



**A network of marine protected areas does not confer
community structure resilience to marine heatwave impacts
across multiple coastal ecosystems**

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Complete List of Authors:	<p>Smith, Joshua; University of California Santa Barbara National Center for Ecological Analysis and Synthesis; Monterey Bay Aquarium, Conservation and Science Division</p> <p>Free, Christopher; University of California Santa Barbara, Bren School of Environmental Science and Management; University of California Santa Barbara, Marine Science Institute</p> <p>Lopazanski, Cori; University of California Santa Barbara, Bren School of Environmental Science and Management; University of California Santa Barbara National Center for Ecological Analysis and Synthesis</p> <p>Brun, Julien; University of California Santa Barbara, National Center for Ecological Analysis and Synthesis</p> <p>Anderson, Clarissa; University of California San Diego Scripps Institution of Oceanography</p> <p>Carr, Mark; University of California Santa Cruz, Ecology and Evolutionary Biology</p> <p>Claudet, Joachim; National Center for Scientific Research, PSL Université Paris, CRIOBE, CNRS-EPHE-UPVD, Laboratoire d'Excellence Corail</p> <p>Dugan, Jenifer; University of California Santa Barbara, Marine Science Institute</p> <p>Eurich, Jacob; Environmental Defense Fund; University of California Santa Barbara National Center for Ecological Analysis and Synthesis; University of California Santa Barbara, Bren School of Environmental Science and Management</p> <p>Francis, Tessa; University of Washington Tacoma, Puget Sound Institute</p> <p>Hamilton, Scott; Moss Landing Marine Laboratories,</p> <p>Mouillot, David; University of Montpellier, MARBEC; Institut Universitaire de France</p> <p>Raimondi, Pete; University of California, Santa Cruz, Department of Ecology and Evolutionary Biology</p> <p>Starr, Richard; Moss Landing Marine Laboratories,</p> <p>Ziegler, Shelby; University of Georgia, Odum School of Ecology</p> <p>Nickols, Kerry; California State University Northridge, Biology</p> <p>Caselle, Jennifer; University of California Santa Barbara, Marine Science Institute</p>
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Abstract:	<p>Marine protected areas (MPAs) have gained attention as a conservation tool for marine ecosystems to build resilience to climate change. However, empirical evidence that explicitly links MPAs to enhanced ecological resilience is limited and mixed. To better understand whether MPAs provide a buffer to climate impacts, we tested the resistance and recovery of marine communities to the 2014-2016 Northeast Pacific heatwave in the largest scientifically designed MPA network in the world off the coast of California, USA. We compared fish, benthic invertebrate, and macroalgal community structure inside MPAs and at reference sites across the rocky intertidal, kelp forest, shallow reef, and deep reef nearshore habitats in California's Central Coast region from 2007-2020. We also explored whether MPA features, including age, size, historic fishing pressure, habitat diversity, connectivity, and fish biomass response ratios, conferred climate resilience for kelp forest and rocky intertidal habitats spanning the entire California MPA network. Our results show that ecological communities dramatically shifted as a result of the marine heatwave across all four nearshore habitats, and that MPAs did not facilitate habitat-wide resistance or recovery. The rocky intertidal was the only habitat where community structure significantly resisted marine heatwave impacts in MPAs. Community shifts were associated with a pronounced decline in the relative proportion of species with cold-water thermal affinities and an increase in those with warm-water thermal affinities. We also found that MPA features did not explain resistance or recovery to the marine heatwave. Collectively, our findings suggest that MPAs may have limited ability to mitigate the impacts of marine heatwaves on community structure. Given that mechanisms of resilience to climate perturbations are complex, there is a clear need to expand assessments of ecosystem-wide consequences resulting from acute climate-driven perturbations, and the potential role of regulatory protection in mitigating community structure changes.</p>

A network of marine protected areas does not confer community structure resilience to marine heatwave impacts across multiple coastal ecosystems

Joshua G. Smith^{1,2*}, Christopher M. Free^{3,4}, Cori Lopazanski^{1,3}, Julien Brun¹, Clarissa R. Anderson⁵, Mark H. Carr⁶, Joachim Claudet⁷, Jenifer E. Dugan⁴, Jacob G. Eurich^{8,1,3}, Tessa B. Francis⁹, Scott L. Hamilton¹⁰, David Mouillot^{11,12}, Peter T. Raimondi⁶, Richard M. Starr¹⁰, Shelby L. Ziegler¹³, Kerry J. Nickols¹⁴, Jennifer E. Caselle⁴

¹ National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, Santa Barbara, CA, USA

² Conservation and Science Division, Monterey Bay Aquarium, CA, USA

³ Bren School of Environmental Science and Management, University of California, Santa Barbara, Santa Barbara, CA, USA

⁴ Marine Science Institute, University of California, Santa Barbara, Santa Barbara, CA, USA

⁵ Scripps Institution of Oceanography/Southern California Coastal Ocean Observing System, University of California, San Diego, Scripps Institution of Oceanography, La Jolla, CA 92037, USA

⁶ Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA, USA

⁷ National Center for Scientific Research, PSL Université Paris, CRIOBE, CNRS-EPHE-UPVD, Maison de l'Océan, Paris, France

⁸ Environmental Defense Fund, Santa Barbara, CA, USA

⁹ Puget Sound Institute, University of Washington, Tacoma, WA, USA

¹⁰ Moss Landing Marine Laboratories, San Jose State University, Moss Landing, CA, USA

¹¹ MARBEC, University of Montpellier, CNRS, IFREMER, IRD, Montpellier, France

¹² Institut Universitaire de France, IUF, Paris, France

¹³ Odum School of Ecology, University of Georgia, Athens, GA, USA

¹⁴ Department of Biology, California State University Northridge, Northridge, CA, USA

* **Corresponding author:** National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, Santa Barbara, CA, USA; joshsmith@nceas.ucsb.edu

Running Title: MPAs do not confer climate resilience

Abstract

Marine protected areas (MPAs) have gained attention as a conservation tool for marine ecosystems to build resilience to climate change. However, empirical evidence that explicitly links MPAs to enhanced ecological resilience is limited and mixed. To better understand whether MPAs provide a buffer to climate impacts, we tested the resistance and recovery of marine communities to the 2014-2016 Northeast Pacific heatwave in the largest scientifically designed MPA network in the world off the coast of California, USA. We compared fish, benthic invertebrate, and macroalgal community structure inside MPAs and at reference sites across the rocky intertidal, kelp forest, shallow reef, and deep reef nearshore habitats in California's Central Coast region from 2007-2020. We also explored whether MPA features, including age, size, historic fishing pressure, habitat diversity, connectivity, and fish biomass response ratios, conferred climate resilience for kelp forest and rocky intertidal habitats spanning the entire California MPA network. Our results show that ecological communities dramatically shifted as a result of the marine heatwave across all four nearshore habitats, and that MPAs did not facilitate habitat-wide resistance or recovery. The rocky intertidal was the only habitat where community structure significantly resisted marine heatwave impacts in MPAs. Community shifts were associated with a pronounced decline in the relative proportion of species with cold-water thermal affinities and an increase in those with warm-water thermal affinities. We also found that MPA features did not explain resistance or recovery to the marine heatwave. Collectively, our findings suggest that MPAs may have limited ability to mitigate the impacts of marine heatwaves on community structure. Given that mechanisms of resilience to climate perturbations are complex, there is a clear need to expand assessments of ecosystem-wide consequences resulting from acute climate-driven perturbations, and the potential role of regulatory protection in mitigating community structure changes.

Keywords: California, marine protected area networks, marine heatwaves, community composition, community structure, resilience, climate change

1. Introduction

Climate change can rapidly reshape the distribution of species and the composition of ecological communities (Smale et al., 2019). In particular, episodic periods of anomalous ocean warming, hereafter 'marine heatwaves', are driving pronounced shifts in species distributions across marine ecosystems (Azzurro & D'Amen, 2022; Olsen et al., 2022), with direct implications for ecological processes and associated human benefits (Smale et al., 2019; Cheung et al., 2021; Payne et al., 2021; Cinner et al., 2022; K. E. Smith et al., 2023). While the urgency to plan for resilience in the face of climate change is clear, as marine heatwaves increase in frequency and severity (Holbrook et al., 2019), pathways to enhance resilience are mixed. Therefore, understanding how ecological communities resist, recover from, or are transformed by climate perturbations, such as marine heatwaves, represents one of the most pressing challenges for building ecosystem resilience capacity (Mason et al., 2022).

Marine protected areas (MPAs) are an important conservation strategy for preserving biodiversity, enhancing ecosystem services, and rebuilding depleted fisheries (Gronrud-Colvert et al., 2021). MPAs may provide network-scale population connectivity that can enhance spillover and the replenishment of individuals to populations in both protected and fished areas (Harrison et al., 2012; Williamson et al., 2016; M. Di Lorenzo et al., 2020; Goetze et al., 2021). Although most MPAs were initially designed to reduce the effects of overfishing and habitat loss, they are frequently hypothesized to provide long-term protection against climate impacts (Roberts et al., 2017; Hofmann et al., 2021). For example, networks of MPAs may provide refugia as species redistribute in response to climate change, owing to lower anthropogenic stressors and higher population sizes resulting from reduced harvest (McLeod et al., 2009; Carr et al., 2017). MPA features such as habitat diversity, historic fishing pressure, age, and size may also influence the capacity for MPAs to provide ecological resilience (Jacquemont et al., 2022). As such, MPAs and MPA networks are being increasingly highlighted as a key tool for enhancing climate resilience (IUCN-WCPA, 2008; Jacquemont et al., 2022).

Despite the growing number of studies examining MPAs as a tool for mitigating climate impacts, the effectiveness of MPAs (both individually and as networks) for enhancing the resilience (i.e., resistance to and recovery from disturbance; Bates et al., 2019) of marine communities to climate change remains contested (Johnson et al., 2022). Climate change stressors (e.g., ocean acidification, sea level rise, hypoxia, warming) may have effects on populations and communities that occur regardless of regulatory protection (Bates et al., 2019;

Bruno et al., 2019). Marine heatwaves can also reduce connectivity, a key design attribute for many MPA networks, by changing prevailing current patterns (Lima et al., 2021). Mixed evidence surrounding the efficacy of MPAs in providing climate resilience may be explained in part by the single-habitat (e.g., coral reef, seagrass, kelp forest, etc.) focus of many studies, and also in part by the ways in which assemblages of species are partitioned.

Our understanding of whether and how MPAs confer ecological resilience to climate change can be improved by synthesizing the effects of regulatory protection across multiple habitats and ecosystems. Potential mechanisms producing ecological shifts in response to climate change may include altered mortality due to physiological environmental tolerances, changes in species interactions (e.g., competition, predation, disease, facilitation), adult movement across habitats and along the coast, ontogenetic shifts, and changes in recruitment success (Harley et al., 2006). Moreover, the ways in which species responses are evaluated (e.g., trait-based, functional groups, feeding guilds, trophic position, etc.) can influence detection of climate-driven outcomes. Therefore, long-term monitoring across multiple habitats subjected to similar (or the same) perturbations is needed to thoroughly examine the impacts of climate change on marine ecosystems, to test whether MPAs confer climate resilience, and to assess the relative resilience among ecosystems. Such cross-ecosystem studies are rare, especially those that include monitoring across networks of MPAs before, during, and after extreme climate change-driven perturbations.

In 1999, California passed the Marine Life Protection Act (MLPA), which expanded its system of MPAs to function as a coherent ecological network and to address six goals aimed at conservation, fisheries, and other human benefits (Marine Life Protection Act, 1999; Gleason et al., 2013). Guided by these goals, California established a network of 124 MPAs distributed along the state's entire 1,100-mile coastline that protects 16% (850 square miles) of state waters. The network protects hard- and soft-bottom habitats ranging in depth from the intertidal to 1000 m, however with few exceptions, the ecological monitoring studies have emphasized hard-bottom habitats. Leading up to and following MPA implementation, an extensive ecological monitoring effort of these habitats began in order to support adaptive management of the network (Botsford et al., 2014). During the course of California's MPA monitoring, a major marine heatwave occurred that was the consequence of two environmental anomalies: a 2014-2016 warming event known as "the Blob," and a major El Niño event in 2015-2016 (Bond et al., 2015; Di Lorenzo & Mantua, 2016; Gentemann et al., 2017). This pronounced climate perturbation was the largest marine heatwave on record (Laufkötter et al., 2020).

This study leveraged over a decade of monitoring across the rocky intertidal, kelp forest, shallow reef, and reef habitats to evaluate whether a network of MPAs confers community structure resilience to climate disturbances. Specifically, we tested the hypotheses that: (1) the 2014-16 marine heatwave event resulted in the reorganization of community structure across multiple nearshore habitats, (2) MPAs enhance the ability for ecological communities to resist and recover from the impacts of climate perturbations, and (3) species traits (thermal affinities) explain differential responses to the marine heatwave in relation to regulatory protection (MPAs). After testing these hypotheses, we explored whether MPA features (size, age, historic fishing pressure, habitat diversity, and connectivity) enhance ecological community resilience across habitats to inform the design of MPA networks resilient to climate change.

2. Methods

2.1. MPA sampling and data collection

As part of the State of California's long-term MPA evaluation and monitoring program, several habitat-specific research groups conduct annual surveys designed to monitor ecological changes over time inside MPAs and at associated reference sites (Supplementary Appendix *Methods*). Our analyses focused on four habitats that have extensive long-term monitoring data: rocky intertidal, kelp forest, shallow reef, and deep reef (Supplementary Appendix, **Figure S1**). Across the four habitats included in our analyses, three organismal groups were sampled: fishes (kelp forest, shallow reef, and deep reef), invertebrates (rocky intertidal and kelp forest), and macroalgae (rocky intertidal and kelp forest). We focused our community structure analyses on MPAs located along the temperate central coast of California (**Figure 1A**) because this area was the most comprehensively sampled region of the MPA network and had sufficient pre-marine heatwave data to evaluate baseline community structure (Supplementary Appendix, **Figure S1**). To evaluate MPA features as drivers of ecological resilience, we included MPAs across all of California for two of the habitats (rocky intertidal and kelp forest), where more extensive spatial and temporal coverage exists (see section 2.6).

Two general types of data were used in our analyses: species counts (kelp forest, shallow reef, deep reef), and the proportional cover of invertebrates and macroalgae (rocky intertidal, and kelp forest invertebrates and algae). While biomass is often used as a common measurable response across taxa (Duffy et al., 2017), it is not suitable for our analyses because

of the large number of taxa for which it is difficult to accurately measure biomass (e.g., macroalgae and invertebrates). Therefore, we elected to use a taxonomic abundance-based approach to compare changes in community structure. All analyses were conducted using published data for each habitat (Brooks et al., 2022; Cieri et al., 2022, p. 20; Malone et al., 2022; MARINe et al., 2022).

2.2. Changes in community structure associated with the marine heatwave

We used non-metric multidimensional scaling (nMDS) to visualize community structure before (2007-13), during (2014-16), and after (2017-20) the 2014-16 marine heatwave. Prior to ordination, a base similarity matrix was constructed for each habitat type using Bray-Curtis dissimilarity on Hellinger-transformed counts or percent cover of species. The Hellinger transformation converts absolute counts to the square root of proportional counts, which reduces the disproportionate contribution of highly abundant species (Legendre & Gallagher, 2001). Each MPA or reference site surveyed in a single year represents a single unit of replication. To visualize the state of each ecological community, we plotted centroids and 95% confidence ellipses that represent the generalized position of the community in ordinated 2-dimensional nMDS space before, during, and after the marine heatwave event.

We used a pairwise permutational analysis of variance (PERMANOVA) to test three hypotheses surrounding community structure changes (**Figure 2A**). First, if MPAs do not mitigate heatwave impacts on community structure, then communities inside MPAs should respond similarly (i.e., comparable change in Bray-Curtis distance) to reference sites. Second, if MPAs confer resistance, then communities inside MPAs should remain unchanged while those in reference sites shift. Finally, if MPAs enhance recovery, then communities inside MPAs should shift during the marine heatwave, but return to or move back in the direction of their previous state following the disturbance. To test these hypotheses, a single PERMANOVA was performed for each habitat and site type (MPA or reference) using pairwise comparisons between marine heatwave periods (before vs. during, before vs. after) using the *vegan* package (Oksanen et al., 2022) in R (R Core Team, 2021).

2.3. Effect of MPAs on community structure resistance and recovery

We used a multivariate distance-based approach to test whether MPAs conferred ecological community resistance to or recovery from the marine heatwave. We define resistance

as community structure (i.e., relative abundance of species) that remained unchanged during the marine heatwave (low change in distance-based centroids), and recovery as a community that returned to a similar structure post-heatwave. Resistance was evaluated by calculating the vector distance (in high dimensional space using the Bray-Curtis distance matrix) of the centroid of the ecological community between the periods before (2007-2013) and during (2014-2016) the marine heatwave (e.g., high resistance is indicated by a smaller change in distance-based centroids). Recovery was evaluated by calculating the distance between the before (2007-2013) and after period (2017-2020) centroids. We calculated the change in distance between centroids using the *betadisper* function in the *vegan* package (Oksanen et al., 2022). The *betadisper* function returns the principal coordinates of centroids, which we used to calculate distance after ensuring positive-definite eigenvalues. Finally, significance was tested using a PERMANOVA on community structure resistance (before vs. during) and recovery (before vs. after).

To explore whether the timing of community shifts coincided with temporal changes in oceanographic variables, we used a Granger causality test on Bray-Curtis dissimilarity. For this analysis, annual dissimilarity was calculated for each site (MPA or reference) and habitat relative to 2007. Dissimilarity was then offset (lagged) against oceanographic variables (see section 2.5) in one-year increments for a maximum of three years (maximum lag based on length of the time series). We used 2007 as the baseline year because it preceded the marine heatwave and because we were interested in lag effects specifically related to the marine heatwave, rather than gradual environmental and community changes over time. However, 2008 was used as the baseline year for the deep reef habitat because surveys were not extensively conducted in 2007. It is important to note that the Granger test only examines lagged time series between community change and the environmental variables, it does not examine correlations which are explored using a different test described section 2.5.

2.4. Species associated with community changes

To evaluate which species were associated with community change, we used two approaches. First, we used a Similarity Percentage Analysis (SIMPER) to decompose species composition using Bray-Curtis dissimilarity and to examine the percent contribution of each species to the before versus after marine heatwave communities. However, because SIMPER is known to confound the mean between group variation and dispersion (Warton et al., 2012), we validated the SIMPER output using the *mvabund* package (Wang et al., 2022) in R. The

mvabund package uses fitted generalized linear models to account for nonlinear mean to variance relationships of each species. This combination of approaches allowed us to determine the contribution of individual taxa to observed community structure differences. Additionally, because the PERMANOVA analyses revealed that community change was similar inside MPAs and reference sites, we analyzed compositional changes overall rather than within each site protection status. Finally, we constructed an analysis of deviance table using the multivariate generalized linear model fits to test whether species composition changed as a result of the marine heatwave (before vs. after). Test statistics and p-values for each species were generated through PIT-trap resampling.

2.5. Environmental correlates and species traits

We explored oceanographic conditions before, during, and after the marine heatwave to evaluate whether community structure shifts were explained by environmental anomalies (**Figure 1B-E**). For these environmental analyses, we used sea surface temperature (SST) at 1 km daily resolution from MURSST (Chin et al., 2017), MPA bottom temperature (BT) at 8 km daily resolution from GLORYS (Jean-Michel et al. 2021), the Biologically Effective Upwelling Transport Index (BEUTI; Jacox et al., 2018) calculated at 1 degree latitude bins, and the Multivariate Oceanographic Climate Index (MOCI), which is a long-term (30 year) indicator of several oceanographic and atmospheric conditions (García-Reyes & Sydeman, 2017) calculated at the study area level. We selected these environmental products because they provide biologically meaningful climatology at the best available spatial resolution for our study area.

To process the environmental data, we first calculated the monthly mean SST, BT, BEUTI, and quarterly MOCI values at each long-term monitoring site. We then calculated monthly anomalies for SST, BT, and BEUTI as the difference between the observed monthly mean and the baseline average (long-term average for each month, 1988-2012 for BEUTI, 1993-2012 for BT, and 2002-2012 for SST; start year of the historical climatology reflects the first year with data). Baseline averages were calculated through 2012 to accommodate a 2-year buffer before the onset of the marine heatwave in 2014. For MOCI, we calculated the annual mean (2000-2020) at each site as a standard index. To visualize and pair the environmental data with the long-term biological monitoring data, we calculated the mean anomalies across all calendar months for each year (**Figure 1B-E**). Finally, to determine whether observed shifts in community structure were associated with changes in oceanographic conditions, we used the

envfit function in the *vegan* package (Oksanen et al., 2022) to overlay the four environmental variables as vectors on the ordinated community data.

We used a trait-based fourth-corner model to evaluate effects of environmental variables and species thermal affinities on the relative abundance of all recorded taxa. Species thermal affinities were obtained from literature reported classifications and expert judgment (Supplementary Appendix, *Methods*). The fourth-corner model relates the interaction between the environment and species traits (thermal affinities) on variation in the abundance of taxa (Brown et al., 2014). Briefly, we used the *mvabund* package to fit simultaneous generalized linear models for counts of all species at each site as a function of the oceanographic conditions (SST, BT, BEUTI, MOCI), the relative representation of thermal affinities, and their interaction.

2.6. Drivers of resistance and recovery

The ecological and design context of California's network is well documented, allowing us to explore whether certain traits or MPA features conferred community structure resilience to the marine heatwave. These analyses were spatially expanded to include a subset of MPAs covering the entire network from northern to southern California, thereby providing a greater scope of MPA trait diversity. However, only the kelp forest and rocky intertidal habitats contained sufficient pre-heatwave monitoring data with consistent annual surveys in all bioregions of the state to appropriately examine drivers of ecological resilience among MPAs at the network level (Supplementary Appendix, **Figure S1**). MPA features included habitat richness and diversity (including depth-stratified hard and soft bottom, proportion of rock, and the extent of kelp forest canopy, rocky intertidal, sandy beach, coastal marsh, tidal flats, and armored shore), historic fishing pressure, MPA age and size, connectivity, and fish biomass response ratios (as a proxy for MPA performance, see Supplementary Appendix *Methods*).

We developed a two-stage multivariate model to examine the effect of MPA traits on community resistance and recovery. First, we used a PERMANOVA to identify MPAs that significantly resisted or recovered from the marine heatwave (building on the methods outlined in section 2.3). We then used a logistic regression to evaluate the probability that specific MPA traits enhanced resistance or resilience. For the logistic regression, any MPA community that significantly resisted or recovered from the marine heatwave was assigned a target level of '1', and any MPA community that did not resist or recover from the marine heatwave a '0.'

3. Results

3.1. MPAs and community structure

Ecological community change was widespread across all habitats, and three habitats (kelp forest, shallow reef, deep reef) showed no clear differences between MPAs and reference sites in the magnitude of community change (**Figure 2B**). Ecological community structure dramatically shifted as a result of the marine heatwave event across all measured nearshore habitats ($n=4$), regardless of whether the communities ($n=5$) were inside MPAs or reference sites (**Figures 2B and S5, Table 1**).

Community structure changes coincided with oceanographic anomalies associated with the marine heatwave (**Figure 1, Tables 2 and 3**). At the onset of the marine heatwave in 2014, sea surface temperature was anomalously warm by as much as 2°C, and bottom temperature was also 1°C above the baseline average. MOCI and BEUTI also experienced precipitous change during the marine heatwave, reflecting reduced upwelling and productivity, and these anomalies persisted until at least mid-2016 (**Figure 1B-E**). Although each oceanographic vector aligned well with community shifts in nMDS space (**Figure 2B**), significant correlations were habitat-specific (**Table 2**). In the rocky intertidal, SST was the only oceanographic variable significantly correlated with community change. However, for shallow reef, kelp forest fishes, and kelp forest invertebrates and algae, warmer SST and BT, and higher MOCI were significantly associated with community change. In the deep reef habitat (fishes only), the only significant oceanographic correlate was BEUTI (**Table 2**). Finally, there were no significant temporal lags determined except for one interaction between the shallow reef and BEUTI ($lag = 3$ for MPA and reference sites, **Table 3**).

For all habitats except the rocky intertidal, MPAs did not impart increased resistance to or recovery from marine heatwave-driven community changes compared to reference sites (**Figure 3, Table 1**). The rocky intertidal and deep reef were the only two habitats that resisted the marine heatwave (based on non-significant PERMANOVA result, **Figure 3A**). The rocky intertidal was the only habitat where community structure inside MPAs was not significantly different either during or post-marine heatwave (**Figure 3B**), although the trajectory of the shallow reef habitat started to move towards the pre-heatwave state beginning in the year 2018, with the biggest shifts towards recovery occurring in the MPA sites (Supplementary Appendix, **Figures S3 and S4**). In the deep reef habitat, interannual changes were more variable, resulting

in a larger resistance distance relative to the other habitats that was not significantly different (**Figures 3A** and **S3**). However, recovery was more variable than resistance. The rocky intertidal and shallow reef habitats showed relatively greater recovery than the kelp forest and deep reef habitats.

3.2. Species responses

The multivariate analyses revealed several species that explained differences between the pre- and post-heatwave periods. Among the three habitat types with monitoring of fish species (kelp forest, shallow reef, deep reef), the blue and deacon rockfish complex (*Sebastes mystinus* and *S. diaconus*) was positively correlated with the post-heatwave period (Supplementary Appendix, **Table S4**). Fish species that declined and were found within the top 80% contribution of pre- vs. post-heatwave community structure included: *Sebastes serranoides* (kelp forest), *S. chrysomelas* or *carnatus* (kelp forest), *S. miniatus* (kelp forest, shallow reef), *Brachyistius frenatus* (kelp forest), *S. semicinctus* (deep reef), and *S. hopkinsi* (deep reef). For invertebrates and algae, the multivariate analyses revealed an uptick in the abundance of purple sea urchins (*Strongylocentrotus purpuratus*) and a decline in macroalgae in both the rocky intertidal and the kelp forest habitats.

3.3. Community structure and thermal traits

The relative proportional representation of thermal affinities significantly changed during the marine heatwave for kelp forest invertebrates algae, kelp forest fishes, and shallow reef fishes ($p < 0.001$, $df = 6$, $F = 62.24$; $p < 0.05$, $df = 6$, $F = 2.18$; $p < 0.001$, $df = 4$, $F = 37.41$, respectively). Cold-temperate species significantly declined during the marine heatwave for these habitats (**Figure 4A**). During the marine heatwave, there was a slight increase in cosmopolitan species for the rocky intertidal and kelp forest (invertebrates and algae), and an even more pronounced increase in warm-temperate and subtropical fish species in the kelp forest, shallow reef, and deep reef habitats. Importantly, these changes in community composition that occurred during the marine heatwave (2014-2016) persisted into the following years (2017 and beyond), which partially explains the lack of observed recovery to the pre-heatwave community structure.

Variation in species abundance was explained by significant interactions between thermal affinities and oceanographic variables for all habitats (**Figure 4B**). In general, species

thermal affinities responded similarly across habitats. The abundance of cold-temperate species declined with increased sea surface temperature anomalies and reduced upwelling (BEUTI), while the abundance of warm-temperate, subtropical, and tropical species increased with the oceanographic conditions that were associated with the onset of the marine heatwave, such as MOCI and warming water temperature. Bottom temperature had the most variable interactive effect across habitats and thermal affinities. Interestingly, thermal associations for the deep reef habitat had an opposite sign for cold-temperate and warm-temperate interactions, relative to the other habitats.

3.4. MPA traits and ecological stability

Community structure responses were highly variable across the state-level network for MPAs, although rocky intertidal habitats showed higher resilience than kelp forests (**Figure 5**). However, none of the evaluated MPA features (age, size, historic fishing pressure, habitat diversity, connectivity, biomass response ratios) were statistically significant drivers of this variability.

4. Discussion

Our findings suggest that the 2014-16 Northeast Pacific marine heatwave impacted ecological community structure across four nearshore habitats, and that MPAs did not confer widespread resistance or recovery. Marine protected areas have gained increased attention as a conservation strategy for mitigating the effects of climate change (Wilson et al., 2018), but evidence of their efficacy in providing ecosystem-wide resilience to climate disturbances remains mixed (Roberts et al., 2017; Bates et al., 2019; Jacquemont et al., 2022). Critically, international efforts to conserve 30% of marine habitats by the year 2030 (IUCN, 2014) highlight the need for planning that considers the effect of large climate driven perturbations on local ecological processes. Therefore, while MPAs may be implemented with specific conservation targets, our study suggests that extreme climate perturbations, such as marine heatwaves, can overwhelm intended climate benefits of MPAs over the short-term (< 5 years following a marine heatwave). These results highlight the ecosystem-wide consequences of acute climate-driven perturbations despite regulatory protection.

Several ecological processes may explain the pronounced shifts observed across habitats, such as altered adult movement, changes to recruitment regimes, tropicalization,

deborealization, and shifts in species interactions such as herbivory, competition, predation, and disease (Vergés et al., 2014; García Molinos et al., 2016; Wernberg et al., 2016; Free et al., 2019; Mignot et al., 2022). First, our study found that the relative proportion of warm-temperate and subtropical species increased during and after the marine heatwave. The increased proportional representation of species with warm-water thermal affinities may be explained by adult movement into the study area, changes in recruitment patterns, or displacement of cold-temperate species (Sanford et al., 2019; Walker et al., 2020; Fredston et al., 2021). For example, the large increase in blue rockfish in kelp forest, shallow reef, and deep reef habitats was associated with strong recruitment and pelagic young-of-the-year abundance of rockfishes in midwater trawl surveys at the start of the marine heatwave period (Field et al. 2021). Large increases in the subtropical wrasse, seniorita (*Oxyjulis californica*), were also observed in multiple habitats, contributing to community change. Second, during the marine heatwave, a large-scale outbreak of herbivorous sea urchins occurred throughout the study region that coincided with precipitous declines in macroalgae and the loss of an important benthic mesopredator, the sunflower sea star, due to a large-scale marine disease outbreak (Harvell et al., 2019; Smith et al., 2021).

Species life history traits in relation to the marine heatwave event may explain why the rocky intertidal was the only habitat where community structure exhibited resilience. Variation in stress tolerance to air temperature is a fundamental driver of rocky intertidal community structure. Although 2014 was the warmest year on land in California, the sustained sea surface temperature anomalies associated with ocean warming during the marine heatwave may have impacted the rocky intertidal less than the subtidal habitats. Within the rocky intertidal, resilience in MPAs may be explained by increased propagule delivery to MPAs, particularly by long-lived foundation species that stabilize the community (Raimondi & Smith, 2022), or by the removal (through harvest) of habitat-forming mussels (*Mytilus spp.*) in reference sites. Additionally, the rocky intertidal is the only habitat that used a fixed-plot design (Supplementary Appendix, *Methods*) and this methodological form of sampling could have resulted in smaller propagated spatial variance perceived as enhanced resilience relative to the sampling used in the other habitats. More research is needed to distill the mechanistic processes associated with MPA resilience in the rocky intertidal.

The primary regulation associated with MPAs in California involves a restriction of fishing activities. Therefore, it is not surprising that community shifts occurred in MPAs and reference sites simultaneously for most habitats, since many of the species exhibiting the biggest changes

are not directly targeted by fishing activities. Moreover, other studies have documented increases in targeted species biomass inside of MPAs within this system, which is a focal MPA conservation objective (Field et al. 2021). Similar responses to the marine heatwave in southern California fish communities were reported by Freedman et al. (2020), who found that non-targeted subtropical species were most responsible for community reorganization. Ziegler et al. (Ziegler et al., 2023) also reported that fish species diversity recovered more quickly after the heatwave inside of MPAs.

Although the anomalously warm environmental conditions subsided after 2016, changes in community structure persisted, especially in the kelp forest, shallow reef, and deep reef habitats. These results are particularly interesting in the context of ecosystem stability and transition dynamics. Given the highly variable recruitment of the dominant fishes in the study region (Schroeder et al., 2019; Field et al., 2021), it is possible that sufficient time has not elapsed for the communities to return to a pre-perturbed state. Lagged effects due to ontogenetic shifts and methodological sampling that disproportionately select for adults may also contribute to the observed lack of recovery. Declines in vermilion rockfish in the shallow reef habitat coincided with increases in the deep reef habitat, likely reflecting ontogenetic movements from shallow to deep habitats. In addition, the shallow reef habitat monitoring program used hook and line sampling, which disproportionately selects individuals that are older than 2-3 years, which is why lagged effects of oceanography were more likely to be detected in this habitat (Ziegler et al. 2023). Moreover, many species in the California Current are slow-growing, late to mature, long-lived, and relatively sedentary with small home ranges (Field et al., 2021). These life history traits may create inertia to resistance or recovery from change. However, the persistence of novel community structure configurations observed in this study despite the return of pre-heatwave environmental conditions highlights the need for further assessments of community transition dynamics over ecologically meaningful timescales.

Our finding of no effect of MPA features on dampening marine heatwave-driven responses in the rocky intertidal and kelp forest habitats is particularly interesting given that habitat mosaics, historic fishing effort, and connectivity have been linked to MPA conservation capacity (Bastari et al., 2016). However, this finding does not diminish the importance of MPA networks for addressing conservation priorities; rather, because MPA networks may not inherently provide resilience and absorb climate perturbations, conservation goals may be limited in their capacity to fully achieve intended outcomes related to climate change mitigation. For example, the widespread effects of marine heatwaves and other climate perturbations may

overwhelm local stressors (e.g., fishing, marine pollution) that MPAs were initially successful at mitigating (Bruno et al., 2019). These results highlight the need for management frameworks that include climate adaptation strategies and the protection of range-shift corridors (Burrows et al., 2014).

Increasing our understanding of the pathways through which marine heatwaves restructure ecological communities is central to developing adaptive management solutions. In our study, we used a taxonomic (i.e., species) based approach to evaluate changes in community structure, but functional diversity may also be impacted by warming events and should be explored (McLean et al., 2019; Murgier et al., 2021). Prolonged warming events may differentially impact groups and guilds of species with similar functional traits (Harvey et al., 2021). Moreover, in order to understand the ability of MPA networks to resist and recover from future marine heatwaves, it is critical to have sufficient monitoring across multiple habitats and regions. Because pre-perturbation data are essential for establishing baselines and comparatively evaluating ecological responses, consistent monitoring is fundamental to capture the effect of marine heatwave events. Although the timing of marine heatwaves is unpredictable, evidence suggests that the frequency and magnitude of abrupt warming events are expected to increase (Frölicher et al., 2018; Holbrook et al., 2020). Finally, the outcomes of resilience can vary depending on the analytical procedures used, and therefore performance measures should be carefully and clearly defined.

Evidence of MPAs as a tool for mitigating the effects of climate change remains controversial, especially since most MPAs were initially designed for other conservation priorities. Our analysis of ecological community change across a network of MPAs highlights that widespread effects of climate-driven stressors such as marine heatwaves can dramatically restructure ecological communities, regardless of regulatory protection. Improved resilience capacity of MPA networks will require integrating adaptive management with careful consideration of how abrupt climate change-driven perturbations may inhibit intended conservation outcomes.

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489 Author Contributions Statement

490 JGS, CMF, CL, SH, RS, DM, KN, and JEC conceived the ideas and designed methodology;
491 JGS, CMF, CL, JB, MC, SH, PR, SZ, and JEC collected the data; JGS, CMF, CL, JB, and CA
492 analyzed the data; JGS led the writing of the manuscript. All authors contributed substantially to
493 revisions. The authors have agreed to be listed and approve the manuscript for submission.

494 Conflict of Interests Statement

495 The authors have no conflicts of interest to declare.

496 Data Availability Statement

497 All source code and data are available on GitHub: <https://github.com/NCEAS/ca-mpa>

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Table 1. Results from a series of pairwise permutational analysis of variance (PERMANOVA) tests on community resistance (before-during) and resilience (before-after). PERMANOVAs were performed separately for each habitat and calculated on Bray-Curtis dissimilarity matrices. Pseudo p-values were generated using 999 permutations of residuals.

Habitat	MPA type	Transition	B-C distance	Sum of squares	R-squared	Psuedo F	P(perm)
Rocky intertidal	Reference	Resistance	0.059	0.155	0.020	1.883	0.071
		Recovery	0.053	0.219	0.025	2.635	0.006*
	MPA	Resistance	0.064	0.154	0.026	1.824	0.114
		Recovery	0.063	0.174	0.026	1.946	0.091
Kelp forest inverts and algae	Reference	Resistance	0.085	0.490	0.061	4.381	0.001*
		Recovery	0.125	0.921	0.099	8.211	0.001*
	MPA	Resistance	0.080	0.333	0.047	2.823	0.003*
		Recovery	0.142	0.849	0.102	7.189	0.001*
Kelp forest fishes	Reference	Resistance	0.081	0.249	0.047	3.220	0.007*
		Recovery	0.100	0.640	0.109	9.098	0.001*
	MPA	Resistance	0.066	0.210	0.050	2.944	0.015*
		Recovery	0.124	0.505	0.109	7.569	0.001*
Shallow reef	Reference	Resistance	0.073	0.146	0.061	2.349	0.064
		Recovery	0.071	0.586	0.188	9.515	0.001*
	MPA	Resistance	0.066	0.159	0.093	3.676	0.002*
		Recovery	0.112	0.486	0.225	11.882	0.001*
Deep reef	Reference	Resistance	0.136	0.198	0.124	1.839	0.064
		Recovery	0.167	0.681	0.308	6.687	0.001*
	MPA	Resistance	0.104	0.121	0.082	1.163	0.296
		Recovery	0.107	0.337	0.163	2.530	0.015*

Table 2. Envfit scores indicating the significance level of correlations between oceanographic conditions and community change in non-metric multidimensional scaling (NMDS) space.

Habitat	Oceanographic variable	NMDS1	NMDS2	R-squared	P
	SST	-0.7912547	0.61148669	0.04470378	0.082
Rocky intertidal	BEUTI	0.69836497	-0.7157418	0.04526633	0.089
	MOCI	-0.7073517	0.70686181	0.02268704	0.294
	SST	-0.9996435	0.02669789	0.09539347	0.004*
Kelp forest inverts and algae	BEUTI	0.9825685	0.18590091	0.03408813	0.128
	MOCI	-0.9999658	-0.0082756	0.07069741	0.009*
	BT	-0.9656009	0.26002862	0.16787102	0.001*
	SST	-0.8460518	-0.5331007	0.06414416	0.016*
Kelp forest fishes	BEUTI	0.5656038	0.82467711	0.05077399	0.029*
	MOCI	-0.6502115	-0.7597532	0.1197755	0.002*
	BT	-0.9838682	-0.178895	0.07219366	0.012*
	SST	0.2728423	-0.9620588	0.17089017	0.002*
Shallow reef	BEUTI	-0.5025552	0.86454515	0.02234512	0.401
	MOCI	0.2317249	-0.9727814	0.28615304	0.001*
	BT	0.24773479	-0.9688279	0.16047632	0.002*
	SST	0.99894071	0.04601577	0.04552869	0.524
Deep reef	BEUTI	-0.9103123	-0.4139221	0.25415853	0.014*
	MOCI	0.9987318	-0.0503467	0.02164017	0.726
	BT	0.67510729	-0.7377196	0.02604815	0.699

Table 3. Granger causality test results between community dissimilarity and oceanographic anomalies using a maximum lag of 3 years. Only one significant lag effect was detected (shallow reef-reference-BEUTI; bolded and marked with an asterisk). Note that the Granger test only examines temporal lags, it does not test for associations (included in Table 2).

Habitat	MPA type	Variable	Res.Df	F	P	Lag order (years)
Rocky intertidal	Reference	SST	6	0.307	0.821	—
		BEUTI	6	1.712	0.335	—
		MOCI	6	2.545	0.232	—
	MPA	SST	6	0.065	0.975	—
		BEUTI	6	0.338	0.802	—
		MOCI	6	1.644	0.346	—
Kelp forest inverts and algae	Reference	SST	6	1.212	0.439	—
		BT	6	1.049	0.485	—
		BEUTI	6	1.609	0.353	—
	MPA	MOCI	6	0.285	0.835	—
		SST	6	0.156	0.919	—
		BT	6	0.471	0.724	—
Kelp forest fishes	Reference	BEUTI	6	3.043	0.193	—
		MOCI	6	0.308	0.820	—
	MPA	SST	6	1.170	0.450	—
		BT	6	0.289	0.832	—
		BEUTI	6	0.292	0.831	—
	MPA	MOCI	6	1.136	0.459	—
Shallow reef	Reference	SST	6	2.253	0.261	—
		BT	6	0.872	0.543	—
		BEUTI	6	1.035	0.489	—
	MPA	MOCI	6	0.559	0.678	—
		SST	6	0.675	0.623	—
		BT	6	0.574	0.670	—
Shallow reef	Reference	BEUTI	6	267.647	0.001*	3
		MOCI	6	0.435	0.744	—
	MPA	SST	6	0.321	0.812	—
		BT	6	0.239	0.865	—
		BEUTI	6	10.288	0.044*	3
	MPA	MOCI	6	0.586	0.664	—
Deep reef	Reference	SST	3	0.075	0.810	—
		BT	3	0.237	0.674	—
		BEUTI	3	0.219	0.686	—
	MPA	MOCI	3	0.167	0.722	—
		SST	3	0.597	0.521	—
		BT	3	5.568	0.142	—
Deep reef	MPA	BEUTI	3	3.814	0.190	—
		MOCI	3	0.410	0.587	—

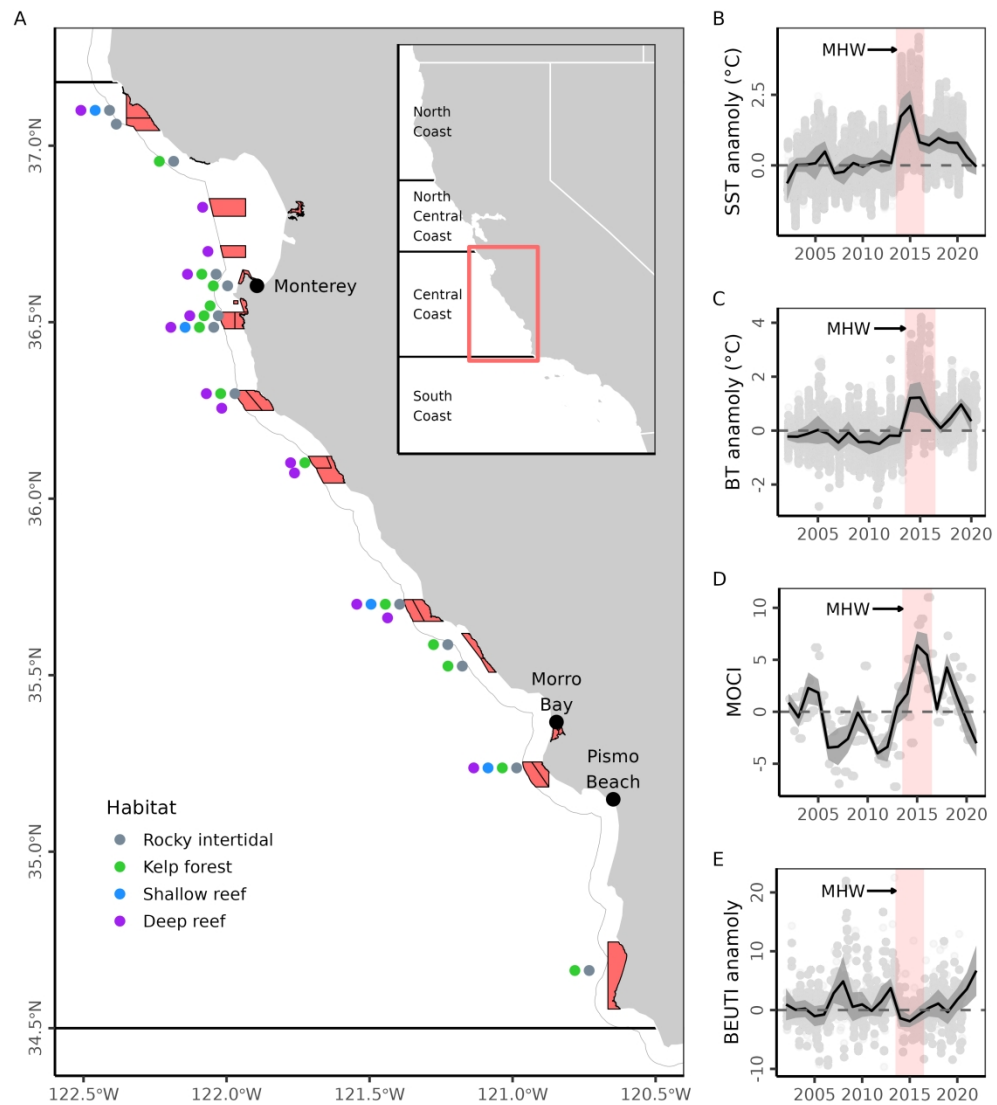


Figure 1. The (A) coverage of ecological monitoring in marine protected areas (MPAs) in California's Central Coast region and (B-E) exposure of these MPAs to four indicators of oceanographic conditions. In (A), points indicate which habitats were monitored both inside MPAs and reference sites (i.e., points indicate data availability, not the location of sampling sites), the dark horizontal lines delineate the Central Coast region, and the thin gray line indicates state waters (3 nautical miles offshore and all of Monterey Bay). Oceanographic indicators include: (B) sea surface temperature (SST); (C) bottom temperature (BT); (D) the multivariate oceanographic climate index (MOCI); and (E) the biologically effective upwelling index (BEUTI). Lines indicate the median and shading indicates the 95% confidence interval. The 2014-2016 marine heatwave (MHW) is indicated by the vertical red rectangle.

374x419mm (236 x 236 DPI)

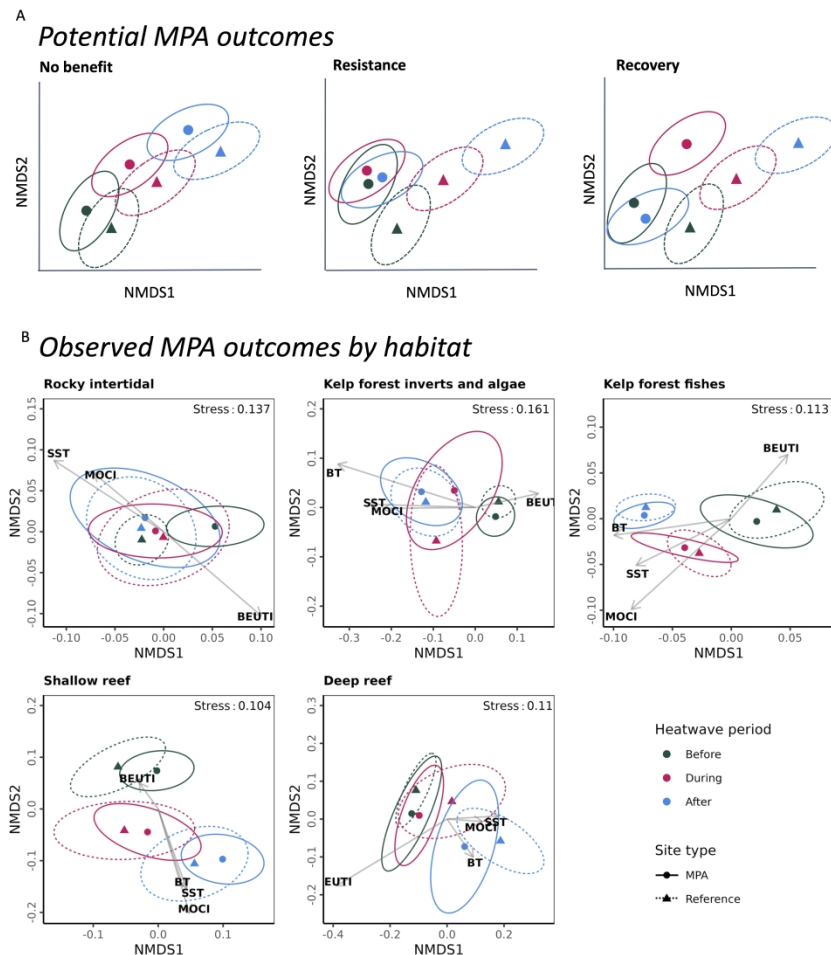


Figure 2. (A) Potential and (B) observed shifts in community composition from 2007 to 2020. Panel A illustrates a typology of potential community composition shifts: (1) “No benefit”, where communities inside MPAs respond similarly to reference sites; (2) “Resistance”, where communities inside MPAs remain stable while those in reference sites shift; and (3) “Recovery”, where communities inside MPAs shift during the heatwave, but return to their previous state following the disturbance while reference sites do not return. Panel B shows observed shifts in community composition before (2007–2013), during (2014–2016), and after (2017–2020) the marine heatwave inside MPAs (circles) and reference sites (triangles) in the Central Coast region of California. Each sub-panel represents a habitat and each point depicts the centroid position with 95% confidence ellipses. Also included are vectors for each environmental indicator: sea surface temperature (SST), bottom temperature (BT), the multivariate ocean climate index (MOCI), and the biologically effective upwelling transport index (BEUTI). The trajectory of each vector reflects its correlation with community structure (Table 2). Therefore, indicators that are highly correlated with changes in community structure are aligned with the centroids (points).

1481x2116mm (72 x 72 DPI)

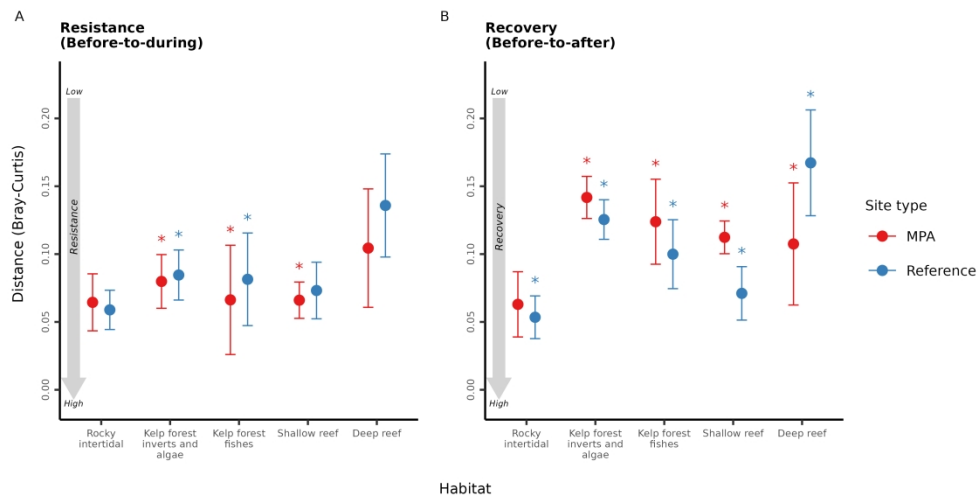


Figure 3. Community resistance (before-to-during marine heatwave comparison) and recovery (before-to-after marine heatwave comparison) as measured by distance between centroids. Each point depicts the distance between the pre-heatwave centroid (before) and the during-heatwave or the post-heatwave centroid inside MPAs and reference sites. Therefore, higher values indicate less resistance or recovery. Error bars depict the pooled standard error between centroids and the asterisks denote significant differences in community composition between heatwave periods, as derived from a pairwise permutational analysis of variance (PERMANOVA). Points without asterisks indicate resistance or resilience (as measured by non-significant PERMANOVA). Note that some communities have inherently greater interannual variability, potentially resulting from variation in sampling methodology, which can lead to larger mean distances that are not significantly different (Supplementary Appendix, Figure S6).

452x387mm (236 x 236 DPI)

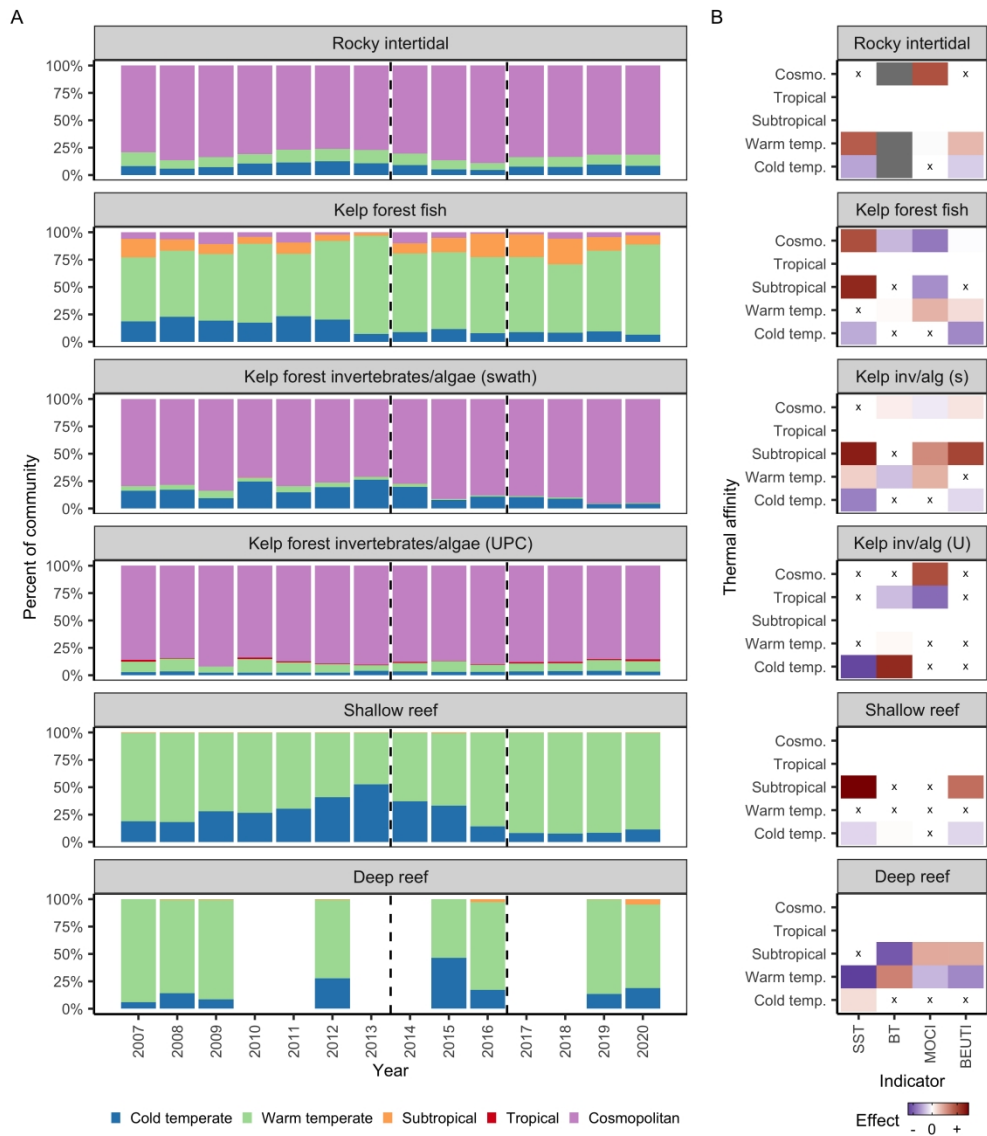


Figure 4. The (A) proportional community composition by thermal affinity groups from 2007-2020 and the (B) interactive effect of oceanographic indicators (sea surface temperature anomaly, SST; bottom temperature anomaly, BT; multivariate oceanographic climate index, MOCI; biologically effective upwelling transport index, BEUTI) and species traits on variance in the abundance of species over the same time period. In (A), vertical lines bound the 2014-2016 marine heatwave years. In (B), colors indicate the standardized beta coefficients for all trait-oceanographic indicator interaction terms, based on multiple generalized linear-LASSO models. Beta coefficients were scaled to unit variance to make them visually comparable. Darker squares indicate stronger associations; positive associations are red and negative associations are blue. Black x's mark interaction terms dropped in model selection. White squares without x's indicate traits that were never observed. Dark gray squares indicate non-applicable indicators.

1375x1587mm (72 x 72 DPI)

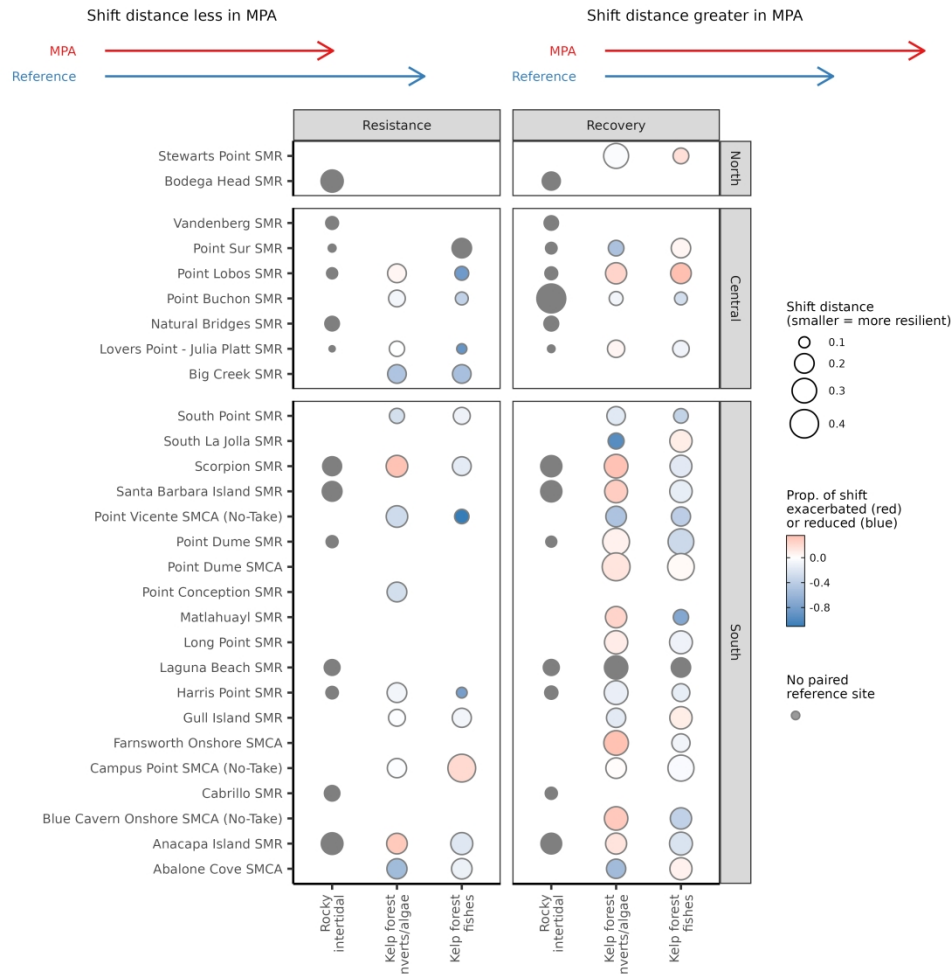


Figure 5. Resistance (before-to-during marine heatwave comparison) and resilience (before-to-after marine heatwave comparison) of community structure to the 2014-2016 marine heatwave by marine protected area (MPA) and habitat type along a latitudinal gradient. Point size indicates the Bray-Curtis distance change in the MPA relative to the reference site $[(\text{DistanceMPA} - \text{DistanceReference}) / \text{DistanceMPA}]$. Therefore, smaller points indicate MPAs that exhibited greater resistance or recovery (i.e., communities inside the MPA shifted smaller distances). Point color indicates the magnitude of the shift of community structure in a given MPA relative to its paired reference site. Red shades indicate MPAs where the change in distance was greater than the paired reference site (i.e., shift exacerbated in MPAs relative to reference sites). Blue shades indicate MPAs where the change in distance was greater in the paired reference site than in the MPA (i.e., community structure changes were less in the MPA). Note that the rocky intertidal does not use a paired MPA-reference sampling design (reference site selection is described in Supplementary Appendix, Methods) and therefore the grey points indicate MPAs without the necessary data from adjacent reference sites. Missing points indicate insufficient data to evaluate changes.

419x419mm (236 x 236 DPI)