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Marine Protected Areas That Preserve Trophic Cascades Promote Resilience of Kelp Forests to Marine Heatwaves

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ABSTRACT

Under accelerating threats from climate-change impacts, marine protected areas (MPAs) have been proposed as climate-adaptation tools to enhance the resilience of marine ecosystems. Yet, debate persists as to whether and how MPAs may promote resilience to climate shocks. Here, we use 38 years of satellite-derived kelp cover to empirically test whether a network of 58 temperate coastal MPAs in Central and Southern California enhances the resistance of kelp forest ecosystems to, and their recovery from, the unprecedented 2014–2016 marine heatwave regime that occurred in the region. We also leverage a 22-year time series of subtidal community surveys to mechanistically understand whether trophic cascades explain emergent patterns in kelp forest resilience within MPAs. We find that fully protected MPAs significantly enhance kelp forests' resistance to and recovery from marine heatwaves in Southern California, but not in Central California. Differences in regional responses to the heatwaves are partly explained by three-level trophic interactions comprising kelp, urchins, and predators of urchins. Urchin densities in Southern California MPAs are lower within fully protected MPAs during and after the heatwave, while the abundances of their main predators—lobster and sheephead—are higher. In Central California, a region without lobster or sheephead, there is no significant difference in urchin or kelp densities within MPAs as the current urchin predator, the sea otter, is protected statewide. Our analyses show that fully protected MPAs can be effective climate-adaptation tools, but their ability to enhance resilience to extreme climate events depends upon region-specific environmental and trophic interactions. As nations progress to protect 30% of the oceans by 2030, scientists and managers should consider whether protection will increase resilience to climate-change impacts given their local ecological contexts, and what additional measures may be needed.

1 | Introduction

Marine protected areas (MPAs) are an essential conservation tool whose coverage has globally expanded in the past decades (Duarte et al. 2020; Lubchenco and Grorud-Colvert 2015). Their importance is reflected in recent international policies aiming to protect 30% of coastal and open oceans, as specified within Target 3 of the Kunming-Montreal Global Biodiversity Framework (Convention of Biological Diversity 2022). Following mounting evidence of increasing impacts of climate change on marine ecosystems (Schoeman, Bolin, and Cooley 2023), the new conservation framework includes climate mitigation and adaptation in Target 8 (Convention of Biological Diversity 2022). The assumption underlying this framework is that protected areas may enhance climate adaptation and ecosystem resilience. While some empirical evidence supporting this expectation exists for individual MPAs and species (Jacquemont et al. 2022), clear empirical evidence at regional scales and for whole ecosystems is lacking. There is strong consensus that well-managed and fully protected (i.e., no-take) MPAs promote biodiversity and habitat conservation (Gill et al. 2017; Lester et al. 2009; Sala and Giakoumi 2018), but the extent to which MPAs confer ecological resilience to climate change impacts remains poorly understood.

One prominent manifestation of anthropogenic climate change is the increase in the frequency and intensity of extreme climate shocks, in particular marine heatwaves (MHWs) (Oliver et al. 2018). MHWs have caused mass mortality of sessile or low-mobility species (Garrabou et al. 2022; Szuwalski et al. 2023), losses of habitat-forming species such as corals and kelp, and regime shifts, among other impacts (Arafeh-Dalmau et al. 2019; McPherson et al. 2021; Smale et al. 2019; Wernberg 2021). For example, MHWs in Australia and in the northeast Pacific Ocean have caused extensive losses of kelp over large areas and a shift into alternative stable ecosystem states dominated by less-productive algae or by sea urchin “barrens,” that have resulted in large-scale economic losses (Rogers-Bennett and Catton 2019; Wernberg 2021). Given that MHWs are becoming more frequent and longer (Oliver et al. 2018), it is a research priority to understand whether and how MPAs might increase resilience to their impacts.

Whether MPAs provide resilience to ecosystems experiencing climate shocks is debated and challenging to study (White et al. 2025). The operational definition for resilience used here is resistance to and recovery from disturbance (Connell and Sousa 1983), although resilience is a multifaceted concept (O'Leary et al. 2017). MPAs are designed to provide protection from local anthropogenic disturbance, primarily from extractive activities. They cannot directly mitigate the broad-scale impacts of climate shocks (Filbee-Dexter et al. 2024; Tittensor et al. 2019). However, by reducing extractive activities such as fishing, MPAs may allow the recovery of key species for ecosystem functioning, which in turn can promote resilience to climate shocks (Benedetti-Cecchi et al. 2024; Jacquemont et al. 2022; Roberts et al. 2017; Sala and Giakoumi 2018; Schindler, Armstrong, and Reed 2015). The empirical evidence surrounding this argument is still emerging and mixed. Some studies have found no evidence that MPAs confer resilience to climate impacts (Bruno, Côté, and Toth 2018; Freedman et al. 2020; Smith et al. 2023). On the other hand, other studies have shown increased resilience to climate change in MPAs: for instance, in Baja California, Mexico, juvenile recruitment and adult abundance of pink and green abalone recovered faster within MPAs following a mass mortality of benthic invertebrates due to climate-driven hypoxia and warming (Micheli et al. 2012; Smith et al. 2022). In California, USA, species diversity recovered 75% faster from a series of MHWs within MPAs compared to adjacent unprotected areas (Ziegler et al. 2023). Additionally, a recent global analysis found that well-enforced MPAs can buffer the impacts of MHWs on reef fish by promoting the stability of fish at the community and metacommunity levels (Benedetti-Cecchi et al. 2024). Ultimately, a clear understanding of the conditions under which MPAs can provide climate resilience for whole ecosystems, including habitat-forming species and their associated communities, remains limited, due to the challenge of detecting resilience within MPAs.

One key challenge with detecting resilience emerges from the scarcity of long-term, sufficiently replicated and spatially extensive data needed to characterize the state of the marine systems within and outside MPAs, before, during, and after climate extremes occur. MPAs must also be sufficiently large and be in place for a sufficient duration for any benefits of protection to emerge (Claudet et al. 2008). With a general paucity of studies with the necessary experimental design and statistical power, it is challenging to characterize the natural temporal variability and the inherent spatial heterogeneities of marine environments to achieve consensus on whether and under what circumstances MPAs might increase resilience to climate change impacts.

Here we overcome these challenges by utilizing long-term datasets to evaluate whether MPAs can promote kelp forest resilience to an unprecedented series of MHWs in California. During 2014–2016, the California coast was subjected to one of the largest and longest MHW regimes ever documented on Earth, with consistent mean temperature anomalies of 1°C–4°C (Cavole et al. 2016; Di Lorenzo and Mantua 2016; Frölicher and Laufkötter 2018), providing a unique opportunity to investigate the dynamics of MPAs and ecosystem resilience. The combination of the 2014 warm-water anomaly and the 2015–2016 El Niño Southern Oscillation led to extremely warm waters (Cavole et al. 2016; Frölicher, Fischer, and Gruber 2018) that caused species range shifts (Favoretto, Sánchez, and Aburto-Oropeza 2022; Sanford et al. 2019; Smith et al. 2023), a widespread loss of kelp forests from Northern California to Baja California Sur, Mexico (Bell et al. 2023), and an outbreak of sea urchins that eroded kelp forest resilience (Rogers-Bennett and Catton 2019). Additionally, California has a network of MPAs that cover 16% of state waters (Saarman and Carr 2013), decades of satellite-derived estimates of kelp cover (Bell et al. 2023), and underwater surveys of kelp forest communities (Malone et al. 2022). With the rich ecological monitoring data that exist in this ecosystem, we can evaluate for the first time the resilience of kelp forest ecosystems to MHWs within MPAs at a regional scale and the underlying mechanisms that facilitate this resilience.

Trophic cascades are one of the proposed mechanisms by which MPAs can provide climate resilience. It has been hypothesized that, by protecting key predators of sea urchins (a voracious grazer of kelp) MPAs may indirectly control sea urchin abundance, thus increasing both kelp resistance to, and recovery from, MHWs (Ripple et al. 2016). Outside MPAs, where fishers target urchin predators, there are fewer predators and more urchins (Eisaguirre et al. 2020). When a disturbance leads to severe kelp loss, urchins can shift their behavior from hiding in protective cracks and eating drift kelp to being exposed, eating any remaining kelp and preventing kelp establishment (Harrold and Reed 1985; Kriegisch et al. 2019). Overharvesting and depletion of urchin predators can then lead to a high abundance of urchins that overgraze kelp forests (Cowen 1983). If MPAs protect and foster greater abundances of urchin predators (which otherwise would be commonly fished), then protected kelp forests may be more likely to recover and even resist change in the face of a disturbance, compared to unprotected kelp forests.

In this study we investigated the recovery of the giant kelp (*Macrocystis pyrifera*) and bull kelp (*Nereocystis luetkeana*), henceforth "kelp," following the 2014–2016 MHWs in Central and Southern California. The main objectives were to determine (1) whether kelp forests within a network of MPAs were more resilient to the 2014–2016 MHWs compared to unprotected kelp forests, (2) whether resilience of kelp forests differed between regions, and (3) whether there is evidence that trophic cascades are a mechanism underlying resilience to climate shocks. To address these questions, we assessed changes in kelp area during and after the 2014–2016 MHW using satellite-derived estimates of kelp area spanning 1984–2021 and analyzed 22 years of subtidal monitoring datasets to investigate possible evidence for trophic cascades. We tested the following hypotheses: (i) kelp resistance and recovery are higher within fully protected and partially protected MPAs compared to unprotected areas in both Central and Southern California during and after the MHWs; (ii) urchin abundances are lower within MPAs compared to unprotected areas during and after the MHWs, enabling the recovery of kelp forests; and (iii) abundances of giant kelp, urchins, and urchin predators are inversely related, as predicted by the trophic cascade hypothesis.

2 | Materials and Methods

2.1 | Study Area

This study spans Central and Southern California as defined by the Marine Life Protection Act (2013), encompassing the region where giant kelp is the dominant surface canopy-forming kelp species in the USA, from the US Mexico border (~32.5°N) to Pigeon Point, California (~37.2°N), and bull kelp becomes increasingly present north of Point Conception (Figure 1). Central and Southern California are separated into two different biogeographic regions at Point Conception (~34.5°N), which is a transition zone between the cooler temperate ecosystems of Central California and the warmer ecosystems of Southern California (Murray, Littler, and Abott 1980). In Southern California, the primary predators of sea urchins include the California sheephead (*Semicossyphus pulcher*) and spiny lobsters (*Panulirus interruptus*), while in Central California, sea otters (*Enhydra lutris*) and sunflower sea stars (*Pycnopodia helianthoides*) are

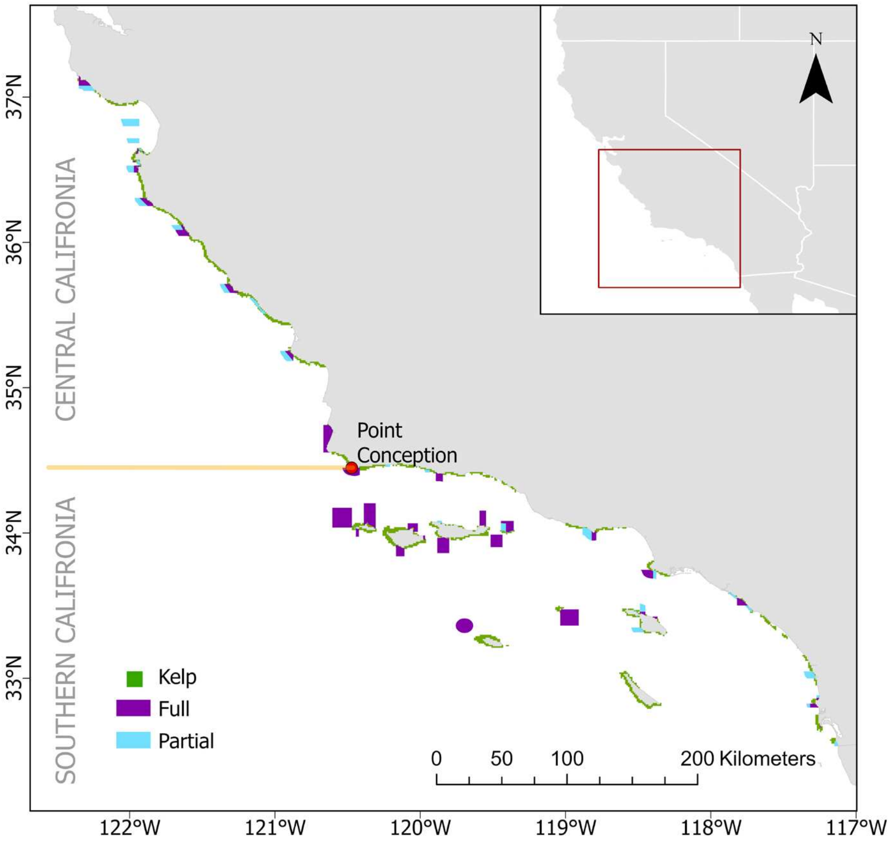

FIGURE 1 | The study area with the distribution of giant kelp and the network of MPAs in Central and Southern California. The yellow horizontal line at 34.4°N represents the biogeographic barrier at Point Conception, where Central California is separated from Southern California. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

the primary predators of urchins—although sunflower sea stars are functionally extirpated in California due to a mass mortality event starting in 2013 (Burt et al. 2018; Eisaguirre et al. 2020). As such, sea otters, which are protected statewide, are currently the sole top predator of urchins within Central California and are known to be a primary driver for changes in kelp (Eisaguirre et al. 2020; Nicholson et al. 2024). California sheephead and spiny lobsters, which are both fished, fill this role of predation in Southern California (Eisaguirre et al. 2020). The range of purple (*Strongylocentrotus purpuratus*) and red urchins (*Mesocentrotus franciscanus*) both span from Alaska to Baja California.

2.2 | Quantifying the Resilience of Kelp Forests to MHWs

We used 38 years (1984–2021) of estimates of kelp area based on remote sensing from the Santa Barbara Coastal LTER time series dataset (Bell 2023) to estimate the resilience of kelp forests. The dataset contains quarterly estimates of kelp canopy area in m^2 (referred to as kelp area from now on) from three Landsat sensors: Landsat 5 Thematic Mapper (1984–2011), Landsat 7 Enhanced Thematic Mapper+ (1999–present), and Landsat 8 Operational Land Imager (2013–present). Each Landsat sensor has 30-m resolution and does not distinguish between giant and bull kelp. We aggregated the original dataset to 1-km resolution to reduce spatial autocorrelation in the data by summing the kelp area in the native 30-m pixels. We followed previous approaches for cleaning the Landsat data (Bell et al. 2023) and excluded those quarters of a year that had no data for more than 25% of the 30-m pixels. We also removed from our dataset 1-km pixels that consisted of fewer than five 30-m pixels. Next, we removed 1-km pixels for which more than two quarters of kelp area were missing in a given year. Finally, the quarterly 1-km data were aggregated to a yearly scale by taking the maximum quarterly kelp area for each year, as a preliminary data analysis did not show a consistent quarter with maximum kelp forest cover. Our final dataset thus uses the maximum annual kelp area per 1-km^2.

Conceptually we define resistance as the ability of the major habitat-forming taxa (kelp) to persist during the MHWs. We define recovery as the ability of the major habitat-forming taxa to recover coverage to baseline levels within 5 years following the MHWs. To develop a metric of kelp resistance to and recovery from the 2014–2016 MHWs, we calculated the relative change in kelp area. For each 1-km^2 pixel, we first determined the long-term historic baseline of kelp coverage, defined as the average kelp area across the 30 years (1984–2013) before the 2014–2016 MHWs. Next, we calculated the ratio of each subsequent year's (2014–2021) kelp area relative to that baseline. We measured resistance (i.e., during the MHW) as the average percentage of kelp forests per pixel ($1\,\text{km}^2$) in 2014–2016 relative to the pre-2014, historic baseline mean. Similarly, we measured recovery (i.e., after the MHW) as the average percentage of kelp forests per pixel in 2017–2021, relative to the historic baseline mean. Accordingly, values close to 100% represented stable kelp cover with respect to the average kelp forest cover during the 1984–2013 baseline; values $<100\%$ represented kelp decline with respect to the pre-MHW baseline, and values $>100\%$ represented expansion of kelp coverage with respect to the historical baseline.

2.3 | Evaluating the Resilience of Kelp Forests Within MPAs Using Landsat Data

2.3.1 | The MPA Dataset

We downloaded the spatial layers, age, and level of fishing restriction for California's MPAs from NOAA's MPAs Inventory (Office of National Marine Sanctuaries 2024). We removed all MPAs that were national sanctuaries, national parks, or primarily estuarine. All MPAs which did not contain kelp were also removed. The final dataset includes 58 MPAs, 19 in Central California and 39 in Southern California. All MPAs were categorized as fully protected or partially protected. Fully protected MPAs do not allow any extractive activities, including the removal of urchins, California sheephead, lobster, or kelp, while partially protected MPAs allow some form of fishing for at least one of these species of interest. Detailed methods can be found in the Data S1, Section 1 along with a list of the MPAs used (Data S2).

Next, we overlaid the MPA layer on the 1-km^2 resolution kelp layer resulting in 53 of the total 58 MPAs being used for this analysis. This procedure allowed us to categorize the level of protection of each pixel as (i) unprotected, (ii) partially protected, or (iii) fully protected. We then classified the MPAs into two age categories based on their year of implementation. Previous studies have found that MPA age is correlated with increased fish biomass (Claudet et al. 2008; Micheli et al. 2004; Ziegler et al. 2023), so we classified MPAs established before 2007 as "old" and those established between 2007 and 2012 as "new." We chose 2007 as the cutoff between new and old MPAs because this was the first year that regulations under the Marine Life Protection Act were implemented in California, specifically Central California.

We also considered that if MPAs are more likely to have been placed in highly productive habitat or those with otherwise distinct human or environmental impacts, apparent differences in kelp resilience or recovery inside MPAs may not be attributable to protection status itself. Therefore, we compiled additional variables for each pixel including depth, surface nitrate, wave height, metrics of thermal history, and an index of human exposure (Table S1). We used a principal components analysis to visually assess whether there were differences in these variables among site types both before, during, and after the MHWs (Figure S1, Data Section 2).

2.3.2 | Permutation Analysis

We used a one-tailed permutation analysis to test whether the differences in resistance and recovery of kelp area during and after the 2014–2016 MHWs were affected by protection status that is, fully protected versus partially protected versus unprotected areas. As there are known latitudinal differences in water temperature, in oceanographic regimes, and in other drivers of kelp coverage, we repeated the analysis for Southern and Central California separately. Given the high year-to-year variability in kelp cover, we used a permutation test because it is nonparametric (Figure S3). Specifically, we tested the following hypotheses: (i) relative kelp area during and after the MHWs within fully protected MPAs is higher than relative kelp area within partially protected MPAs or unprotected areas, and (ii) relative kelp area during and after the MHWs within partially protected MPAs is higher than that in unprotected areas.

For each region, we first computed the observed differences in the medians of the relative kelp area during the response period (2014–2016) and in the recovery period (2017–2021) for each category (i.e., fully protected vs. unprotected; partially protected vs. unprotected, fully protected vs. partially protected). Next, to derive the null distribution, we randomly shuffled each pixel to one of the three protection categories and computed the differences in the median values among the three categories of the randomized set. These values were saved and then the same calculation was replicated 10,000 times, each time randomly shuffling the protection categories. The respective null distributions of the difference in the median values among the three categories were derived by using the 10,000 randomized replicates, and a one-sided pseudo p-value was calculated as 1 less than the percentile of the observed value under the corresponding null distribution. Since we generated multiple p-values for each hypothesis, we applied Bonferroni's correction, multiplying p-values by the number of comparisons undertaken (six). This analysis was implemented first across the entire study area and then repeated for each region individually. We also explored the effect of the age of MPAs on our results, repeating the permutation analyses for both old (established before 2007) and new (established between 2007 and 2012) MPAs separately.

The distribution of relative kelp area was highly right skewed with most pixels having kelp coverage after the MHW equal to, or lower than, corresponding coverage before MHW. However, in some pixels, the relative differences in the median coverage during and after MHW with respect to the historical baseline exceeded 100% by several orders of magnitude. These substantial changes in kelp reflect the fact that some areas that contained very little kelp historically experienced a large increase in kelp area during 2014–2021. To test the impact of pixels with very small pre-MHW kelp forest area on the results of the permutation analysis, we conducted a sensitivity analysis that involved removing pixels with the lowest 5%–30% of mean historic kelp area from the analysis in increments of 5% (Table S8) and then re-running the permutation analysis.

2.4 | Mechanism of Resilience: Trophic Cascades

2.4.1 | Processing of Subtidal Dataset

To investigate whether species interactions—sea urchin grazing and trophic cascades—may be a mechanism driving differences in kelp recovery between protected and unprotected areas, we used subtidal surveys of kelp forest communities that include giant kelp, urchins, and their main predators from the Monitoring and Evaluation of Kelp Forest Ecosystems in the MLPA Marine Protected Area Network long-term dataset, referred to as the “MLPA dataset” for this paper (Carr et al. 2024; Malone et al. 2022). We spatially joined the master MLPA master sites dataset within our study area with the MPA layer to produce a layer with the sites, protection status, and region, depicted in Figure S2 (additional methods in Data S1, Section 1). The MLPA data overlapped with 45 of the 58 MPAs included in our study. Next, we developed a dataset of all the unique transects where divers surveyed our species of interest for both the fish and benthic invertebrate (swath) surveys. We filtered the MLPA data from 2002 to 2023. We chose 5 years after the strong 1997–1998 El Niño as the start year to ensure any effects on kelp ecosystems from the El Niño, including sheephead recruitment, had mostly dissipated. We terminated the series in 2023 because this was the last year of available data. Additionally, we focused on adult organisms and did not include urchin recruits and California sheephead that were <15 cm in total length, as these are not large enough to eat adult urchins (Hamilton and Caselle 2015).

For the fish surveys, we calculated the number and biomass of sheephead recorded on each bottom-level transect and joined these data to the dataset of all unique fish transects. For the invertebrate surveys, we calculated the total number of urchins (summing red and purple urchins), individual adult (height >1 m) canopy-forming kelp (*Macrocystis pyrifera* and *Nereocystis luetkeana*), and spiny lobsters recorded on each transect, and again joined these data to the dataset of all unique swath transects. Because searches were performed for all species of interest, a value of zero was assumed wherever one of the species was not reported. We estimated California sheephead biomass using length-weight equation for California sheephead $b = 0.0144^* \, l^{3.04}$, where b is the biomass in g and l is the total length in cm (Hamilton and Caselle 2015). Next, we summarized these data to average annual densities per transect per site, joined the fish and invertebrate data together, and then calculated the average (and standard error) annual abundance for the species of interest across sites from 2002 to 2023. For urchins, we also kept the total number of urchins counted at each site and the total number of transects to model urchin counts using a negative binomial generalized linear mixed-effects model (GLMM). Thus, each site is equally weighted and the lowest unit of replication is the average density per site per year. Finally, we added a variable called “heatwave” and assigned its values as “before” (2002–2013), “during” (2014–2016), and “after” (2017–2023), according to the year the data were collected.

Data were available for a total of 306 monitoring sites in 45 MPAs, with 95 sites in 29 fully protected MPAs, 41 sites in 16 partially protected MPAs, and 170 sites unprotected. Divided by region, there were 184 sites (covering 30 MPAs) within Southern and 122 sites (15 MPAs) within Central California. Some sites had only invertebrate data and some only reported fish counts. We used all available data for each analysis. All sites with data we used for analyses are visualized in Figure S2.

2.4.2 | Regression Models

First, we used GLMMs to model kelp densities in both Central and Southern California as a function of protection level, period (relative to MHWs), and interaction between protection and period. We used a Tweedie likelihood with a log-link function, and in fitting these models we estimated the Tweedie power parameter jointly with the model coefficients. We fit site-level random intercepts and slopes within both models to account for repeated sampling at each site. The models including random intercepts and slopes were selected based on diagnostic plots of the model residuals, as well as the fact that these models had lower AIC values than those including only random intercepts. A site-level autoregressive order-1 (AR(1)) error structure based on year was included in the Central California model lowering the AIC value, but not Southern California as it led to worse model diagnostics. Diagnostic plots for the final models are in Figures S9, S10.

Next, we hypothesized that higher abundances of sheephead and lobster (mesopredators targeted by California fisheries) inside MPAs in Southern California would result in greater predation pressure on sea urchins, thereby decreasing sea urchin kelp herbivory and allowing for greater kelp area and/or faster kelp recovery. We focused on Southern California to examine whether trophic cascades may be a mechanism underlying kelp resilience because only in this region are the main predators of sea urchins directly targeted by fisheries, and therefore benefit from protection in MPAs. To investigate these hypotheses, we first used two GLMMs to explore the variability in urchin abundances among time periods and locations. First, we modeled urchin abundances in Central California and Southern California as a function of protection level, period (relative to the MHWs), and interactions between protection and period, the same predictors as the kelp density models. Second, we assessed whether there were greater abundances of urchin predators in fully and partially protected MPAs after the full MPA network was implemented. Third, we tested for the direct and indirect relationships predicted by the trophic cascade hypothesis, allowing for linear and quadratic effects for the direct relationships.

For the first set of urchin analyses, we selected a negative binomial distribution with a log-link function to model the total number of urchins at each site, with an offset of the log of the number of transects, which is equivalent to modeling the average density of urchins while allowing for a non-uniform relationship between the mean and variance of the response variable. We fit site-level random intercepts and slopes within both models to account for repeated sampling at each site. The models including random intercepts and slopes were selected based on diagnostic plots of the model residuals, as well as the fact that these models had lower AIC values than those including only random intercepts. Following model fitting, we assessed whether there was evidence of residual temporal autocorrelation in the model by computing the lag-1 autocorrelation on the residuals of each site separately. We found that the average residual autocorrelation among sites was low (0.19). To be sure, we ran both models with and without consideration of a site-level autoregressive order-1 (AR(1)) error structure on the basis of year. No large differences were detected in the outputs from the models describing the relationship between protection, MHWs period, and urchin abundances; therefore, we chose the simpler models without the autoregressive function.

Next, we constructed three GLMMs to test whether there were greater abundances of spiny lobsters and California sheephead, and greater biomass of California sheephead within fully and partially protected sites from 2012 onward. We selected a Tweedie distribution with a log-link function for all models again and we fit the models with a site-level AR(1) error structure, and site-level random intercepts and slopes, except for sheephead abundance model where random slopes were redundant as indicated by an estimated correlation $|\rho| = 1$ between random intercepts and slopes.

To investigate the relationships predicted by the trophic cascade hypothesis, we focused on Southern California and modeled the density of giant kelp (average individuals per 60 m^2) as a function of urchin densities, and then in a separate model, giant kelp as a function of the densities of California sheephead and lobster. In each case, we used a Tweedie model with a log-link function, estimating the Tweedie power parameter jointly with the model coefficients. The relationship between urchins and their predators was first modeled using the same method above, but residual diagnostics indicated this model was a poor fit. So, urchin counts and their predator densities were modeled using a negative binomial distribution with a log-link function with an offset of the log of the number of transects. For all three models, we fit full site-level random intercepts to account for repeated sampling at each site. Diagnostics for all of these models can be found in Figures S11–S15.

For all GLMMs, we used the R packages "glmmTMB" to fit our models, "car" to compute Wald Tests of the main effects, and "DHARMa" to assess the model residuals (Brooks et al. 2017; Fox and Weisberg 2019; Hartig 2022). We derived bias-corrected estimated marginal means and variable effects as well as conducted Tukey-adjusted pairwise comparisons among heatwave and MPA status categories, using the "emmeans" package (Lenth 2024).

Finally, we also used a two-way fixed-effects model to test whether accounting for the year of MPA implementation (spanning from 1973 to 2012) modified the effect of protection on urchin abundance in Southern California. In this instance, we used an ordinary least-squares estimation with fixed effects for both site and year, and Driscoll-Kraay standard errors (Driscoll and Kraay 1998) (Figure S8). All data and statistical analyses were carried out in R (version 4.3.1). All code used for the data preparation, statistics, and figures can be found on the GitHub repository: https://github.com/jkumagai96/Kelp_Forests_and_MPAs.

3 | Results

3.1 | Resilience of Kelp Within MPAs to MHWs

Central California experienced little kelp loss during the MHWs of 2014–2016 with an average of 14.97 km^2 kelp canopy area during this time compared to the historic baseline of 17.26 km^2, a loss of 13.3%. From 2017 to 2021, kelp canopy area decreased to 12.98 km^2 for an average loss of 24.8% compared to the historic baseline (Figure 2a). In contrast, Southern California experienced much higher losses during the MHWs. There was an average loss of 46.4% of kelp canopy area, dropping from the baseline value of 17.13 to 9.18 km^2 during this time period. From 2017 to 2021, there was some recovery, but coverage remained 39.1% below the historic baseline at 10.43 km^2 (Figure 2c).

During and after the MHWs, there was significantly higher relative kelp area within fully protected MPAs than unprotected

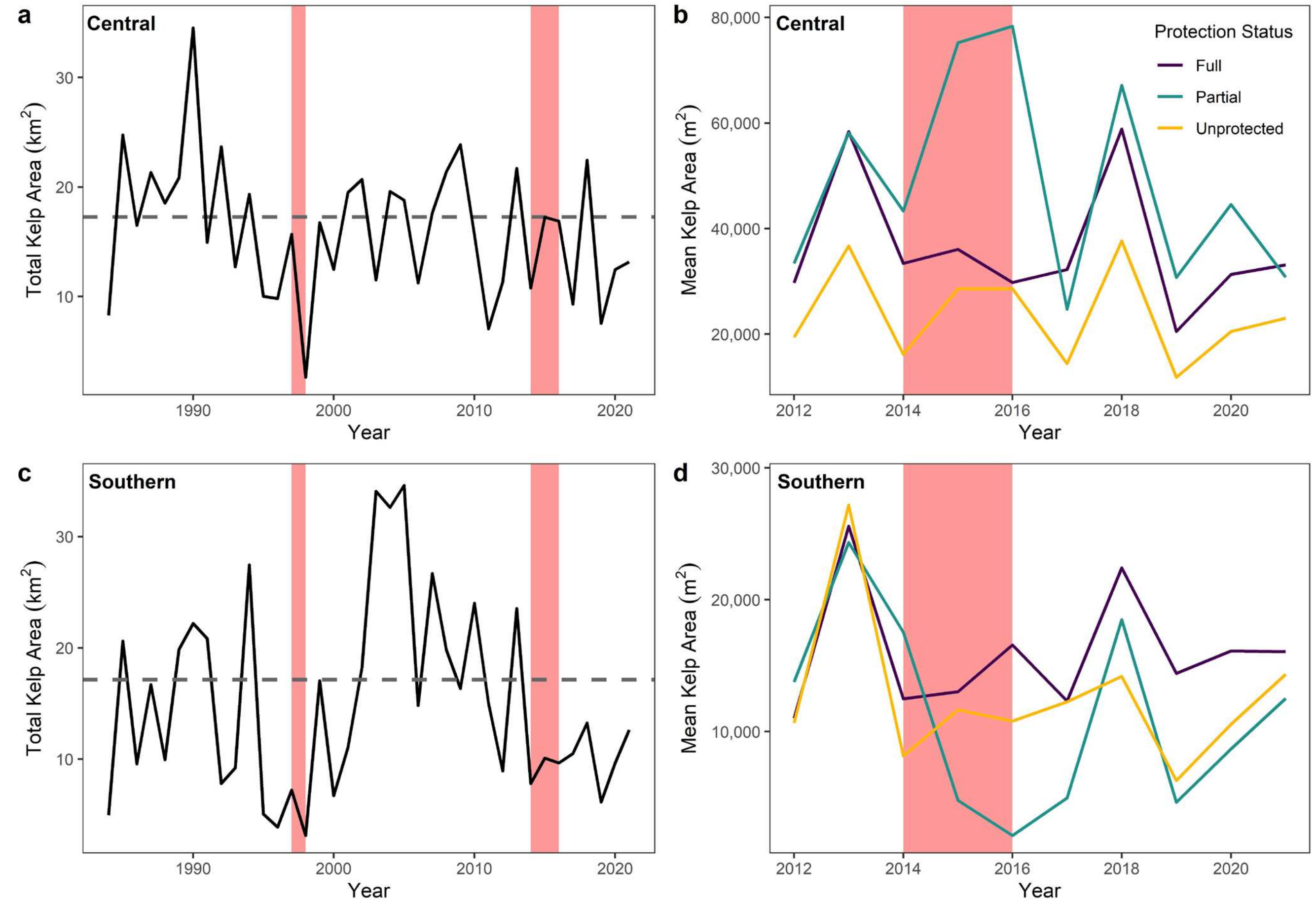

FIGURE 2 | Kelp area through time for the study area. Left: Total kelp area (km^2) within Central (a) and Southern California (c) with the mean baseline kelp area between 1984 and 2013 represented as a horizontal dashed line. Right: Mean kelp area in m^2 per 1-km^2 pixel by protection category from 2012 to 2021, for all MPAs established in Central (b) and Southern California (d). Note that axis ranges differ among panels and MHWs (the 1997–98 extreme ENSO event and 2014–16 MHWs) are denoted with transparent red.

areas (Figure 3, $p < 0.005$), while there were no significant differences in kelp area between partially protected MPAs and unprotected areas (Figure 3a,b; Table S2). However, this pattern is driven by responses in Southern California (Figure 2d). When analyzed by region, the only significant differences in relative kelp area in Central California were between partially protected and unprotected areas during the MHW (Figure 3; Table S2), with more kelp within partially protected MPAs during the MHW (Figures 2b and 3c). In Southern California, there was significantly higher resistance to, and recovery from, MHWs within fully protected MPAs compared to partially protected MPAs and unprotected areas ($p < 0.05$, Figure 3e,f). Importantly, we found no significant difference between relative kelp area within partially protected MPAs and unprotected areas in Southern California. Based on this evidence, fully protected MPAs appear to confer resilience to MHWs, both in terms of resistance and recovery, depending on the region.

When assessing the impact of MPA age on these results in Southern California, we found that kelp forests within fully protected MPAs consistently had significantly higher resistance to the MHWs irrespective of MPA age but that the effect was stronger in MPAs established before 2007 compared to the younger MPAs (Figure S5). However, recovery was indistinguishable between new and old MPAs, albeit that new MPAs exhibited significantly higher relative area of kelp in fully protected MPAs compared to partially protected MPAs (Figure S5). These results were generally robust to the exclusion of pixels with low initial kelp density (Table S8). A principal component analysis failed to find evidence for differences in environmental variables (i.e., temperature, depth, MHW intensity) between protection categories from before (2013), during (2015), and after (2019) the 2014–2016 MHWs, suggesting that protection status is not a result of the preferential placement of MPAs in habitat more favorable to kelp recovery (Figure S1).

These results were corroborated with the underwater surveys conducted from 2002 to 2023 (Figure 4). In Central California, averaging across protection categories, there was a significant and large decrease in kelp density (individuals, not stipes) starting from a modeled average of 0.21/m^2 before the MWHs to 0.09/m^2 after ($\chi^2 = 39$, $\mathrm{df} = 2$, $p < 0.0001$), a twofold decrease. Also, there was no overall significant interaction between protection status and MHWs period (Figure 4b), suggesting that the effect of MHWs on kelp densities was independent of protection status, although there was significantly more kelp in unprotected sites compared to fully protected sites after the MHWs ($p = 0.013$). In contrast, within sites in Southern

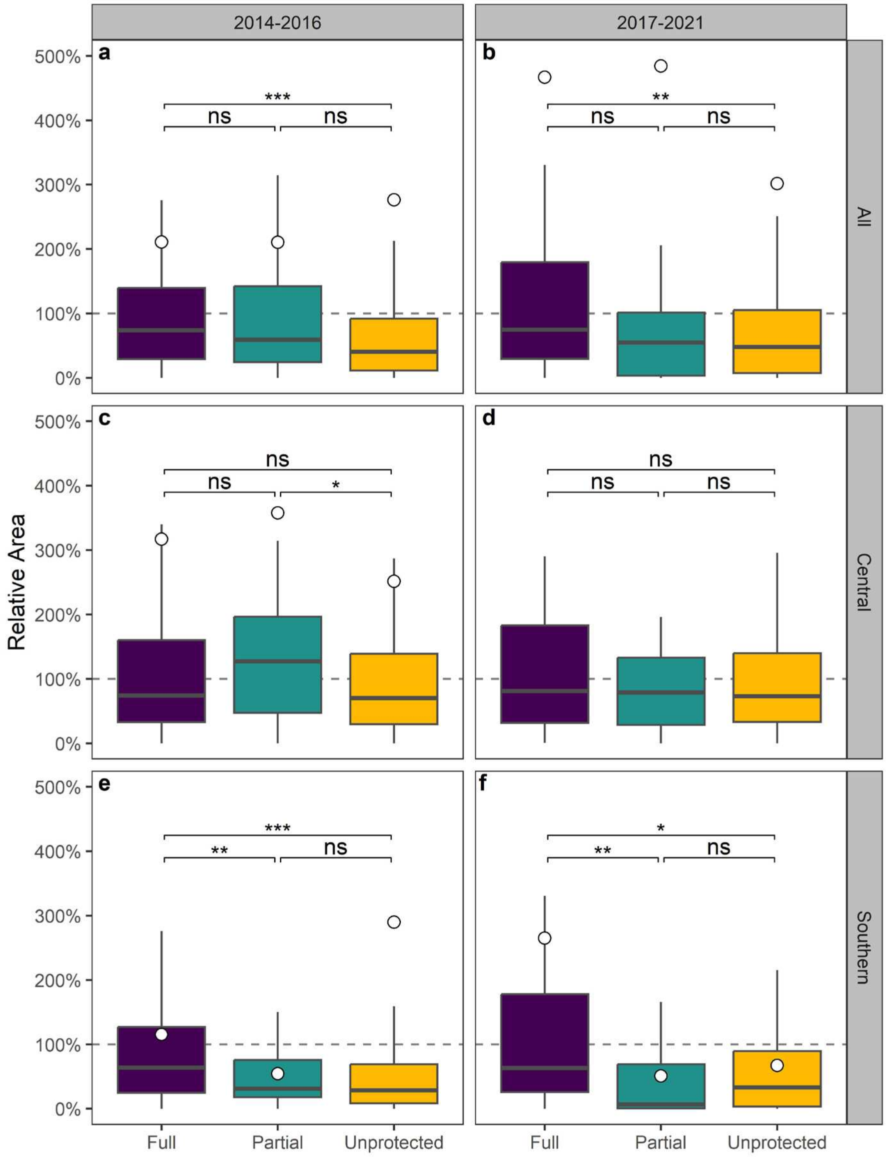

FIGURE 3 | Resilience of kelp forests during (2014–2016) and after the MHWs (2017–2021). Boxplots of relative area of kelp (averaged annual kelp canopy area relative to the historic baseline area within each pixel) within fully protected, partially protected, and unprotected areas for (a, b) all regions, (c, d) Central California, and (e, f) Southern California. White points represent averages, which are heavily skewed by instances of very large changes in kelp cover. Average points in Central California in 2017–2021 are outside the plot extent and not visualized (Table S7), and outliers are also removed from the plot for ease of visualization. Pseudo *p*-values were computed via Bonferroni-corrected permutation analyses; non-significant group differences are indicated with "ns" while significant comparisons (after Bonferroni correction) are denoted with asterisks: $p < 0.05$ (*), < 0.01 (**), and < 0.001 (***).

California, there was an overall significant effect of protection status ($\chi^2 = 12$, $\mathrm{df} = 2$, $p < 0.01$) and the interaction between protection status and MHWs period on giant kelp densities ($\chi^2 = 18$, $\mathrm{df} = 4$, $p < 0.01$). For kelp in fully protected sites, before the MHWs there was no difference in kelp density compared to kelp in unprotected sites ($p = 0.12$). This changed with the MHWs, as there was slightly more kelp both during ($p = 0.16$) and significantly more after ($p = 0.0001$) the MHWs in fully protected sites compared to unprotected sites, again suggesting some resistance and clear recovery within fully protected MPAs (Figure 4b). For partially protected sites in Southern California, the results differ from those for the satellite-based kelp canopy estimates. Before the MHWs, there was less kelp in partially protected sites compared to unprotected sites ($p = 0.07$), but during and after the MHWs, there were no significant differences between underwater kelp density in partially protected MPAs compared to either fully protected or unprotected areas respectively (Figure 4). Taking both the satellite canopy estimates and underwater surveys together, there is evidence of kelp resistance to and recovery from the MHWs in fully protected MPAs compared to unprotected areas in Southern California, but not in Central California.

3.2 | Mechanism of Resilience: Trophic Cascades

In Central California, urchin densities significantly increased overall from 2014 to 2023 in all protection categories (Figure 5,

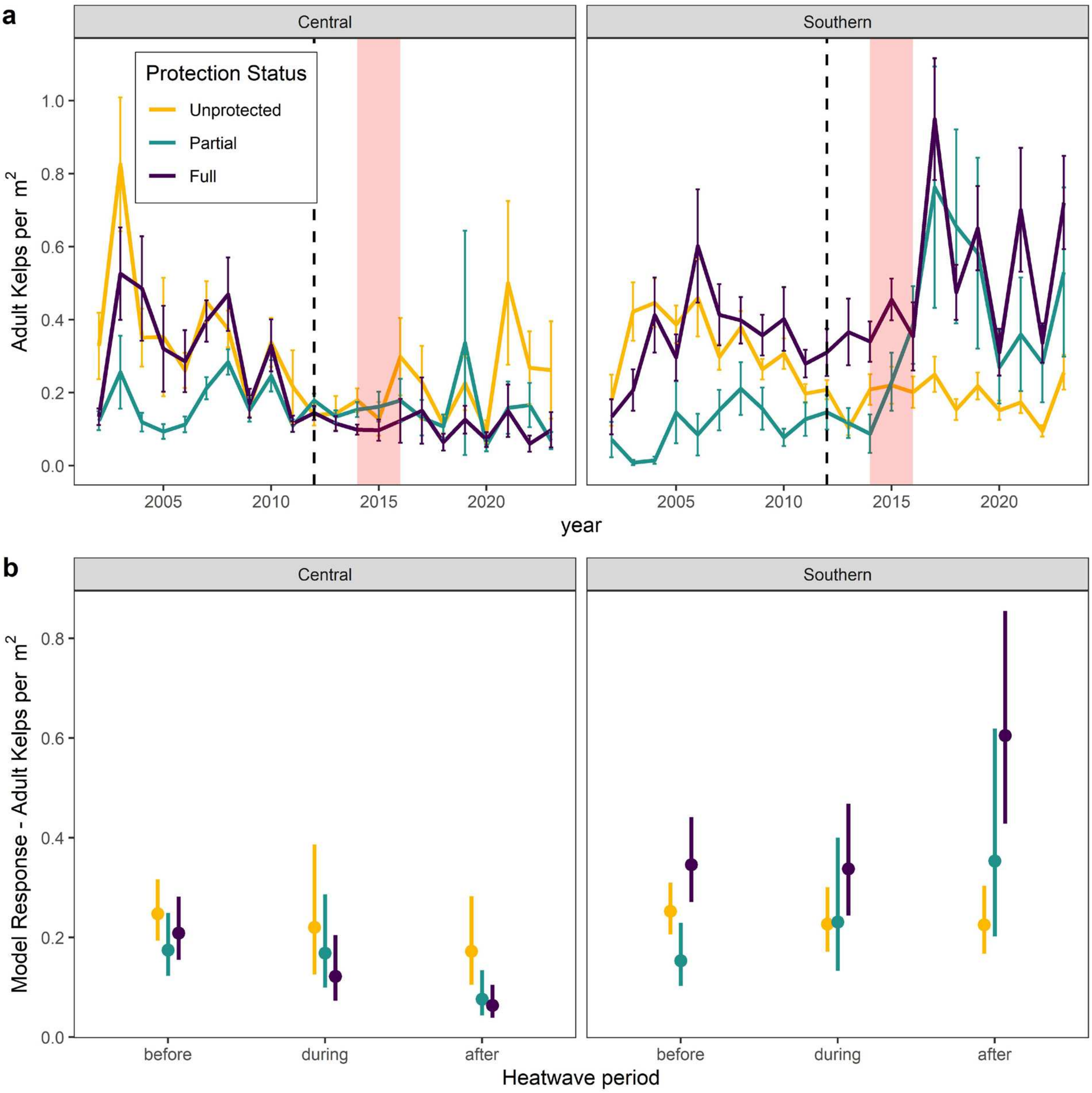

FIGURE 4 | Kelp densities through time by level of protection in Central and Southern California. (a) Mean giant and bull kelp densities per site and level of protection (number of adult individuals per m^2, not stipes). Error bars represent standard errors. Data before 2012 include sites that were protected at that time or would become protected in 2012. The 2014–2016 MHWs are depicted in transparent red. (b) Variation in giant kelp densities across protection levels (full, partial, and unprotected) and MHWs periods (before, during, and after) for both regions. Estimates and their 95% confidence intervals for mean giant kelp density are from fitted GLMMs. The dashed line at 2012 represents the implementation of the most recent MPAs declared under the Marine Life Protection Act.

$\chi^2=579$, df$=2$, $p<0.0001$). Average urchin density across all protection categories was only 0.18 ± 0.04 (mean ± SE) per m^2 before the MHWs but increased to 4.74 ± 1.15 per m^2 during the MHWs and 10.96 ± 2.54 per m^2 after the MHWs. There was no significant interaction between protection category and MHWs period, suggesting that protection status had no effect on urchin abundances or their increase during and after the MHWs.

In Southern California before the MHWs, overall modeled urchin density in unprotected sites (5.82 ± 0.89 per m^2) was not significantly different from that in partially (6.52 ± 2.10 per m^2, $p=0.95$) or fully protected (7.04 ± 1.38 per m^2, $p=0.72$) sites. However, we found that the difference in urchin densities between protection categories varied through time ($\chi^2=56$, df$=4$, $p<0.0001$). In contrast with Central California, urchin densities in Southern California were lower in fully protected sites during the MHWs ($p=0.098$) and significantly lower after ($p=0.0086$) the MHWs than in unprotected sites. Modeled urchin densities also declined in partially protected sites during (3.00 ± 1.06 per m^2) and after (2.89 ± 1.05 per m^2) compared to before (6.52 ± 2.10 per m^2) the MHWs, but these densities were not significantly different from those for unprotected sites (Figure 5). There were also fewer urchins in fully protected sites (2.34 ± 0.54 per m^2) compared to partially protected sites (2.89 ± 1.05 per m^2) after the MHWs, but these

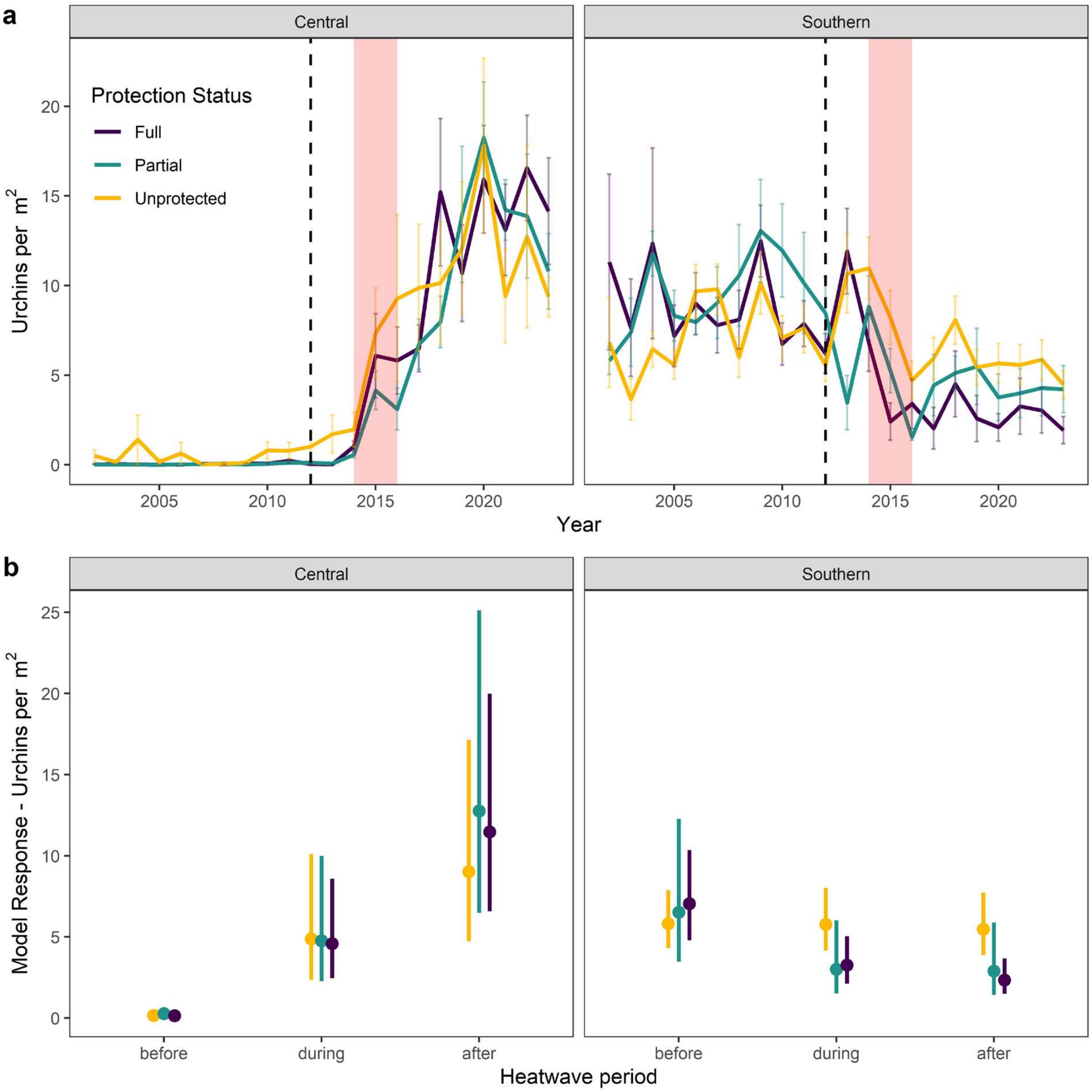

FIGURE 5 | Urchin densities through time by level of protection in Central and Southern California. (a) Mean urchin abundances per site and level of protection (number of individuals per m^2). Red and purple urchin densities were combined. Error bars represent standard errors. Data before 2012 include sites that were protected at that time or would become protected in 2012. The 2014–2016 MHWs are depicted in transparent red. (b) Variation in urchin densities across protection levels (full, partial, and unprotected) and heatwave periods (before, during, and after) for both regions. Estimates of mean urchin density and their 95% confidence intervals are from a GLMM. The dashed line at 2012 represents the implementation of the most recent MPAs declared under the Marine Life Protection Act.

differences were not statistically significant ($p = 0.87$). Using a two-way fixed-effects model, we found that urchin abundances declined with MPA age, particularly in fully protected MPAs and stabilized after 12 years for both fully and partially protected areas (Figure S8). Taken together, these results indicate that the difference in urchin densities between unprotected and fully protected MPAs increased during and after the MHWs.

After the full implementation of the Marine Life Protection Act and the establishment of all MPAs, completed in 2012, there was a significant increase in the densities and biomass of urchin predators in Southern California. After 2012, spiny lobster densities were significantly higher within fully protected sites compared to unprotected sites ($p < 0.0001$), while being marginally lower in partially protected sites compared to unprotected sites (Figure 6a; $p = 0.08$). For California sheephead, there was also a significant increase in both abundance and biomass in fully (abundance—$p = 0.005$; biomass—$p < 0.0001$) and partially ($p = 0.0007$; $p = 0.002$) protected sites compared to unprotected sites (Figure 6b,c). If we re-assign protection status based only on restrictions applied to California sheephead (Data S1, Section 3, Figure SA) their biomass is greater in fully protected than partially protected MPAs, and both are significantly different than unprotected areas ($p < 0.0001$; $p = 0.04$) respectively. Interestingly, sheephead abundance increased at all sites during

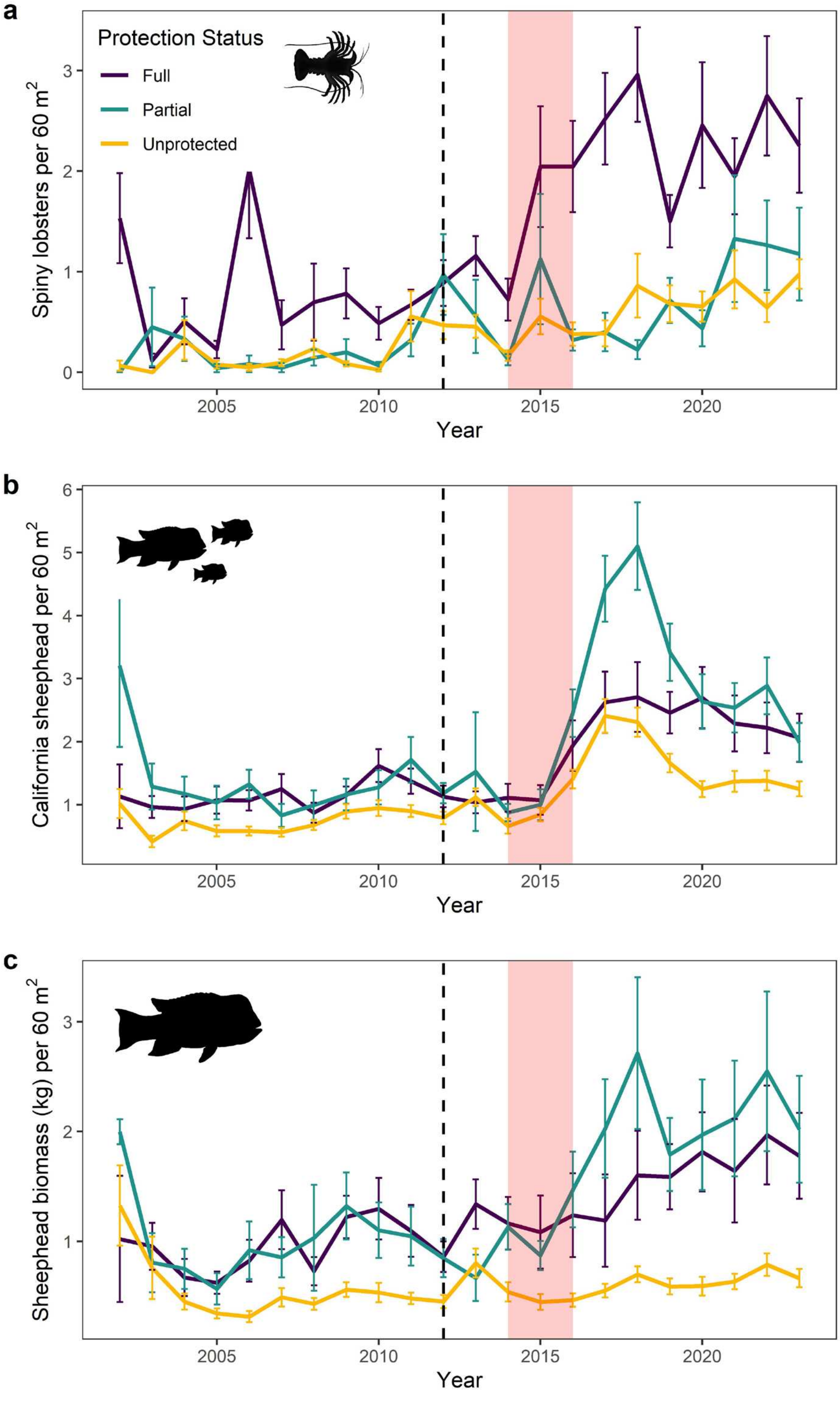

FIGURE 6 | Average abundances of urchin predator population size per site and level of protection for Southern California from 2002 to 2023. (a) Mean abundances of spiny lobsters per site (number of individuals/60 m^2), (b) mean abundance of California sheephead per site (number of individuals/60 m^2), and (c) mean biomass of California sheephead (kg/60 m^2). The dashed line at 2012 represents the implementation of the most recent MPAs declared under the Marine Life Protection Act. Error bars represent standard errors. Data before 2012 includes sites that were protected or would become protected in 2012. The MHWs in 2014–2016 are depicted in transparent red.

the MHW due to large recruitment events during 2015–2016 (Figure 6b, Figure S16).

Finally, we found evidence for direct and indirect relationships characteristic of a trophic cascade between kelp, urchins, and their predators in Southern California. As expected, we found a negative relationship between the densities of giant kelp and urchins (Figure 7a; $p < 0.0001$). With urchins absent, this model predicts ~26 (±2, SE) giant kelp individuals per 60 m^2 transect, falling to 20 (±1.5) at the median density of urchins in the data

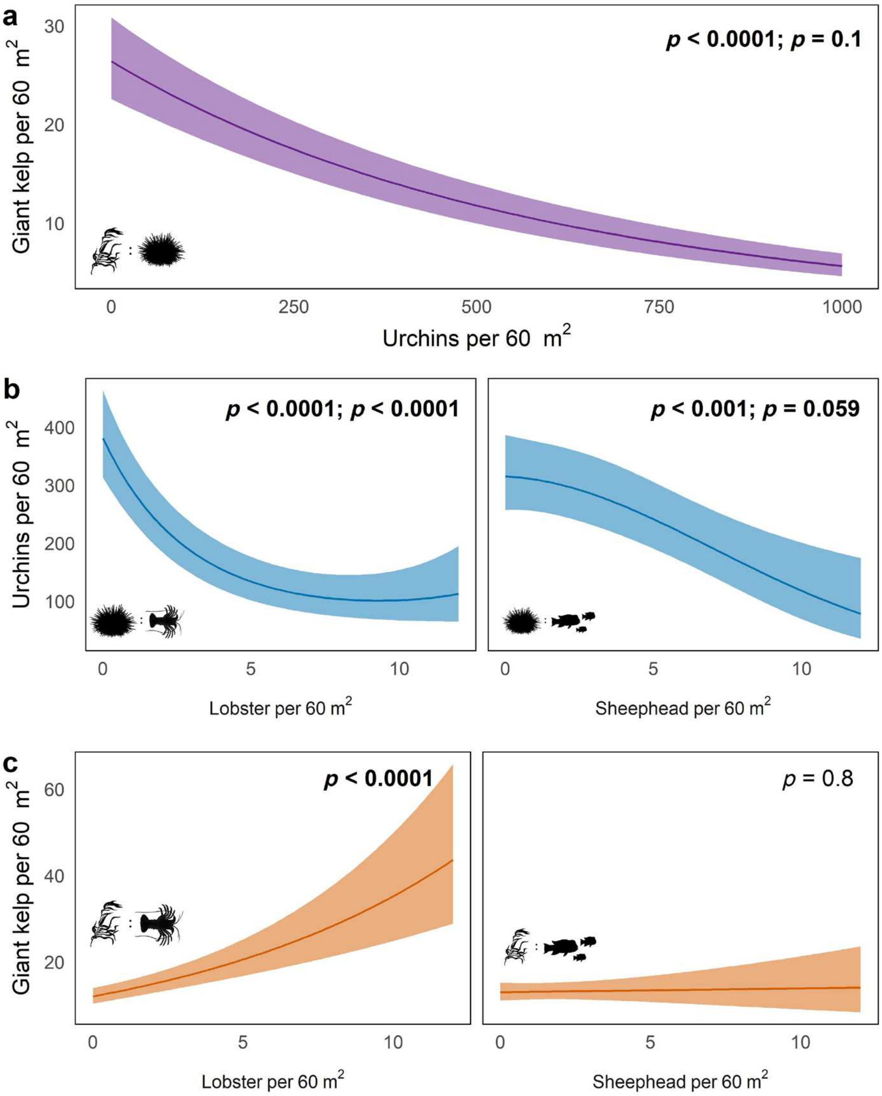

FIGURE 7 | Partial effects plots from three models depicting the direct and indirect trophic interactions in Southern California between (a) giant kelp and urchins, (b) urchins and their predators: lobster and sheephead, and (c) the indirect relationship between giant kelp and lobster and sheephead. On each panel there are two *p* values, the left-most *p* value corresponds to the log-linear effects, while the right-most *p* value corresponds to the log-quadratic effects. The models are based on data from yearly site-level means. The indirect relationships were modeled only with log-linear effects. Plots for model residuals can be found in the supporting information (Figures S13–S15).

(~162 urchins per 60 m^2 transect). Urchin densities were also lower with higher densities of both California sheephead ($p < 0.0001$) and lobster (Figure 7b; $p < 0.0001$). This model suggests a proportionally higher decrease in the densities of urchins with increasing lobster abundance, compared to California sheephead, for which decreases in urchin densities were not apparent until approximately 5 sheephead per 60 m^2 transect (Figure 7b). When holding the other predator's abundance at their mean value, the model predicts ~242 (±32) urchins if there are ~5 sheephead on a transect, and ~134 (±21) urchins if there are ~5 lobsters on a transect. When testing the indirect relationship between giant kelp and urchin predators, we found that there was a significant positive relationship between giant kelp and lobster ($p < 0.0001$), but not between giant kelp and sheephead (Figure 7c; $p = 0.8$). When holding sheephead abundance at its mean value, the model predicts ~12 (±1) giant kelps when there are no lobsters, and ~20 (±2) kelps when there are ~5 lobsters (Figure 7c).

4 | Discussion

This study provides empirical evidence that fully protected MPAs can promote the resilience of kelp forests to climate impacts specifically when natural predators of urchins are protected, resulting in reduced grazing on kelp. Full protection improved both kelp resistance to and recovery from extreme MHWs, an effect evident from both satellite-based canopy estimates and underwater surveys, but this effect varied by region. In Central California, where the main urchin predators were extirpated by a disease outbreak (i.e., sunflower sea stars) or are protected statewide and therefore not directly influenced by MPA status (i.e., sea otters), kelp decreased and sea urchins increased dramatically during and after the MHW, across both protected and unprotected sites. In contrast, in Southern California, MPAs had significantly greater abundances of urchin predators and fewer urchins within both partially and fully protected MPAs during and after the 2014–2016 MHWs. These results lend support to the role of trophic cascades as a mechanism for ecological resilience, and fully protected MPAs as an effective climate-adaptation tool.

Our findings provide evidence that trophic cascades may be a mechanistic path through which MPAs provide climate resilience to kelp forest ecosystems; however, these benefits are context-dependent and vary regionally. Multiple studies have shown that fully protected MPAs increase the biomass and abundance of the predators of urchins (Caselle et al. 2015; Hamilton and Caselle 2015; Lenihan et al. 2022), which exert top-down control on urchin populations, thereby supporting stability and resilience of kelp populations (Ling et al. 2009; Peleg, Blain, and Shears 2023). Here, we show that this mechanism also applies under climate impacts because we observed that there were fewer sea urchins, less loss of kelp, and greater recovery of kelp populations inside fully protected MPAs during and after the 2014–2016 MHW in Southern California. Corroborating this interpretation of our results, we found that urchin abundances were negatively correlated with those of spiny lobster and California sheephead and that giant kelp densities were positively correlated with spiny lobster abundances. One potential reason that there is not a similar positive correlation between densities of giant kelp and California sheephead is the large recruitment event of sheephead during 2015 and 2016 (Figure S16) while kelp suffered losses. This indirect relationship was previously documented before the MHWs in Hamilton and Caselle et al. (2015), consistent with the trophic cascade hypothesis. Overall, these results suggest that the recovery from overfishing of urchin predators within MPAs is likely controlling urchin populations and potential behavior, thus preventing overgrazing and allowing kelp to recover faster from disturbances than in unprotected areas.

In Central California, we found no measurable effect of protection status on kelp resistance and recovery, likely because spatial protection does not confer additional benefits to the main mesopredators of urchins in the region—sea otters and sunflower sea stars—whose dynamics are largely independent of fishing effort and, consequently, protection status. Sea otters are federally protected and have not been actively hunted for over a century, thus benefiting from protection throughout their range. Further, sea urchin abundance started to increase exponentially both inside and outside MPAs following the mass mortality of sunflower stars due to the outbreak of sea star wasting disease in 2013–2015, which led this sea urchin predator to near extinction (Harvell et al. 2019; Montecino-Latorre et al. 2016; Rogers-Bennett and Catton 2019). We assume that the level of protection has no influence on recovery of sunflower stars, as this species is not fished and has yet to recover. These results support the notion that following major MHWs, multiple predators are needed to prevent urchin outbreaks and maintain kelp abundance through time in Central California (Selgrath et al. 2024). Also, these observations illuminate how non-spatial policies, such as species-specific interventions (i.e., the federal protection conferred over sea otters, and possibly the proposed active restoration of depleted seastar populations) may be needed to promote ecosystem resilience.

Interestingly, during the MHWs we see opposing population trends of urchins within Central and Southern California. In Southern California, there was a consistent decline in urchins across all categories of protection during 2014–2016, although densities were still high with an average of 3.89 m^2 in 2016. This may be explained by the large increase in the number of California sheephead during these years or that purple sea urchins are already living closer to their upper thermal limit in Southern California (Hammond and Hofmann 2010), thus a temperature anomaly of a few degrees may have caused mortality in Southern California but not Central California. However, hundreds of kilometers further south in Baja California, Mexico, purple sea urchins have increased their abundance after the MHWs (Arafeh-Dalmau et al. 2020), indicating that the conditions are suitable. Most importantly, after the MHWs there were fewer urchins in fully protected MPAs in Southern California, providing evidence that trophic cascades play a role in lowering urchin abundances.

Our results expand on other studies in the region, emphasizing evidence for trophic cascades—preserved by MPAs—as the mechanism separating healthy kelp forests from urchin barrens. For example, trophic cascades were found to enhance macroalgal abundances in MPAs in the northern Channel Islands a year after the MHWs (Eisaguirre et al. 2020). However, another study in the Channel Islands found contrasting evidence: there was an increase of urchins within MPAs, in part due to the release of red urchins from fishing pressure within MPAs, which outweighed any effect of trophic cascades (Malakhoff and Miller 2021), though the authors of this study did not consider the response of urchins to the MHWs. In comparison, we found fewer urchins within MPAs, but only during and after the MHWs. Notably, when we took into consideration the year of establishment of the MPAs, we found that protection led to fewer urchins in Southern California through time (Figure S8). Therefore, by expanding the spatial and temporal scale of analysis, our results reconcile previously contrasting conclusions.

Our work is also subject to some limitations. First, kelp canopy area is an estimate from satellite imagery, which may add some sources of error (Alix-Garcia and Millimet 2022). However, ongoing methodological improvements have addressed most detection gaps (see Bell et al. 2020 for more detail). For the subtidal data, while we have size structure information for California sheephead that allows us to evaluate biomass, such data are not available for spiny lobsters as it is difficult to measure their size in the field. Also, accurate estimates of lobster density are difficult to obtain from this type of general long-term monitoring of the benthos, as larger and more-tailored surveys, which investigate all crevices, are needed to obtain accurate counts. However, the method used to estimate lobster densities in this study is consistent for all sites and years; therefore, potential accuracy limitations are less likely to influence the overall findings of this study. Moreover, we did not include in our analyses other smaller species, such as crabs, which may benefit from MPAs and influence urchin populations by feeding on juveniles (Clemente et al. 2013). We excluded these species because of the current limited understanding of their role as urchin predators. Finally, we were not able to explore evidence for trophic cascades within Central

California as there is no population data for otters at the same scale and resolution of the MLPA data.

Besides trophic interactions, there are additional potential reasons why spatial protection in Central California was not associated with increased climate resilience for kelp forests. First, this region was less impacted by the MHWs themselves. Notably, on average kelp area remained 1.5–3 times higher in Central than Southern California during and after the MHW (Figure 2), although the underwater densities are similar (Figure 4). It is no surprise that level of protection had no effect in Central California because, regardless of protection, giant and bull kelp forests were not as impacted from the MHWs, even though they experienced a steady decline after the MHWs. In addition, large areas of Central California are less accessible to people and therefore are less impacted by human activities, including fishing (Free et al. 2023), than in Southern California, and because density of the remaining urchin predators (federally protected sea otters) is largely uncorrelated with protection status. Our results are in general agreement with previous studies that also found limited contribution of MPAs to climate resilience for kelp forest communities in Central California (Smith et al. 2023). These findings suggest that it is a priority to assess the benefits of MPAs for providing climate resilience in regions that are more impacted by climate change and human activities. Our study casts new light on differences in climate resilience between two regions in California and, most importantly, highlights the importance of the local ecological context in determining whether MPAs can be expected to buffer climate extremes.

Our findings have important implications for evaluating the benefits that MPAs can confer in terms of mitigating the impacts of climate change, and also for informing approaches to climate-smart management and establishment of new MPAs (Arafeh-Dalmau et al. 2023) as nations make progress toward protecting 30% of the oceans by 2030 while adapting to climate change (Convention of Biological Diversity 2022). Understanding which mechanisms confer climate resilience at different levels of biological organization (species, population, and ecosystem), and at local to regional scale, is crucial to inform realistic expectations of the climate benefits that MPAs or other management options may provide. There is a need for deeper understanding of the mechanisms that drive ecosystem resilience to understand where placing MPAs may increase climate resilience. Furthermore, such understanding requires continued investment in long-term monitoring and standardized metrics to define and measure ecological resilience to evaluate the conditions under which MPAs confer resilience to climate impacts.

The most important implication of our findings is that protection of top predators confers benefits that propagate through the ecosystem, boosting resilience to and recovery from acute impacts of climate change. While this goal often underpins the establishment of MPAs, its effectiveness in providing climate resilience is seldom supported by empirical evidence. Additional research is required to assess the generality of our findings, but they provide a strong motivation to carefully manage fishing pressure in the coastal zone as climate extremes become more frequent and intense (Oliver et al. 2018; Schoeman, Bolin, and Cooley 2023). MPAs offer many benefits from preventing continued destruction of habitats (including blue carbon ecosystems such as seagrass and mangroves), increasing food security, and increasing resilience to climate shocks and environmental variability, ultimately increasing overall ecosystem resilience (Aburto-Oropeza et al. 2011; Jacquemont et al. 2022; Miteva, Murray, and Pattanayak 2015; Selig and Bruno 2010). However, MPAs are not a panacea to the ongoing and projected impacts of climate change. In particular, our results of context-dependent roles of MPAs in conferring climate resilience highlight the urgency to carefully consider what and where additional measures are needed, such as the protection of wide-ranging top predators to the active restoration of habitat and critical species interactions. Crucially, the root causes of climate change and global biodiversity loss must be urgently addressed before the efficacy of our adaptation tools is lost (Mills et al. 2023).

Author Contributions

Joy A. Kumagai: conceptualization, data curation, formal analysis, investigation, methodology, software, validation, visualization, writing – original draft, writing – review and editing. **Maurice C. Goodman:** data curation, formal analysis, methodology, software, validation, visualization, writing – review and editing. **Juan Carlos Villaseñor-Derbez:** data curation, formal analysis, methodology, writing – review and editing. **David S. Schoeman:** conceptualization, investigation, writing – review and editing. **Kyle C. Cavanaugh:** conceptualization, writing – review and editing. **Tom W. Bell:** conceptualization, writing – review and editing. **Fiorenza Micheli:** funding acquisition, conceptualization, investigation, writing – review and editing. **Giulio De Leo:** funding acquisition, investigation, methodology, supervision, writing – review and editing. **Nur Arafeh-Dalmau:** conceptualization, formal analysis, investigation, methodology, supervision, validation, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.14188853. The kelp canopy and environmental variable dynamics data are available from the Environmental Data Initiative at https://doi.org/10.6073/pasta/c40db2c8629cfa3fbe80fdc9e086a9aa. The spatial layers, age, and level of fishing restriction data are available from NOAA's Marine Protected Areas Inventory at https://marineprotectedareas.noaa.gov/dataanalysis/mpainventory/(2023-2024). The subtidal surveys of kelp forest communities are available from the California Ocean Protection Council database at https://doi.org/10.25494/P6/MLPA_kelpforest.9.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.