2023). Recent network-scale work during the 2014–2016 marine heatwaves shows that fully protected MPAs in Southern California had higher kelp resistance and recovery than unprotected areas, coincident with lower urchin densities and higher abundances of urchin predators (lobster, sheephead)—a pattern consistent with a trophic cascade. By contrast, no kelp advantage occurred in Central California where predator context differs (otters are protected statewide and sea stars were lost; Kumagai et al. 2024). Addressing this research gap is vital for improving understanding of how humans impacts alter ecosystem function and for setting realistic expectations regarding the benefits provided by protection.

Marine protected areas (MPAs) have been shown to increase the size and abundances of formerly targeted predatory fishes and invertebrates (Barrett et al. 2009, Edgar et al. 2014, Caselle et al. 2015, 2015, Lenihan et al. 2021) with corresponding increases in predation rates (Shears and Babcock 2002, Pederson and Johnson 2006, Cheng et al. 2019, Yates et al. 2020). These changes in structure and function due to the establishment of MPAs are, however, often highly context

dependent. For instance, time since implementation, reserve size, reserve enforcement, and life history characteristics are all important to the effectiveness of protected area implementation (Edgar et al. 2014, Cinner et al. 2020, Ziegler et al. 2024). Given the numerous examples of trophic cascades in marine ecosystems (Estes et al. 1978, Menge 1995, Pinnegar et al. 2000) and their relative strength in marine systems (Shurin et al. 2002), these MPA-induced shifts in abundance and size of predators have the potential to restore or strengthen trophic cascades. However, few studies have clearly documented MPA-induced trophic cascades. Notable exceptions include temperate marine reserves of New Zealand and Tasmania, and coral reefs in Kenya (Shears and Babcock 2002, Babcock et al. 2010, Sangil et al. 2012). The current dearth of evidence for MPA-induced trophic cascades in marine systems may be due to incomplete sampling across trophic levels (due to a focus on metrics related to targeted species) making it impossible to test for the presence of trophic cascades, and/or time lags in the responses of direct versus indirect effects of protection.

As kelp forests decline globally (Krumhansl et al. 2016), factors that contribute to their resilience and/or restoration are increasingly of interest to managers and policy makers. In particular, MPAs have been touted as tools to enhance marine ecosystem restoration through the strengthening or reestablishment of trophic cascades, but their potential appears to be highly context dependent (Morris et al 2020). For instance, ten years after implementation, Barrett et al. (2009) found significant increases in the size and abundance of predatory lobsters as well as declines in some grazer species, but no effect on macroalgae within MPAs in Tasmania. Shears and Babcock (2003) found strong evidence of trophic cascades within a single reserve in New Zealand where corresponding increases in lobsters and fish, declines in sea urchins, and increases in primary producers were seen 25 years after MPA establishment. Yet, when additional MPAs were considered, the potential for MPA-induced trophic cascades became dependent on abiotic factors, such as sedimentation, depth, and wave exposure (Shears et al. 2008). Within kelp forests in southern California, several studies have shown that increases in large-bodied predators (i.e., fish and lobsters) are correlated with declines in important herbivorous grazers [i.e. sea urchins, (Lafferty 2004, Barrett et al. 2009, Caselle et al. 2015, Eisaguirre et al. 2020)]. Conversely, MPA protection has been associated with increased the abundances of red sea urchins, *Mesocentrotus franciscanus* in the Channel Islands (Malakhoff and Miller 2021). While *M. franciscanus* is not

the primary barren forming species in California (but see REF for Alaska), they are still an important grazing species and reach much larger sizes than *S. purpuratus*. However, *M. franciscanus* is also subject to harvesting outside of protected areas and may benefit from protection (Malakhoff and Miller 2021). In all of these studies, there were no differences in kelp abundances inside and outside of MPAs, despite measurable differences in predatory fish or grazer abundances. A recent network-scale analysis combining 38 years of Landsat kelp canopy with 22 years of subtidal surveys reported that fully protected MPAs in Southern California exhibited greater kelp resistance and recovery during and after the 2014–2016 heatwaves, alongside fewer urchins and more predators, implicating a predator–urchin–kelp cascade (Kumagai et al. 2024). Their permutation and GLMM framework prioritized regional resilience to a specific climate shock, but did not explicitly pair MPAs to immediately adjacent reference reefs. Together, past work suggests that MPAs have the potential to induce trophic cascades, but factors contributing to their success may be more nuanced and requires further analysis.

Here we test the hypothesis that MPA implementation induces trophic cascades in kelp forest ecosystems, where predators are heavily harvested in unprotected areas and herbivory by sea urchins can drive shifts in ecosystem states (i.e., kelp forest vs urchin barrens). Testing this hypothesis can be challenging because protected areas are rarely replicated units; however, networks of MPAs offer a unique opportunity to do so. In this study, we focus on a network of MPAs within the southern California bight, where we synthesize nearly 40 years of satellite-derived estimates of kelp biomass with over 30 years of SCUBA diver-based surveys of fish, invertebrate, and kelp abundance to determine whether the establishment of MPAs enhances the biomass of giant kelp (i.e., increases primary production) with corresponding changes to key predator and herbivore species consistent with trophic cascades. We utilize a before-after-control-impact-paired-series (BACIPS) analysis where data exists prior to MPA implementation or a control-impact (CI) analysis when data was only collected after implementation. Satellite data were derived from Landsat imagery at an annual resolution (Bell et al. 2023), while SCUBA surveys were collected annually as part of the long-term kelp forest monitoring programs conducted by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), the Vantuna Research Group (VRG), the Santa Barbara Coastal Long Term Ecological Research program (LTER), and the National Parks Service Kelp Forest Monitoring

program (KFM). Specifically, we focused on the following question: (i) Did MPA implementation increase the biomass and/or density of key predators (i.e., California sheephead, California spiny lobster), decrease the density of key herbivores (i.e., purple sea urchin, red sea urchin), and increase the biomass and/or density of the main habitat forming seaweed, the giant kelp *Macrocystis pyrifera*, due to the strengthening of trophic cascades.

METHODS

Landsat kelp canopy biomass

We obtained derived estimates of kelp canopy biomass to assess the effect of MPA designation on giant kelp, *Macrocystis pyrifera*. Estimates were derived from Landsat satellite imagery and were available as 900 m² pixels for the entire southern California bight from 1984-2022 (Bell et al. 2023). This time series allowed us to utilize a before-after-control-impact approach, which is the gold standard for impact assessment. We used polygons delineating marine protected area boundaries to calculate maximum annual kelp biomass at each MPA using data processing methods outlined in Bell et al. (2023). At each MPA, adjacent reference sites were created by delineating areas of kelp forest greater than 1 km upcoast and downcoast from the paired MPA boundary. Reference sites were similar in area to MPA sites and were also at least 1 km from any other MPA boundary. For each MPA, we averaged annual maximum biomass across reference pixels to obtain a single mean value, hereafter referred to as the control site, and a single mean value from pixels inside of the MPA, hereafter referred to as the impact site. Data were then converted to a proportion of maximum determined from each individual MPAs paired control and impact time series. This paired approach controls for any site-specific variability in kelp biomass that is independent of protection and is crucial for impact assessment in the southern California bight, where an environmental mosaic can greatly influence local ecosystem dynamics (REF).

Diver-based surveys

To better understand the impacts of MPA implementation on key species that are known to be important members of trophic cascades within kelp forests, we utilized SCUBA survey data collected as part of four separate subtidal monitoring programs in the region. The National Parks Service Kelp Forest Monitoring Program (KFM) began in 1982 and has collected data annually

thereafter, conducting surveys exclusively in the channel islands. The Santa Barbara Coastal Long Term Ecological Monitoring Research program (SBC-LTER) began surveys in 2000 and is primarily located on the mainland within the Santa Barbara channel. The Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) and the Vantuna research group (VRG) utilize comparable methods and began monitoring in the channel islands and mainland in 1999, though at most locations monitoring began at or around the time of MPA implementation (i.e. 2003 for channel islands and 2011 for mainland). PISCO and VRG data were combined into a single dataset, hereafter referred to as PISCO given the similarity in data collection methods.

We estimated kelp biomass using relationships between stipe density (number of stipes per m²) and biomass (kilograms dry mass per m²) established by SBC-LTER [B = SD * slope * 1000, where SD = stipe density and B = biomass]. A slope = 0.085 was used since this was determined to be the average of empirically derived coefficients calculated from May - October (Rassweiler et al. 2025).

We also focused on the two most abundant sea urchin species, the purple sea urchin, *Strongylocentrotus purpuratus*, and the red sea urchin, *Mesocentrotus franciscanus*. These sea urchin species directly reduce kelp biomass through grazing, though, in southern California *S. purpuratus* is more important for urchin barren formation (REFS). We obtained data on sea urchin abundances that were sampled using either quad or swath survey methods (Malone et al. 2022, add REFS). In addition, at most locations and years, size frequency sampling was also conducted off transect. We pooled size frequency data collected from all sites (i.e., across monitoring programs) inside or outside of a respective MPA at each year data were available to construct size frequency distributions using as many individuals as possible. For each site and year, we randomly sampled (with replacement) from the respective MPA, status (i.e., inside vs outside), year, and species-specific size frequency distribution the total number of urchins observed on transect. Sea urchin sizes were transformed to biomass using test diameter-weight relationships [*M. franciscanus*: W = 0.00059 X TD^{2.917}; *S. purpuratus*: W = 0.00059 X TD^{2.870}, TD= test diameter in mm; (Reed et al. 2016)]. We calculated total biomass as the average of 1000 resampling iterations of estimated biomass based on size frequency distributions and density estimates for each site * year * species combination.

We focused on two important predators, the California spiny lobster, *Panulirus interruptus*, and the California sheephead, *Semicossyphus pulcher*. These predators are two of the most heavily fished species in the region and both prey upon sea urchin grazers and can therefore indirectly impact kelp biomass through their trophic interactions with grazing taxa. We obtained data on lobster size and abundance collected as a part of swath surveys and CA sheephead size and abundance from underwater visual belt surveys. Biomass of sheephead was calculated by using abundance and length-weight relationships [$W = 0.0144 \times TL^{3.04}$. TL = total length in cm; (Hamilton and Caselle 2015)] that transformed length into weight. The calculation of biomass for lobsters was only possible after 2011 for PISCO/VRG since length of individuals was not estimated prior to this time. When lobster length was not indicated on transect, we randomly sampled from size frequency data collected from other surveys at the same MPA, status, and year, similar to methods above for sea urchins. Biomass of lobsters was calculated by using abundance and length-weight relationships [$W = 0.00135 \times CL^{2.91}$, CL = carapace length in mm; (Reed et al. 2016)] that transformed length into weight. For specifics on methodological differences between programs see S1.

Similar to Landsat analyses, we averaged annual mean density or biomass across sites to obtain a single mean value inside the MPA (impact site), and a single mean value outside of the MPA (control site). All data were then converted to a proportion of maximum for a given MPA, source (i.e., impact, control), and taxa. This conversion allowed all datasets to range from 0-1 regardless of their initial units.

Site Selection

We only included sites where all taxa of interest were protected, that were surveyed within a year of MPA implementation, were also surveyed at least four subsequent years following implementation, and spanned a timeframe of at least ten years. These requirements for inclusion were chosen to be able to understand trends in the relationship between the effect of MPA implementation and time, since changes in trend are common in ecological time series but are not captured by comparing differences in averages [(i.e., BACI),]. Additionally, we did not consider Point Conception State Marine Reserve as our focal predators are not regularly

observed at this site due to cold temperatures. These criteria resulted in the removal of two MPAs (Anacapa Island State Marine Conservation Area, Painted Cave State Marine Conservation Area) which allow the recreational take of two of our focal species, lobster and/or finfish. Finally, we only considered sites within the Anacapa Island State Marine Reserve that were protected in 2005 as protection in other areas of the reserve began over 20 years earlier (1978) and were not surveyed inside and outside of the reserve until 2004 thus making it difficult to compare the effect of protection to the other MPAs in our network.

Statistical analysis

To evaluate whether protection increased the density or biomass of taxa of interest we calculated the difference in response between the proportional Control (outside MPA) and proportional Impact (inside MPA) estimates, as:

$$\ln RR_{i,t,s} = \ln(pI_{i,t,s} + a) - \ln(pC_{i,t,s} + a)$$

where pI represents the proportional response in the impact or control, pC , for a given year, i , of a given taxa, t , and given source, s , and a is a constant added to avoid taking the logarithm of zero and is equal to 0.01. Therefore, positive deltas correspond to higher biomass in the Impact site than the Control site.

For datasets where data was collected both before and after MPA implementation, we utilized a progressive change Before-After-Control-Impact approach [*pBACIPS*; (Thiault et al. 2017)]. We first tested for temporal trends in the data occurring before implementation using linear regression. All sites that showed significant linear trends were removed, since these trends indicate that the control and impact sites are deviating from each other before implementation and therefore may not be appropriate for comparing the effect of an intervention. Our approach differs from recent regional-scale analyses (e.g., Kumagai et al. 2024), which pooled control and impact sites across broad spatial mosaics to evaluate kelp resilience during marine heatwaves. By contrast, our paired BACIPS design explicitly matches each MPA to adjacent reference reefs, controlling for fine-scale environmental heterogeneity that can obscure causal attribution. This difference allows us to isolate the effect of MPA implementation per se, rather than resilience patterns emerging at broader regional scales. The best model was selected based on AICc. All models were checked for assumptions of autocorrelation, normality and homoscedasticity by

visual inspection of the residuals for autocorrelation (or Runs test for non-linear models) and visual inspection of the residuals for normality and Levene's test for homoscedasticity.

We then calculated effect size estimates for each taxa at each available MPA and across all available data sources based on the best fit model. If the best fit model was a “step-change” in response to protection we calculated an effect size (ES) as:

$$ES_{\text{step}} = \mu_{\Delta \text{After}} - \mu_{\Delta \text{Before}}$$

where μ_{Δ} is the mean log response ratio ($\ln RR$) of abundance or biomass *Before* and *After* MPA implementation. For step-change models, the ES is therefore similar to a standard BACI contrast. 95% confidence intervals were calculated for each ES from the pooled standard deviation between time points. However, if the best fit model included a temporal trend (i.e., linear, sigmoidal, asymptotic) then the response varied over time as a consequence of protection. Since the year of MPA implementation differs across our network, we extracted at time, t , equal to zero and at t equal to 11 years using emmeans in R. We chose these years since they correspond to before implementation ($t = 0$) and the age of our youngest MPA in 2023 (eleven years). This allowed us to control for differences in the effect size due to the duration of time since establishment. We extracted both the fitted value as well as the standard deviation around that measurement and calculated 95% confidence intervals from the pooled standard deviation. We calculated the ES as:

$$ES_{\text{trend}} = \ln RR_{Fit, t = 11} - \ln RR_{Fit, t = 0}$$

where $\ln RR_{Fit}$ corresponds to the model fitted abundance or biomass and t represents the year since implementation. All values of t in the *Before* period were set to zero for model fitting.

If insufficient data were collected prior to implementation (i.e., < 3 samples before implementation), then a simpler Control-Impact (CI) assessment was conducted. We assessed whether the log response ratio, $\ln RR$, changed over time since implementation by fitting linear, sigmoidal, and asymptotic models. If one or two data points existed prior to implementation, these data were set to time = 0 and were included in model fitting. We then calculated ES_{trend} of the best fit model using the same equation as for *pBACIPS* models mentioned above. In both *pBACIPS* and CI analyses, if sigmoidal and asymptotic models could not resolve these models

were removed from model selection consideration. For CI analyses, if the linear model was the best fit model, but there was not a significant linear trend, then ES was assumed to be equal to the mean and we calculated 95% confidence intervals around the mean. All models were run using *lm* in R.

To test for an effect of MPA implementation on species biomass/density, we fit multilevel meta-analysis models with restricted maximum-likelihood estimation (REML) using effect size estimates (ES) from *pBACIPS* and/or CI analyses for each taxa using the *rma.mv* function in the *metafor* package. Taxa was a fixed effect (moderator) in meta-analysis models with MPA as a random effect. We ran models separately for the responses of density and biomass since estimates were non-independent. Initially, models were fit using all data. We then assessed the influence of outliers using Cook's distance and removed influential outliers before rerunning analyses.

RESULTS

We obtained data on kelp, sea urchin, and/or predator biomass from a total of 19 MPAs spanning the coast of southern California from San Diego to Santa Barbara and at six islands in the Channel Islands National Marine Sanctuary. The density and/or biomass inside vs. outside MPAs differed greatly throughout time and across MPAs within our network (Fig. 1). Linear models were most likely to best explain the relationship between the difference in density/biomass, Δ , following implementation (Table S1), suggesting that the effect of implementation changes over time. We found that step-change models were the next most likely model to best explain the relationship between the difference in biomass, Δ , following implementation, suggesting that at these sites the effect of implementation was immediate (Table S1).

Predator biomass and density

Across our network, the magnitude and direction of the effect of implementation on predators, the spiny lobster (*P. interruptus*) and the California sheephead (*S. pulcher*) differed across MPAs (Fig. 3). We failed to detect a significant effect of MPA implementation on *P. interruptus* or *S. pulcher* biomass or density (Table 1; Fig. 4).

Herbivore density

The magnitude and direction of the effect of MPA implementation on sea urchin density also differed across MPAs (Fig. 3). We found a significant effect of MPA implementation on the densities of both purple, *S. purpuratus*, and red, *M. franciscanus*, sea urchins (Table 1). Sea urchin densities were higher outside of protected areas compared to adjacent references (Fig. 4). On average, densities were on average ~78% and 51% lower outside of MPAs for purple and red sea urchins respectively.

Giant kelp biomass and stipe density

The effect of MPA implementation on giant kelp also varied considerably across our network (Fig. 3). We found a significant effect of MPA implementation on giant kelp, with kelp an average of ~266% higher inside of protected areas compared to adjacent controls (Table 1, Fig. 4).

DISCUSSION

MPAs are a tool used globally to restore and enhance marine ecosystems. Yet, without rigorous replicated tests of the benefits we hope protection provides, scientists and managers can set unrealistic expectations for stakeholders and erode trust (CITE). Here, we focused on a large network of MPAs with one of the most comprehensive datasets available to better understand whether protection indirectly increased primary production within kelp forests by restoring/enhancing a trophic cascade. We show that protection can increase giant kelp, *M. pyrifera*, biomass (a proxy for primary productivity) within protected areas when compared to adjacent paired reference areas, though the magnitude and direction of the effect differs through time and across our study region. This result is consistent across scales and methodology (i.e., Landsat vs SCUBA diver-based surveys). Protection also led to decreases in the densities of purple sea urchins, *S. purpuratus*, which are common prey of lobster and sheephead and voracious grazer on giant kelp. However, we did not detect an increase in the density or biomass of key predatory species, the California spiny lobster, *P. interruptus*, or the California sheephead, *S. pulcher*. These results suggest that protection may improve ecosystem function, however, the mechanistic link is currently unclear. Our network-wide kelp gains and urchin declines are structurally consistent with a recovering cascade, and they dovetail with event-based evidence

that cascades preserved in fully protected MPAs enhance climate resilience of kelp during marine heatwaves in Southern California (Kumagai et al. 2024). Where we observe variable predator responses, Kumagai et al. documented higher lobster and sheepshead inside fully protected MPAs during and after the heatwaves, suggesting that body-size thresholds, MPA age, and climate context likely modulate when predator signals translate into kelp outcomes.

Long-term time series

Past studies on the effectiveness of MPA implementation have shown temporal lags in both direct and indirect effects. For instance, in some species, recruitment happens over decadal cycles and therefore may severely limit a species ability to recover from disturbance (Barrett et al. 2007). Even after abundances increase, it may take even longer for species to reach the large sizes needed to restore important ecological processes, such as predation. In our system, both lobsters and sheepshead must reach relatively large sizes to have sufficiently high predation on sea urchins to be ecologically relevant (Hamilton and Caselle 2015, Selden et al. 2017, DiFiore and Stier 2023). Consistent with time-dependence, network-scale analyses show urchin densities decline with MPA age and stabilize approximately 12 years post-establishment in Southern California (Kumagai et al. 2024), underscoring that cascade expression strengthens as protected predator cohorts mature. This is further complicated as the density of urchins needed to maintain a barren state is an order of magnitude smaller than the density of urchins needed to create a barren state, making reversal from urchin barren to kelp forest more difficult (Ling et al. 2015). Alternatively, if ecologically important prey species, such as sea urchins, reach large enough sizes to escape predation, then it may take even longer to restore ecosystem functioning as death by old age may be the only way for these systems to return to a baseline (Selden et al. 2017). For these reasons, long-term time series are necessary to detect the true effects of park implementation. In our study system, the effect of MPA implementation was generally linear, meaning that densities within MPAs increased (or decreased, depending on the taxa) over time. We did not find evidence of saturating responses in any of our taxa or time series, which suggests that these kelp forests are still changing in response to protection.

Restored trophic interactions

Although we were unable to directly link information on community structure to our historical dataset on kelp biomass, it's likely that species interactions across trophic levels are driving the patterns seen here. MPAs have been shown to restore trophic linkages by increasing the size and abundances of previously targeted predatory species (REFS). These increases in predators can lead to trophic cascades on coral reefs, however, their effects are more variable on macroalgal dominated reefs, like kelp forests. Gilby and Stevens (Gilby and Stevens 2014) failed to detect differences in macroalgal cover and sea urchin densities between marine protected areas and adjacent reference areas in marine vegetated habitats. Cheng et al. (2019) found that predation risk increased inside parks, but that grazing pressure did not change, suggesting that functional redundancy in the grazer guild may buffer the impacts of increased predation. This work suggests that it may be difficult to detect the indirect effects of protecting targeted species within kelp forests. Nonetheless, direct and indirect links expected of a cascade have been demonstrated at scale: in Southern California, urchins decrease with increasing lobster and sheepshead, kelp is negatively related to urchins, and positively related to lobster, with the strongest indirect kelp benefit emerging via lobster (Kumagai et al. 2024). Our paired design complements this by showing that, outside the confines of a single climate shock, MPA implementation is associated with lower urchin densities and higher kelp biomass relative to adjacent reference reefs. For instance, Hamilton and Caselle (2015) found that nine years after implementation CA sheepshead biomass had increased inside MPAs in the Channel Islands, but that differences in kelp and sea urchins were context dependent. Malakhoff and Miller (2021) found that red urchin densities increased inside of reserves, where they were protected from fishing, but purple urchin densities did not differ between protected and unprotected areas in the northern Channel Islands (a subset of our study region). We found that as purple sea urchin densities decreased within protected areas compared to paired references, kelp biomass increased, though substantial site to site variability exists. However, we did not detect an effect of protection on predators.

Management Implications

Recent declines in canopy forming kelps have led to kelp restoration efforts along the coast of California. Many of these efforts have focused on removing sea urchin grazers and/or seeding kelp on reefs. However, the reestablishment of important trophic interactions may improve restoration efforts, though the effects are context dependent (Heineke et al. 2023). Not

surprisingly, this suggests that ongoing restoration efforts may be most effective inside park boundaries where the potential for intact trophic cascades is more likely.

Conclusion

Our study suggests that by limiting the extraction of marine resources, kelp forest ecosystems have the potential to be more productive. Given that kelp productivity plays an important role in increasing biodiversity, it appears that marine protection could be key to maintaining healthy functioning kelp forest ecosystems. As anthropogenic stressors continue to threaten coastal ecosystems and the communities that rely on them, strategies, such as park designation, will be critical tools for marine management.

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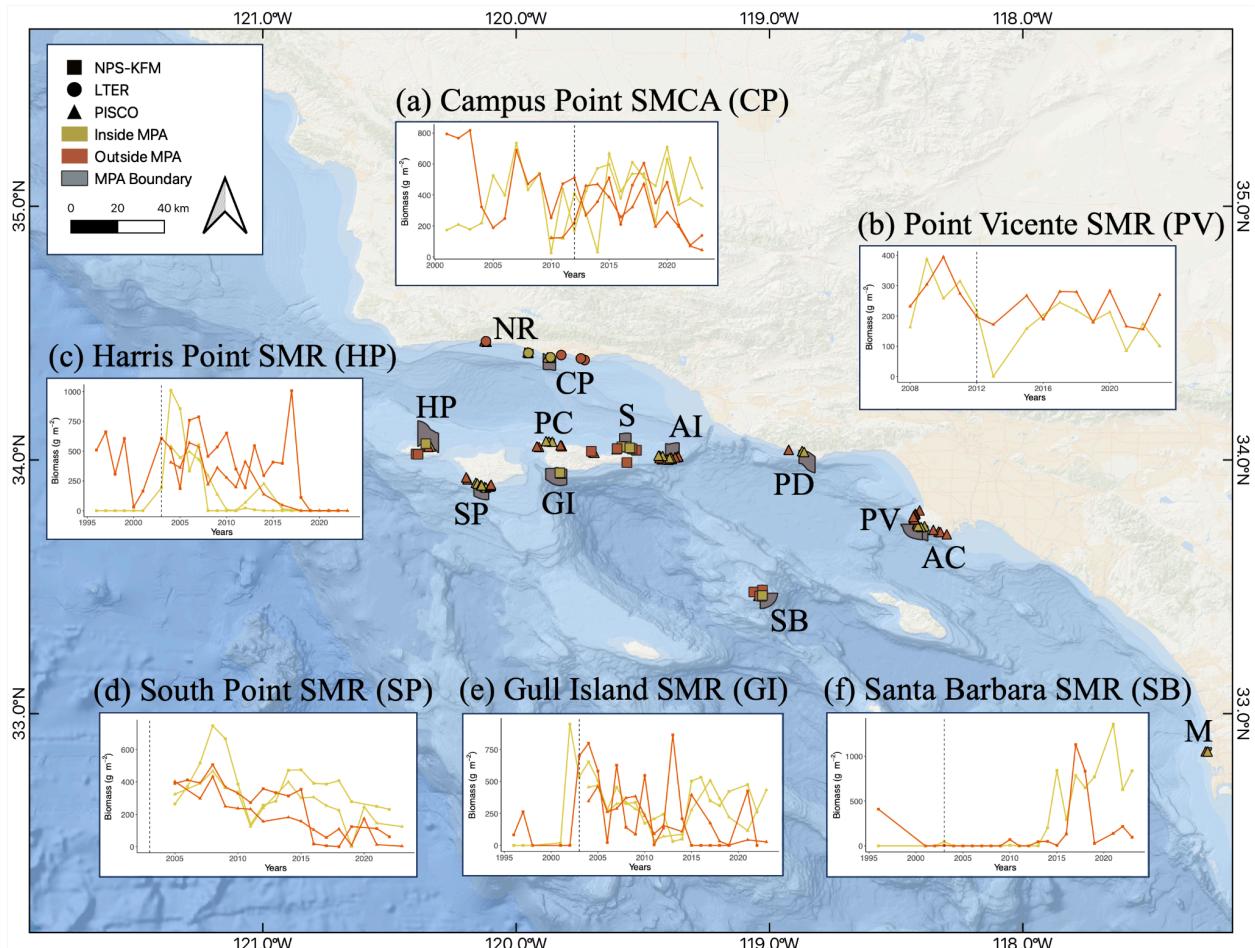


Figure 1. Map shows MPA locations (grey) where NPS KFM (square), LTER (circle), and PISCO (triangle) diver data were collected. Time series show biomass of giant kelp, *M. pyrifera*, at MPA (yellow) and reference (orange) sites at select mainland and channel island locations. Panels show *M. pyrifera* densities at (a) Campus Point SMCA, (b) Point Vicente SMR, (c) Harris Point SMR, (d) South Point SMR, (e) Gull Island SMR, (f) Santa Barbara SMR.

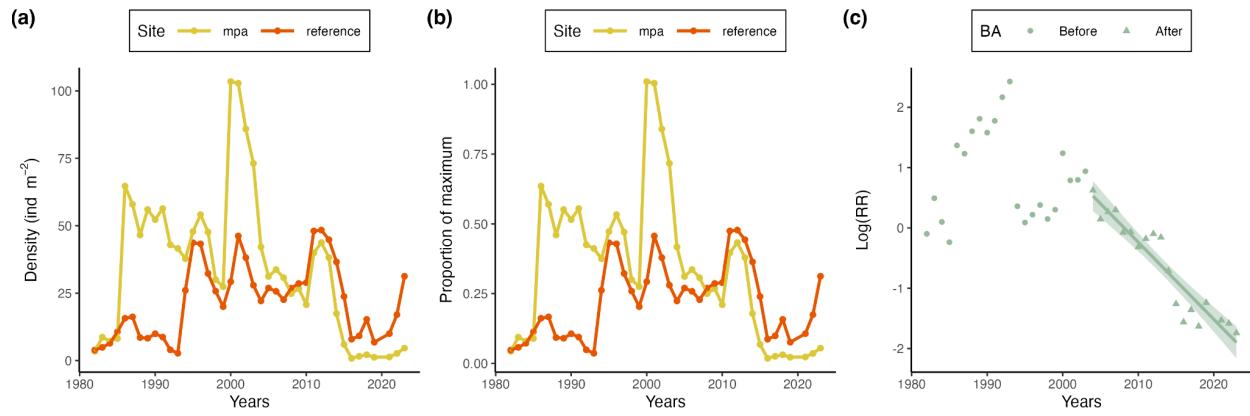


Figure 2. Steps of processing data sets to test for the effects of MPA implementation. First, mean annual density (or biomass) are calculated for each MPA and data source separately (a); next data are transformed to the proportion of maximum (b), finally the difference between MPA and reference data sets are calculated (log response ratio) and models fit to these data (c). Yellow indicates site located within MPA boundary, red indicates paired site outside MPA boundary, green indicates logRR for density, while circles indicate data collected prior to MPA implementation and triangles indicate data collected after MPA implementation.

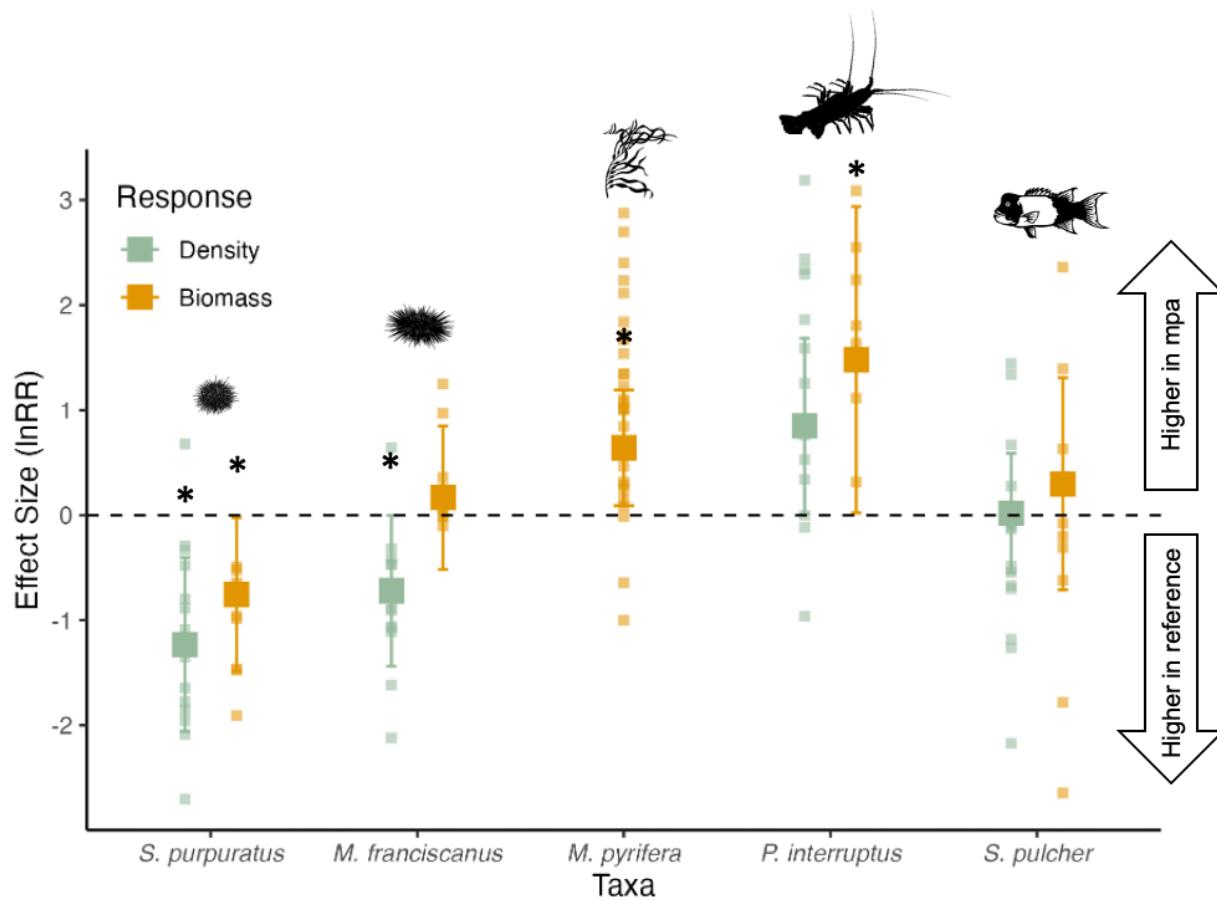


Figure 3. The mean effect of protection on purple sea urchins, *S. purpuratus*, red sea urchin, *M. franciscanus*, giant kelp, *M. pyrifera*, spiny lobster, *P. interruptus*, and sheephead *S. pulcher*. Large squares represent modeled estimates of mean effect sizes and 95% confidence intervals, while small squares represent effect size estimates for each individual MPA*source. Green represents estimates for density, orange represents estimates for biomass. The zero line indicates no effect of protection and stars indicate statistical significance at $p < 0.05$.

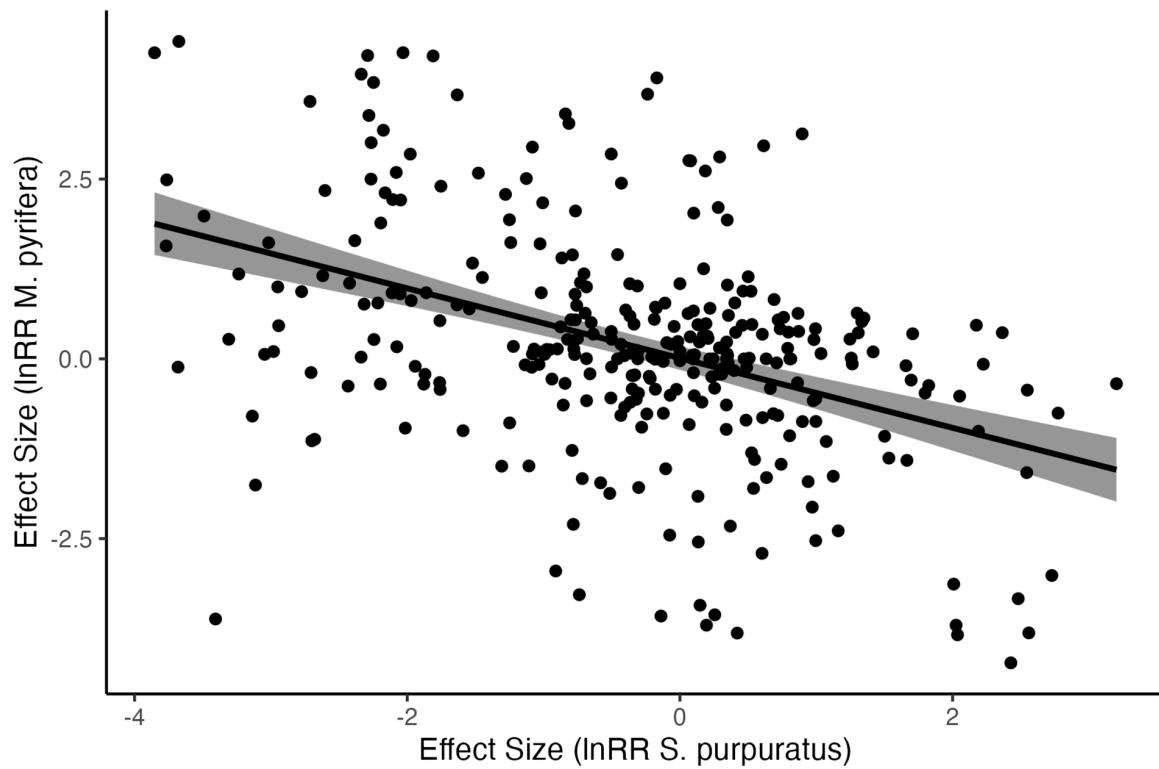


Figure 4. Relationship between log response ratio (lnRR) between paired MPA and reference densities of purple sea urchins, *S. purpuratus*, and density of kelp, *M. pyrifera*, stipes. Each data point represents a single year, MPA, and data source.

Table 1. Average density and biomass of taxa across different survey techniques.

Taxa	Source	Density (stipe or ind m ⁻²)	Biomass (g m ⁻²)
<i>Macrocystis pyrifera</i>	KFM	2.733 ± 0.377	252.816 ± 34.911

<i>Macrocystis pyrifera</i>	LTER	4.181 ± 0.265	386.864 ± 24.477
<i>Macrocystis pyrifera</i>	PISCO	2.296 ± 0.102	212.488 ± 9.455
<i>Mesocentrotus franciscanus</i>	KFM	4.357 ± 0.220	384.146 ± 27.404
<i>Mesocentrotus franciscanus</i>	LTER	0.397 ± 0.055	51.192 ± 10.443
<i>Mesocentrotus franciscanus</i>	PISCO	1.933 ± 0.124	288.566 ± 24.113
<i>Strongylocentrotus purpuratus</i>	KFM	23.765 ± 1.420	178.601 ± 10.987
<i>Strongylocentrotus purpuratus</i>	LTER	2.308 ± 0.272	41.011 ± 4.107
<i>Strongylocentrotus purpuratus</i>	PISCO	5.225 ± 0.367	83.881 ± 6.422
<i>Panulirus interruptus</i>	KFM	0.008 ± 0.001	-
<i>Panulirus interruptus</i>	LTER	0.024 ± 0.004	10.093 ± 1.496
<i>Panulirus interruptus</i>	PISCO	0.013 ± 0.001	8.494 ± 1.157
<i>Semicossyphus pulcher</i>	KFM	0.012 ± 0.001	-
<i>Semicossyphus pulcher</i>	LTER	0.014 ± 0.002	8.142 ± 1.723
<i>Semicossyphus pulcher</i>	PISCO	0.028 ± 0.001	13.541 ± 0.775

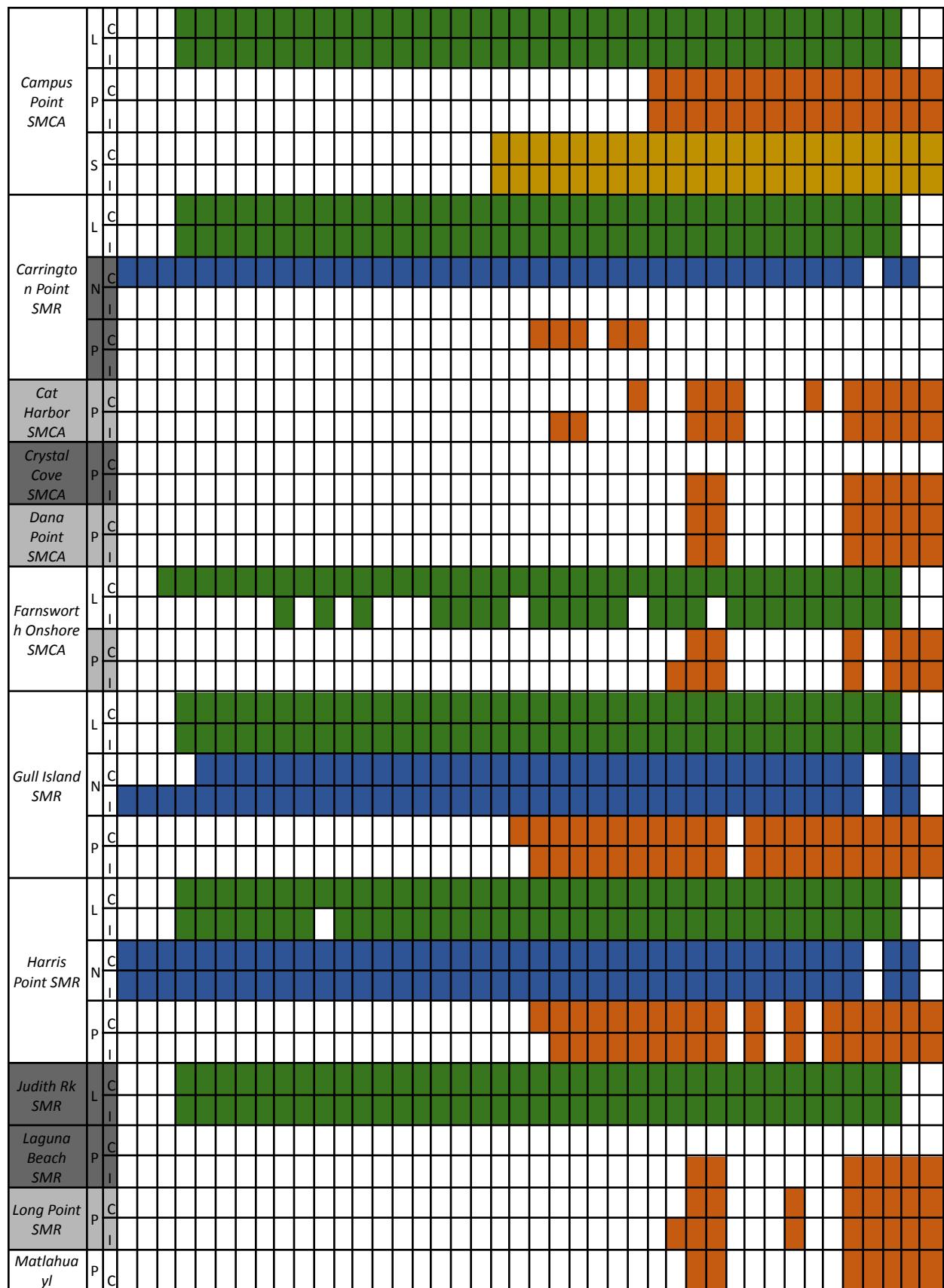
Table 2. Summary statistics from models of the effects of MPA implementation on key taxa within kelp forests. Taxa with significant p-values ($p < 0.05$) indicated in bold.

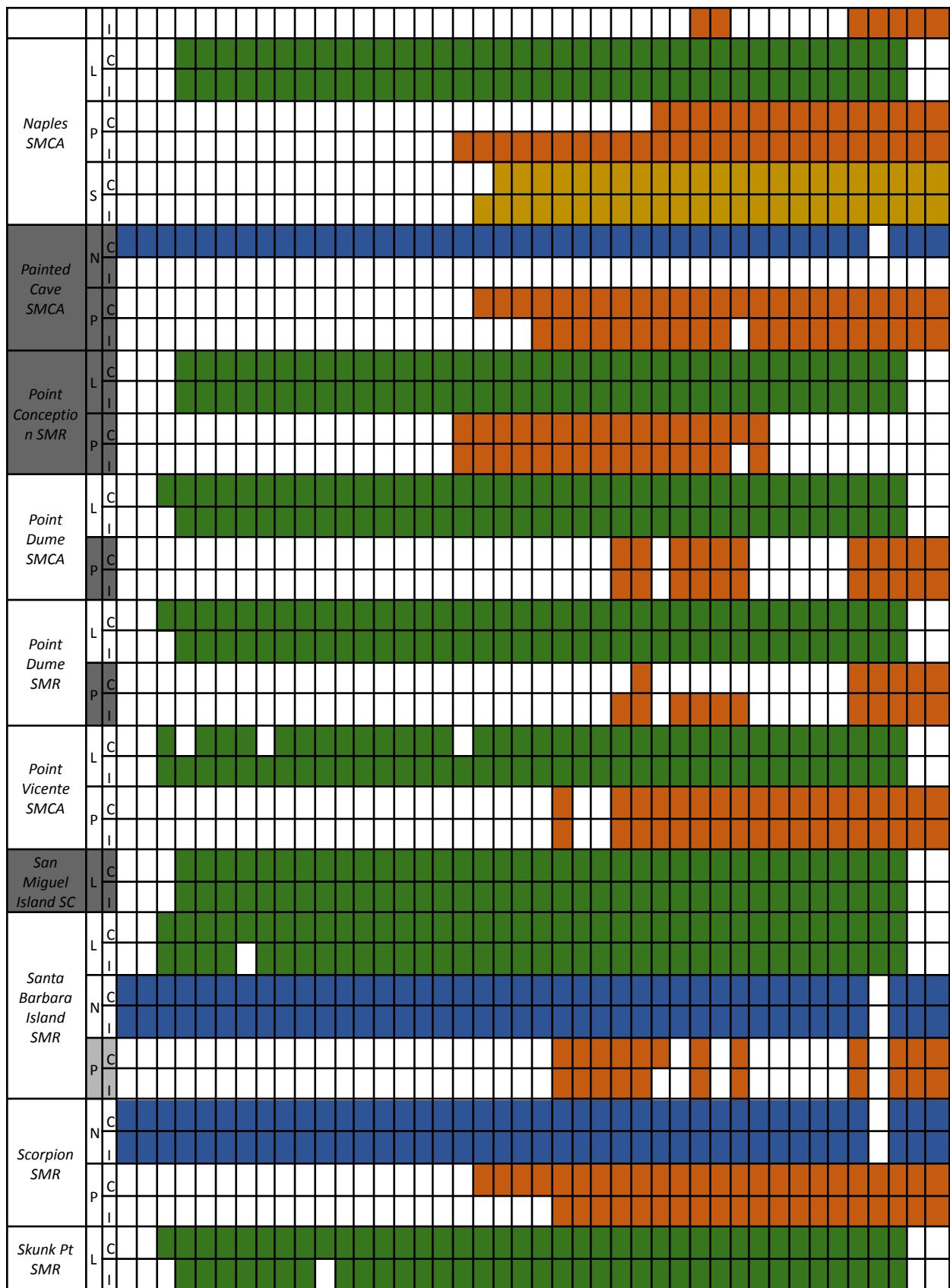
Response	Taxa	estimate	SE	t-value	p-value	CI _{lower}	CI _{upper}
Biomass	<i>S. purpuratus</i>	-0.7561	0.3641	-2.0767	0.0423	-1.4849	-0.0273
	<i>M. franciscanus</i>	0.1673	0.3410	0.4906	0.6256	-0.5153	0.8499
	<i>M. pyrifera</i>	0.6190	0.2742	2.2573	0.0278	0.0701	1.1679
	<i>P. interruptus</i>	1.4789	0.7287	2.0295	0.0470	0.0203	2.9375
	<i>S. pulcher</i>	0.2977	0.5045	0.5900	0.5575	-0.7123	1.3076
Density	<i>S. purpuratus</i>	-1.2337	0.4132	-2.9858	0.0043	-2.0625	-0.4050
	<i>M. franciscanus</i>	-0.7200	0.3573	-2.0153	0.0490	-1.4365	-0.0034
	<i>P. interruptus</i>	0.8490	0.4164	2.0389	0.0465	0.0138	1.6842
	<i>S. pulcher</i>	0.0194	0.2836	0.0682	0.9458	-0.5495	0.5882

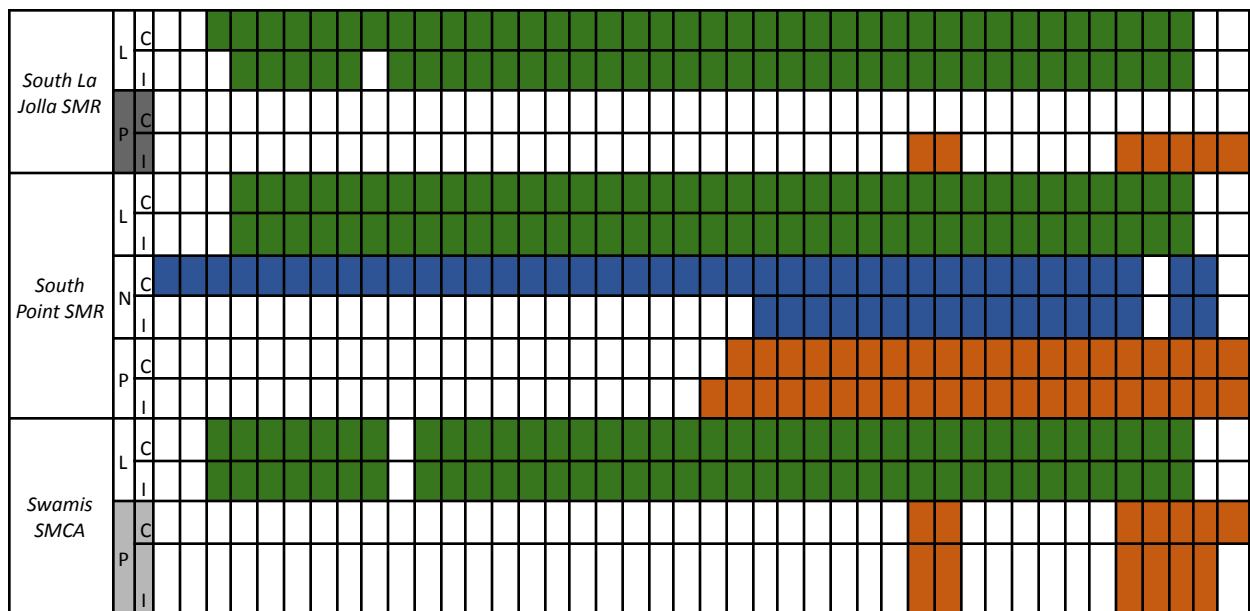
Table 3. Results of linear models between taxa. Significance at $p < 0.05$ noted in bold.

Supplemental Descriptions of PISCO, KFM, LTER, and Landsat datasets

Table S1. Data availability by year and site (protected area) classification (status = Control (C) or Impact (I)) for all datasets (Source: L = Landsat, P = PISCO/VRG, N = NPS, S = SBC-LTER). Dark grey sites indicate that this site did not meet criteria for inclusion. Light grey sites indicate that only *S. pulcher* met the criteria for inclusion. *For PISCO data, biomass of urchins were not included in analyses at Matlahuayl SMR since size frequency data were unavailable in 2011 and 2012 and biomass of lobsters at Anacapa Island SMR, Gull Island SMR, Harris Point SMR, South Point SMR, and Scorpion SMR were not included in analyses since size data were unavailable prior to 2010 and therefore did not meet criteria for inclusion.







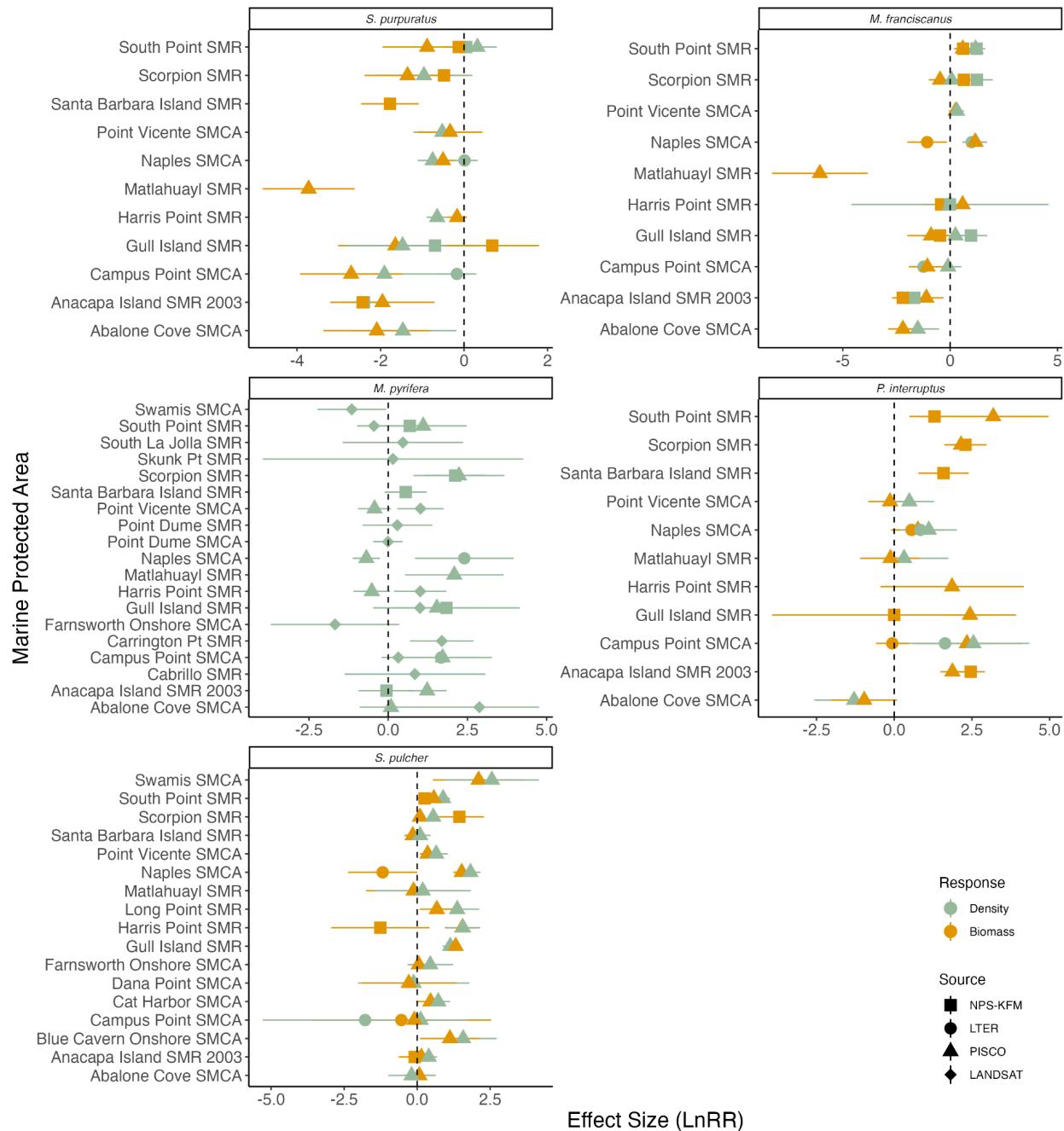


Figure S1. Effect of protection on key taxa across network of MPAs. Symbols indicate which monitoring program the data are from, while colors represent the response metric [either density (green) or biomass (orange)]. Effect size estimates were calculated based on the best fit model from progressive change BACIPs analysis (where before and after data were available) or linear models for CI analysis (where only after data exist).