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1 A marine protected area network does not confer
2 community structure resilience to a marine heatwave
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5 Joshua G. Smith^{1,2*}, Christopher M. Free^{3,4}, Cori Lopazanski^{1,3}, Julien Brun¹, Clarissa R.
6 Anderson⁵, Mark H. Carr⁶, Joachim Claudet⁷, Jenifer E. Dugan⁴, Jacob G. Eurich^{8,1}, Tessa B.
7 Francis⁹, Scott L. Hamilton¹⁰, David Mouillot^{11,12}, Peter T. Raimondi⁶, Richard M. Starr¹⁰, Shelby
8 L. Ziegler¹³, Kerry J. Nickols^{14,15}, Jennifer E. Caselle⁴

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

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

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

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

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

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

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

21 ⁸ Environmental Defense Fund, Santa Barbara, CA, USA

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

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

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

25 ¹² Institut Universitaire de France, IUF, Paris, France

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

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

28 ¹⁵ Current affiliation: Ocean Visions, Leesburg, VA, USA

29

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

32 **Running Title:** MPAs do not confer climate resilience

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37 Abstract

38 Marine protected areas (MPAs) have gained attention as a conservation tool for enhancing
39 ecosystem resilience to climate change. However, empirical evidence explicitly linking MPAs to
40 enhanced ecological resilience is limited and mixed. To better understand whether MPAs can
41 buffer climate impacts, we tested the resistance and recovery of marine communities to the
42 2014-2016 Northeast Pacific heatwave in the largest scientifically designed MPA network in the
43 world off the coast of California, USA. The network consists of 124 MPAs (48 no-take, 76
44 partial-take) implemented at different times, with full implementation completed in 2014. We
45 compared fish, benthic invertebrate, and macroalgal community structure inside and outside of
46 seven no-take MPAs across rocky intertidal, kelp forest, shallow reef, and deep reef nearshore
47 habitats in California's Central Coast region from 2007-2020. We also explored whether MPA
48 features, including age, size, depth, proportion rock, historic fishing pressure, habitat diversity
49 and richness, connectivity, and fish biomass response ratios (proxy for ecological performance),
50 conferred climate resilience for kelp forest and rocky intertidal habitats spanning 28 MPAs
51 across the full network. Ecological communities dramatically shifted due to the marine heatwave
52 across all four nearshore habitats, and MPAs did not facilitate habitat-wide resistance or
53 recovery. Only in protected rocky intertidal habitats did community structure significantly resist
54 marine heatwave impacts. Community shifts were associated with a pronounced decline in the
55 relative proportion of cold-water species and an increase in warm-water species. MPA features
56 did not explain resistance or recovery to the marine heatwave. Collectively, our findings suggest
57 that MPAs have limited ability to mitigate the impacts of marine heatwaves on community
58 structure. Given that mechanisms of resilience to climate perturbations are complex, there is a
59 clear need to expand assessments of ecosystem-wide consequences resulting from acute
60 climate-driven perturbations, and the potential role of regulatory protection in mitigating
61 community structure changes.

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

64 1. Introduction

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

77 Marine protected areas (MPAs) are an important conservation strategy for preserving
78 biodiversity and nature's contributions to people (Grorud-Colvert et al., 2021). MPAs may
79 provide network-scale population connectivity that can enhance spillover of individuals and the
80 replenishment of populations in both protected and fished areas (Harrison et al., 2012;
81 Williamson et al., 2016; Baetscher et al., 2019; Di Lorenzo et al., 2020; Goetze et al., 2021).
82 Although most MPAs were initially designed to reduce the effects of overfishing and habitat loss,
83 they are frequently hypothesized to provide long-term protection against climate impacts
84 (Roberts et al., 2017; Hofmann et al., 2021). For example, networks of MPAs may provide
85 refugia as species redistribute in response to climate change, owing to lower anthropogenic
86 stressors and higher population sizes resulting from reduced harvest (McLeod et al., 2009; Carr
87 et al., 2017). MPA features such as habitat diversity, historic fishing pressure, age, and size
88 may also influence the capacity for MPAs to provide ecological resilience (Jacquemont et al.,
89 2022). As such, MPAs and MPA networks are being increasingly highlighted as a key tool for
90 enhancing climate resilience (IUCN-WCPA, 2008; Jacquemont et al., 2022).

91 Despite the growing number of studies examining MPAs as a tool for mitigating climate
92 impacts, the effectiveness of MPAs (both individually and as networks) for enhancing the
93 resilience (i.e., resistance to and recovery from disturbance, Bates et al., 2019) of marine
94 communities to climate change remains contested (Johnson et al., 2022, but see Jacquemont et
95 al. 2022). Climate change stressors (e.g., ocean acidification, sea level rise, hypoxia, warming)

96 may have effects on populations and communities that occur regardless of regulatory protection
97 (Bates et al., 2019; Bruno et al., 2019). Marine heatwaves can also reduce connectivity by
98 changing prevailing current patterns – a key design attribute for many MPA networks (Lima et
99 al., 2021). Mixed evidence surrounding the efficacy of MPAs in providing climate resilience may
100 be explained in part by the single-habitat (e.g., coral reef, seagrass, kelp forest, etc.) focus of
101 many studies, and also in part by the ways in which assemblages of species are partitioned.

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

117 In 1999, California passed the Marine Life Protection Act (MLPA), which expanded its
118 system of MPAs to function as a coherent ecological network and to address six goals aimed at
119 conservation, fisheries, and other human benefits (Marine Life Protection Act, 1999; Gleason et
120 al., 2013). Guided by these goals, California established a network of 124 MPAs (48 no-take, 76
121 partial-take) distributed along the state's entire 1,300-kilometer coastline that protects 16% of
122 state waters. The network protects hard- and soft-bottom habitats ranging in depth from the
123 intertidal to depths of 1,000 m. However, with few exceptions, ecological monitoring studies
124 focused on hard-bottom habitats. Leading up to and following MPA implementation, an
125 extensive ecological monitoring effort of these habitats began to support adaptive management
126 of the network (Botsford et al., 2014). During the course of California's MPA monitoring, a major
127 marine heatwave occurred that was the consequence of two environmental anomalies: a 2014-
128 2015 warming event known as "the Blob," and a major El Niño event in 2015-2016 (Bond et al.,

129 2015; Di Lorenzo & Mantua, 2016; Gentemann et al., 2017). This pronounced climate
130 perturbation was the largest marine heatwave on record in California (Laufkötter et al., 2020).

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

142 2. Methods

143 2.1. MPA sampling and data collection

144 As part of the State of California's long-term MPA evaluation and monitoring program,
145 several habitat-specific research groups conduct annual surveys designed to monitor ecological
146 changes over time inside MPAs and at areas of comparable habitat outside MPAs (**Figure 1A;**
147 **Figure S1**, Supplementary Appendix *Figures*). Conceptually, while MPAs could be considered
148 the "treatment" or "control" in our analyses (i.e., fishing is considered either the experiment or
149 the control), we take a social-ecological system perspective and consider human activities,
150 including fishing, to be integral system components (Kandel et al., 2022). Thus, in our analytical
151 framework, MPAs are considered the experimental treatment where fishing is removed (e.g.,
152 Pacoureaux et al., 2023).

153 Our analyses focused on four habitats that have extensive long-term monitoring data:
154 rocky intertidal, kelp forest, shallow reef, and deep reef (**Figure 1A; Figure S1**, Supplementary
155 Appendix *Figures*). Across the four habitats included in our analyses, three organismal groups
156 were sampled: macroalgae (rocky intertidal and kelp forest), conspicuous mobile and sessile
157 invertebrates (rocky intertidal and kelp forest), and fishes (kelp forest, shallow reef, and deep
158 reef). We focused our community structure analyses on MPAs located along the temperate

159 Central Coast of California (**Figure 1A**) because this area was the most comprehensively
160 sampled region of the MPA network and had sufficient pre-marine heatwave data to evaluate
161 baseline community structure (**Figure S1**, Supplementary Appendix *Figures*). To evaluate MPA
162 features as potential drivers of ecological resilience, we included MPAs across all of California
163 for two of the habitats (rocky intertidal and kelp forest), where more extensive spatial and
164 temporal coverage exists (see section 2.6).

165 Two general types of data were used in our analyses: species counts (kelp forest,
166 shallow reef, deep reef), and the proportional cover of invertebrates and macroalgae (rocky
167 intertidal and kelp forest invertebrates and algae). While biomass is often used as a common
168 measurable response across taxa (Duffy et al., 2017), it is not suitable for our analyses because
169 of the large number of taxa for which it is difficult to accurately measure biomass (e.g.,
170 macroalgae and invertebrates). Therefore, we elected to use a taxonomic abundance-based
171 approach to compare changes in community structure. All analyses were conducted using
172 published data for each habitat (Brooks et al., 2022; Cieri et al., 2022; Malone et al., 2022;
173 MARINe et al., 2022).

174 2.2. Changes in community structure associated with the marine heatwave

175 We used non-metric multidimensional scaling (nMDS) to visualize community structure
176 before (2007-13), during (2014-16), and after (2017-20) the 2014-16 marine heatwave. Prior to
177 ordination, a base similarity matrix was constructed for each habitat type using Bray-Curtis
178 dissimilarity on Hellinger-transformed counts or on percent cover of species. The Hellinger
179 transformation converts absolute counts to the square root of proportional counts, which
180 reduces the disproportionate contribution of highly abundant species (Legendre & Gallagher,
181 2001). We elected to use the transformation to relative species abundance to improve the
182 robustness, comparability, and ecological interpretation of our community structure analyses.
183 Each site sampled inside or outside of a MPA surveyed in a single year represents a single unit
184 of replication. To visualize the state of each ecological community, we plotted centroids and
185 95% confidence ellipses that represent the generalized position of the community in ordinated
186 2-dimensional nMDS space before, during, and after the marine heatwave event.

187 We used a pairwise permutational analysis of variance (PERMANOVA) to test three
188 hypotheses surrounding community structure changes (**Figure 2A**). First, if MPAs do not
189 mitigate marine heatwave impacts on community structure, then communities inside MPAs

190 should respond similarly (i.e., comparable change in multivariate distance) to those outside.
191 Second, if MPAs confer resistance, then communities inside MPAs should remain unchanged
192 while those outside shift. Finally, if MPAs enhance recovery, then communities inside MPAs
193 should shift during the marine heatwave, but return to or move back in the direction of their
194 previous state following the disturbance. To test these hypotheses, a single PERMANOVA was
195 performed for each habitat and site type (inside or outside a MPA) using pairwise comparisons
196 between marine heatwave periods (before vs. during, before vs. after) using the *pairwiseAdonis*
197 wrapper function (Martinez Arbizu, 2019) in the *vegan* package (Oksanen et al., 2022) in R (R
198 Core Team, 2021).

199 2.3. Effect of MPAs on community structure resistance and recovery

200 We used a multivariate distance-based approach to test whether MPAs conferred
201 ecological community resistance to or recovery from the marine heatwave. We refer to this
202 measurement as ‘multivariate distance’ to distinguish it from ‘geographic distance,’ which is
203 often a measure of climate change impacts on marine species distributions. We define
204 resistance as community structure (i.e., relative abundance of species) that remained
205 unchanged during the marine heatwave (low change in multivariate distance-based centroids),
206 and recovery as a community that returned to a similar structure post-heatwave. Resistance
207 was evaluated by calculating the multivariate vector distance (in high dimensional space using
208 the Bray-Curtis dissimilarity matrix) of the centroid of the ecological community between the
209 periods before (2007-2013) and during (2014-2016) the marine heatwave (e.g., high resistance
210 is indicated by a smaller change in multivariate distance-based centroids).

211 Recovery was evaluated by calculating the multivariate distance between the before
212 (2007-2013) and after period (2017-2020) centroids. We calculated the change in multivariate
213 distance between centroids using the *betadisper* function in the *vegan* package (Oksanen et al.,
214 2022). The *betadisper* function returns the principal coordinates of centroids, which we used to
215 calculate multivariate distance after ensuring positive-definite eigenvalues. Finally, statistical
216 significance was tested using a PERMANOVA on community structure resistance (before vs.
217 during) and recovery (before vs. after).

218 To explore whether the timing of community shifts coincided with temporal changes in
219 oceanographic variables, we used a Granger causality test on Bray-Curtis dissimilarity. For this
220 analysis, annual dissimilarity was calculated for each site (inside or outside a MPA) and habitat

221 relative to 2007. Dissimilarity was then offset (lagged) against oceanographic variables (see
222 section 2.5) in one-year increments for a maximum of three years (maximum lag based on
223 length of the time series). We used 2007 as the baseline year because it preceded the marine
224 heatwave and because we were interested in lag effects specifically related to the marine
225 heatwave, rather than gradual environmental changes over time. However, 2008 was used as
226 the baseline year for the deep reef habitat because surveys were not extensively conducted in
227 2007. It is important to note that the Granger test only examines lagged effects between the
228 time series of community change and the environmental variables, it does not examine
229 correlations, which are explored using other diagnostics described in section 2.5.

230 2.4. Species associated with community changes

231 To evaluate which species were associated with community change, we used two
232 approaches. First, we used a Similarity Percentage Analysis (SIMPER) to decompose
233 community structure using Bray-Curtis dissimilarity and to examine the percent contribution of
234 each species to the before versus after marine heatwave communities. However, because
235 SIMPER is known to confound the mean between group variation and dispersion (Warton et al.,
236 2012), we cross-validated the SIMPER output using the *mvabund* package (Wang et al., 2022)
237 in R. The *mvabund* package uses fitted generalized linear models to account for nonlinear
238 mean-to-variance relationships of each species. Both of these analyses were conducted on the
239 absolute abundance of species (rather than relative abundance) because they are not sensitive
240 to common or rare taxa. This combination of approaches allowed us to determine the
241 contribution of individual taxa to observed community structure differences. Additionally,
242 because the PERMANOVA analyses revealed that community change was similar inside and
243 outside of MPAs, we analyzed compositional changes overall rather than within each site by
244 protection status. Finally, we constructed an analysis of deviance table using the multivariate
245 generalized linear model fits to test whether species structure changed as a result of the marine
246 heatwave (before vs. after). Test statistics and p-values for each species were generated using
247 the PIT-trap (probability integral transform) resampling method.

248 2.5. Environmental correlates and species traits

249 We explored temperature and oceanographic conditions before, during, and after the
250 marine heatwave to evaluate whether community structure shifts were explained by
251 environmental changes (**Figure 1B-F**, **Figure S2** Supplementary Appendix *Figures*). For these

252 environmental analyses, we used air temperature (AT, °C) measured *in situ* at rocky intertidal
253 long-term monitoring sites (as an environmental correlate for rocky intertidal communities only,
254 Supplementary Appendix *Methods*); sea surface temperature (SST, °C) at 1 km daily resolution
255 from MURSST (Chin et al., 2017), sea bottom temperature (SBT, °C) at 8 km daily resolution
256 from GLORYS (Jean-Michel et al. 2021), the Biologically Effective Upwelling Transport Index
257 (BEUTI, $\text{mmol m}^{-1} \text{s}^{-1}$; Jacox et al., 2018) calculated at 1 degree latitude bins, and the
258 Multivariate Oceanographic Climate Index (MOCI), which is a long-term (30 year) indicator of
259 several oceanographic and atmospheric conditions (García-Reyes & Sydeman, 2017)
260 calculated at the regional level (Central California). We selected these environmental indicators
261 and associated products because they provide biologically meaningful climatology at the best
262 available spatial resolution for our study area.

263 To process the environmental data, we first calculated the monthly mean AT, SST, SBT,
264 BEUTI, and quarterly MOCI values at each site. We then calculated monthly anomalies for AT,
265 SST, SBT, and BEUTI as the difference between the observed monthly mean and the baseline
266 average (long-term average for each month, 2000-2012 for AT, 1988-2012 for BEUTI, 1993-
267 2012 for SBT, and 2002-2012 for SST; start year of the historical climatology reflects the first
268 year with data). Baseline averages were calculated through the end of 2012 to accommodate a
269 buffer before the onset of the marine heatwave in 2014. For MOCI, we calculated the annual
270 mean (2000-2020) at each site as a standard index. To visualize and pair the environmental
271 data with the long-term biological monitoring data, we calculated the mean anomalies across all
272 calendar months for each year (**Figure 1B-F**). Finally, to determine whether observed shifts in
273 community structure were associated with changes in oceanographic conditions, we used the
274 *envfit* function in the *vegan* package (Oksanen et al., 2022) to overlay the four environmental
275 variables as vectors on the ordinated community data. The *envfit* function computes the rank-
276 based correlation coefficient and significance is evaluated through permutation-based
277 resampling.

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

285 oceanographic conditions (AT, SST, SBT, BEUTI, MOCI), the relative representation of thermal
286 affinities, and their interaction.

287 2.6. Drivers of resistance and recovery

288 The ecological and design context of California's network is well documented, allowing
289 us to explore whether certain MPA features conferred community structure resilience to the
290 marine heatwave. These analyses were spatially expanded to include a subset of MPAs
291 covering the entire network from northern to southern California, thereby providing a greater
292 scope of MPA feature diversity (**Figure S3**, Supplementary Appendix *Figures*). However, only
293 the kelp forest and rocky intertidal habitats contained sufficient pre-heatwave monitoring data
294 with consistent annual surveys in all bioregions of the state to appropriately examine drivers of
295 ecological resilience among MPAs at the network level (**Figure 1A**; **Figure S1**, Supplementary
296 Appendix *Figures*). MPA features included habitat richness and habitat diversity (calculated
297 using Shannon-Wiener on depth-stratified hard and soft bottom, proportion of rock, and the
298 extent of kelp forest canopy, rocky intertidal, sandy beach, coastal marsh, tidal flats, and
299 armored shore), historic fishing pressure, MPA age and size, connectivity, and kelp forest fish
300 biomass response ratios (as a proxy for MPA ecological performance, see Supplementary
301 Appendix *Methods*).

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

309 3. Results

310 3.1. Community structure resistance and recovery

311 Ecological community change was widespread across all habitats, and three habitats
312 (kelp forest, shallow reef, deep reef) showed no clear differences inside and outside of MPAs in
313 the magnitude of community change (**Figure 2B**). Prior to the marine heatwave, community

314 structure was similar inside and outside of MPAs in all habitats except the rocky intertidal
315 (indicated by the non-overlapping ellipses in **Figure 2B**). However, ecological community
316 structure dramatically shifted as a result of the marine heatwave event across all measured
317 nearshore habitats (n=4), regardless of whether the communities (n=5) were inside or outside of
318 MPAs (**Figures 2B and S8, Table 1**).

319 Community structure changes coincided with oceanographic conditions associated with
320 the marine heatwave (**Figure 1, Tables 1 and 2**). At the onset of the marine heatwave in 2014,
321 sea surface temperature was anomalously warm by as much as 2°C, and sea bottom
322 temperature was also 1°C above the baseline average. MOCI and BEUTI experienced
323 precipitous changes during the marine heatwave, reflecting reduced upwelling and productivity,
324 and these anomalies persisted until at least mid-2016 (**Figure 1 E-F**). Although each
325 oceanographic anomaly aligned well with community shifts in nMDS space (**Figure 2B**),
326 significant correlations were habitat-specific (**Table 2**). In the rocky intertidal, warmer air
327 temperature was the strongest environmental correlate with community structure changes,
328 although warmer SST and declines in upwelling (BEUTI) were also correlated with community
329 change. For shallow reef, kelp forest fishes, and kelp forest invertebrates and algae, SST, SBT,
330 and MOCI were significantly associated with community change, such that communities shifted
331 with increases in surface and bottom water temperature and positive values of the MOCI index.
332 In the deep reef habitat (fishes only), the only significant oceanographic correlate was BEUTI
333 (**Table 2**), where the community shifted in response to reduced upwelling. Finally, there were no
334 significant temporal lags determined except for one interaction between the shallow reef and
335 BEUTI (*lag* = 3 years for sites inside and outside of MPAs, **Table S4**).

336 For all habitats except the rocky intertidal, MPAs did not impart increased resistance to
337 or recovery from marine heatwave-driven community changes compared to sites outside of
338 MPAs (**Figure 3**). The rocky intertidal and deep reef were the only two habitats that resisted the
339 marine heatwave (based on non-significant PERMANOVA result, **Figure 3A**). The rocky
340 intertidal was the only habitat where community structure inside MPAs was not significantly
341 different either during or post-marine heatwave (**Figure 3B**). Kelp forest invertebrates, algae,
342 and fishes all substantially shifted during the marine heatwave, and these changes persisted for
343 several years later with no apparent recovery. The shallow reef habitat responded similarly with
344 pronounced shifts in community structure during the marine heatwave, although the trajectory of
345 the shallow reef habitat started to move towards the pre-heatwave state beginning in the year
346 2018, with the biggest shifts towards recovery occurring inside MPAs (**Figures S5 and S6**,

347 Supplementary Appendix *Figures*). In the deep reef habitat, year-to-year changes were more
348 variable, resulting in a larger multivariate distance relative to the other habitats, but this
349 community change was not significantly different from the baseline year (**Figures 3A** and **S9**
350 Supplementary Appendix *Figures*). However, recovery was more variable than resistance. The
351 shallow reef habitat exhibited relatively greater recovery (i.e., less shift in multivariate distance
352 compared to the pre-heatwave community state) than the kelp forest and deep reef habitats.

353 3.2. Species responses

354 The multivariate analyses revealed several species that explained differences between
355 the pre- and post-heatwave periods. Among the three habitat types with monitoring of fish
356 species (kelp forest, shallow reef, deep reef), the blue and deacon rockfish complex (*Sebastes*
357 *mystinus* and *S. diaconus*) was positively correlated with the post-heatwave period (**Table S5**,
358 Supplementary Appendix, *Tables*). Fish species that declined and were found within the top
359 80% contribution of pre- vs. post-heatwave community structure included: *Sebastes serranoides*
360 (kelp forest), *S. chrysomelas* and *carinatus* (kelp forest), *S. miniatus* (kelp forest, shallow reef),
361 *Brachyistius frenatus* (kelp forest), *S. semicinctus* (deep reef), and *S. hopkinsi* (deep reef). For
362 invertebrates and algae, the multivariate analyses revealed an increase in the abundance of
363 purple sea urchins (*Strongylocentrotus purpuratus*) and a decline in macroalgae in both the
364 rocky intertidal and kelp forest habitats.

365 3.3. Community structure and thermal traits

366 The relative proportional representation of thermal affinities significantly changed during
367 the marine heatwave for kelp forest invertebrates and algae, kelp forest fishes, and shallow reef
368 fishes ($p < 0.001$, $F_{6,708} = 62.24$; $p < 0.05$, $F_{6,700} = 2.18$; $p < 0.001$, $F_{4,315} = 37.41$, respectively).
369 Cold-temperate species significantly declined during the marine heatwave for these habitats
370 (**Figure 4A**). During the marine heatwave, there was a slight increase in cosmopolitan species
371 for the rocky intertidal and kelp forest (invertebrates and algae), and an even more pronounced
372 increase in warm-temperate and subtropical fish species in the kelp forest, shallow reef, and
373 deep reef habitats. Importantly, these changes in community composition that occurred during
374 the marine heatwave (2014-2016) persisted into the following years (2017 and beyond), which
375 partially explains the lack of observed recovery to the pre-heatwave community structure.

376 Variation in species abundance was explained by significant interactions between
377 thermal affinities and oceanographic variables for all habitats from the fourth corner model
378 (**Figure 4B**, **Figure S7** Supplementary Appendix, *Figures*). In general, species thermal affinities
379 responded similarly across habitats. The abundance of cold-temperate species declined with
380 increased sea surface temperature anomalies and reduced upwelling (BEUTI), while the
381 abundance of warm-temperate, subtropical, and tropical species increased with the
382 oceanographic conditions that were associated with the onset of the marine heatwave, such as
383 MOCI and warming water temperature. Sea bottom temperature had the most variable
384 interactive effect across habitats and thermal affinities. Interestingly, thermal associations for the
385 deep reef habitat had an opposite sign for cold-temperate and warm-temperate interactions,
386 relative to the other habitats.

387 3.4. MPA features and ecological stability

388 Community structure responses were highly variable across the state-level network for
389 MPAs. In general, rocky intertidal communities showed higher resistance than kelp forest
390 communities, as indicated by smaller shifts in multivariate distance (**Figure 5C**; smaller points).
391 While shifts in community structure were generally larger in the kelp forest (**Figure 5C**; larger
392 points), in some cases, the magnitude of shifts inside MPAs was less relative to shifts outside of
393 MPAs (**Figure 5A**). In general, MPA protection fostered more resistance than recovery (**Figure**
394 **5C**; i.e., more blue points in the resistance column and more red points in the recovery column),
395 although these results were not statistically significant. For example, kelp forest communities in
396 the Point Buchon, South Point, and Harris Point MPAs resisted and moved towards recovery
397 from the heatwave more than communities outside these MPAs (**Figure 5C**; blue points).
398 However, kelp forest communities in the Scorpion, Anacapa Island, and Campus Point MPAs
399 were less successful at resisting shifts than communities outside these MPAs (**Figure 5C-left**;
400 red points). Similarly, kelp forest communities in the Point Lobos, Santa Barbara, Farnsworth,
401 and Blue Cavern MPAs were less successful at recovering from shifts than communities outside
402 these MPAs (**Figure 5C-right**; red points). None of the evaluated MPA features (age, size,
403 historic fishing pressure, habitat diversity, connectivity, biomass response ratios) were
404 statistically significant drivers of this variability (**Figure S11**, Supplementary Appendix *Figures*).

405 4. Discussion

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

420 Several ecological processes may explain the pronounced shifts observed across
421 habitats, such as altered adult movement, changes to recruitment regimes, tropicalization,
422 deborealization, and shifts in species interactions such as herbivory, competition, predation, and
423 disease (Vergés et al., 2014; García Molinos et al., 2016; Wernberg et al., 2016; Free et al.,
424 2019; Mignot et al., 2022). First, our study found that the relative proportion of warm-temperate
425 and subtropical species increased during and after the marine heatwave. The increased
426 proportional representation of species with warm-water thermal affinities may be explained by
427 adult movement into the study area, changes in recruitment patterns, or by a decline in the
428 relative abundance of cold-temperate species (Sanford et al., 2019; Walker et al., 2020;
429 Fredston et al., 2021). For example, the large increase in blue rockfish in kelp forest, shallow
430 reef, and deep reef habitats was associated with strong recruitment and pelagic young-of-the-
431 year abundance of rockfishes in midwater trawl surveys at the start of the marine heatwave
432 period (Field et al. 2021). Large increases in the subtropical wrasse, seniorita (*Oxyjulis*
433 *californica*), were also observed in multiple habitats, contributing to community change. Second,
434 during the marine heatwave, a large-scale outbreak of herbivorous sea urchins occurred
435 throughout the study region that coincided with precipitous declines in kelp (and other
436 macroalgae) and the loss of an important benthic mesopredator, the sunflower sea star

437 (*Pycnopodia helianthoides*), due to a large-scale marine disease outbreak (Harvell et al., 2019;
438 Smith et al., 2021).

439 Species life history traits in relation to the marine heatwave event may explain why the
440 rocky intertidal was the only habitat where community structure exhibited resilience. Variation in
441 stress tolerance to air temperature is a fundamental driver of rocky intertidal community
442 structure. Although 2014 was the warmest year on record in California, the sustained sea
443 surface temperature anomalies associated with ocean warming during the marine heatwave
444 may have impacted the rocky intertidal less than the subtidal habitats. Resilience in rocky
445 intertidal MPAs may be explained by increased propagule delivery to MPAs, particularly by long-
446 lived foundation species that stabilize the community (Raimondi & Smith, 2022), or through
447 regulatory protection that prohibits the harvest of habitat-forming mussels (*Mytilus spp.*) in
448 MPAs. Additionally, the rocky intertidal is the only habitat that used a fixed-plot design
449 (*Supplementary Appendix, Methods*) and this methodological form of sampling could have
450 resulted in smaller propagated spatial variance, which could be more biased towards
451 conclusions of enhanced resilience relative to the sampling used in the other habitats. More
452 research is needed to distill the mechanistic processes associated with MPA resilience in the
453 rocky intertidal.

454 The primary regulation associated with MPAs in California involves a restriction of fishing
455 activities; thus, we were interested in understanding whether ecological communities inside no-
456 take MPAs are more resilient to marine heatwaves than our control social-ecological system.
457 We consider human activities, such as fishing, as integral parts of the social-ecological system,
458 since fishing occurred decades before MPA establishment and the marine heatwave, with the
459 restriction of harvest through regulatory protection as the primary conservation mechanism.
460 However, there are multiple viewpoints pertaining to interactions between humans and the
461 oceans, and similarly there are many approaches to evaluating the effects of fishing and
462 regulatory protection. Alternative frameworks might consider areas inside MPAs as “reference”
463 locations for places where harvest occurs (Costello 2014). While we believe human and natural
464 systems are now so integrated in coastal areas that there are virtually no pristine ecosystems,
465 the framing of considering MPAs as controls and fished systems as experimental treatments
466 would not impact our results.

467 It is not surprising that community shifts occurred inside and outside MPAs
468 simultaneously for most habitats, since many of the species exhibiting the biggest changes are

469 not directly targeted by fishing activities (e.g., invertebrates and algae). In cases where MPAs
470 do not confer ecological resilience to marine heatwaves, it is important to note that the capacity
471 of MPAs to harbor higher biomass than unprotected sites can still be maintained (Frid et al.,
472 2023). Other studies have documented increases in targeted species biomass inside of MPAs
473 within this system, which is a focal MPA conservation objective (Hamilton et al., 2010; Caselle
474 et al., 2015; Ziegler et al., 2022). Similar responses to the marine heatwave in southern
475 California fish communities were reported by Freedman et al. (2020), who found that non-
476 targeted subtropical species were most responsible for community reorganization. Ziegler et al.
477 (2023) also reported that fish species diversity recovered more quickly after the heatwave inside
478 of MPAs.

479 Although the anomalously warm environmental conditions subsided after 2016, changes
480 in community structure persisted, especially in the kelp forest, shallow reef, and deep reef
481 habitats. These results are particularly interesting in the context of ecosystem stability and
482 transition dynamics. Given the highly variable recruitment of the dominant fishes in the study
483 region (Schroeder et al., 2019; Field et al., 2021), it is possible that sufficient time has not
484 elapsed for the communities to return to a pre-perturbed state. Lagged effects due to
485 ontogenetic shifts and methodological sampling that disproportionately select for adults may
486 also contribute to the observed lack of recovery. For example, declines in vermilion rockfish
487 (*Sebastes miniatus*) in the shallow reef habitat coincided with increases in that species in the
488 deep reef habitat, likely reflecting ontogenetic movements from shallow to deep habitats (Love
489 et al., 2002; Love, 2011). In addition, the shallow reef habitat monitoring program used hook
490 and line sampling, which disproportionately selects individuals that are older than 2-3 years,
491 which is why lagged effects of oceanography were more likely to be detected in this habitat
492 (Ziegler et al., 2023). Moreover, many species in the California Current are slow-growing, late to
493 mature, long-lived, and relatively sedentary with small home ranges (Love et al., 2002; Love,
494 2011). These life history traits may create inertia to resistance or recovery from change.
495 However, the persistence of novel community structure configurations observed in this study,
496 despite the return of pre-heatwave environmental conditions, highlights the need for further
497 assessments of community transition dynamics over ecologically meaningful timescales.

498 Our finding of no effect of MPA features on dampening marine heatwave-driven
499 responses in the rocky intertidal and kelp forest habitats is particularly interesting given that
500 habitat mosaics, historic fishing effort, and connectivity have been linked to MPA conservation
501 capacity (Bastari et al., 2016). The widespread effects of marine heatwaves and other climate

502 perturbations may overwhelm local stressors (e.g., fishing, marine pollution) that MPAs were
503 initially successful at mitigating (Bruno et al., 2019). Indeed, even biodiversity rich spots or deep
504 water communities are susceptible to the impacts of climate change (Kocsis et al., 2021;
505 Emblemsvåg et al., 2022). Our results highlight the need for management frameworks that
506 include climate adaptation strategies, the protection of range-shift corridors, and consideration
507 of the compounding effects of both fishing and marine heatwaves on resilience (Burrows et al.,
508 2014). More investigation is needed to better understand the drivers that can help MPAs to
509 maintain higher fish biomass than unprotected sites under climate change (Frid et al., 2023).

510 Increasing our understanding of the pathways through which marine heatwaves
511 restructure ecological communities is central to developing adaptive management solutions. In
512 our study, we used a taxonomic (i.e., species) abundance-based approach to evaluate changes
513 in community structure, but functional diversity may also be impacted by warming events and
514 should be explored (McLean et al., 2019; Murgier et al., 2021). Prolonged warming events may
515 differentially impact groups and guilds of species with similar traits, such as dispersal ability,
516 thermal tolerance, metabolic rate, and mobility (Duncan et al., 2019; Harvey et al., 2021).
517 Moreover, to understand the ability of MPA networks to resist and recover from future marine
518 heatwaves, it is critical to have sufficient monitoring across multiple habitats, taxa, and regions.
519 Because pre-perturbation data are essential for establishing baselines and comparatively
520 evaluating ecological responses, consistent monitoring is fundamental to capture the effect of
521 marine heatwave events. Although the timing of marine heatwaves is unpredictable, evidence
522 suggests that the frequency and magnitude of abrupt warming events are expected to increase
523 (Frölicher et al., 2018; Holbrook et al., 2020).

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

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

552 Conflict of Interests Statement

553 The authors have no conflicts of interest to declare.

554 Data Availability Statement

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

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Tables and Figures

Table 1. Results from a series of pairwise permutational analysis of variance (PERMANOVA) tests on community resistance (before-during) and recovery (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. Asterisks denote that community structure was significantly different for pairwise comparisons (Resistance = before vs. during, Recovery = before vs. after).

Habitat	MPA type	Transition	B-C distance	Sum of squares	R-squared	Psuedo F	P(perm)
Rocky intertidal	Outside	Resistance	0.059	0.155	0.02	1.883	0.071
		Recovery	0.053	0.219	0.025	2.635	0.006*
	Inside	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	Outside	Resistance	0.085	0.49	0.061	4.381	0.001*
		Recovery	0.125	0.921	0.099	8.211	0.001*
	Inside	Resistance	0.08	0.333	0.047	2.823	0.003*
		Recovery	0.142	0.849	0.102	7.189	0.001*
Kelp forest fishes	Outside	Resistance	0.081	0.249	0.047	3.22	0.007*
		Recovery	0.1	0.64	0.109	9.098	0.001*
	Inside	Resistance	0.066	0.21	0.05	2.944	0.015*
		Recovery	0.124	0.505	0.109	7.569	0.001*
Shallow reef	Outside	Resistance	0.073	0.146	0.061	2.349	0.064
		Recovery	0.071	0.586	0.188	9.515	0.001*
	Inside	Resistance	0.066	0.159	0.093	3.676	0.002*
		Recovery	0.112	0.486	0.225	11.882	0.001*
Deep reef	Outside	Resistance	0.136	0.198	0.124	1.839	0.064
		Recovery	0.167	0.681	0.308	6.687	0.001*
	Inside	Resistance	0.104	0.121	0.082	1.163	0.296
		Recovery	0.107	0.337	0.163	2.53	0.015*

Table 2. EnvFit scores indicating the significance level of correlations between environmental conditions (air temperature °C, AT; sea surface temperature °C, SST; sea bottom temperature °C, SBT, biologically effective upwelling transport index $\text{mmol m}^{-1}\text{s}^{-1}$, BEUTI; multivariate oceanographic climate index, MOCI) and community change in non-metric multidimensional scaling (nMDS) space.

Habitat	Environmental variable	Type	R square	p-value
Rocky intertidal	AT	Anomaly	0.07	0.043*
		Absolute	0.33	0.001*
	SST	Anomaly	0.04	0.149
		Absolute	0.09	0.012*
	BEUTI	Anomaly	0.04	0.121
		Absolute	0.09	0.011*
MOCI	Absolute	0.02	0.324	
Kelp forest inverts and algae	SST	Anomaly	0.10	0.004*
		Absolute	0.04	0.077
	BEUTI	Anomaly	0.03	0.128
		Absolute	0.02	0.323
	MOCI	Absolute	0.07	0.009*
	SBT	Anomaly	0.17	0.001*
Absolute		0.14	0.001*	
Kelp forest fishes	SST	Anomaly	0.06	0.016*
		Absolute	0.04	0.066
	BEUTI	Anomaly	0.05	0.029*
		Absolute	0.03	0.17
	MOCI	Absolute	0.12	0.002*
	SBT	Anomaly	0.07	0.012*
Absolute		0.01	0.635	
Rocky reef fishes	SST	Anomaly	0.17	0.002*
		Absolute	0.18	0.002*
	BEUTI	Anomaly	0.02	0.401
		Absolute	0.03	0.257
	MOCI	Absolute	0.29	0.001*
	SBT	Anomaly	0.16	0.002*
Absolute		0.12	0.009*	
Deep reef fishes	SST	Anomaly	0.05	0.524
		Absolute	0.08	0.292
	BEUTI	Anomaly	0.25	0.014*
		Absolute	0.27	0.016*
	MOCI	Absolute	0.02	0.726
	SBT	Anomaly	0.03	0.699
Absolute		0.15	0.099	

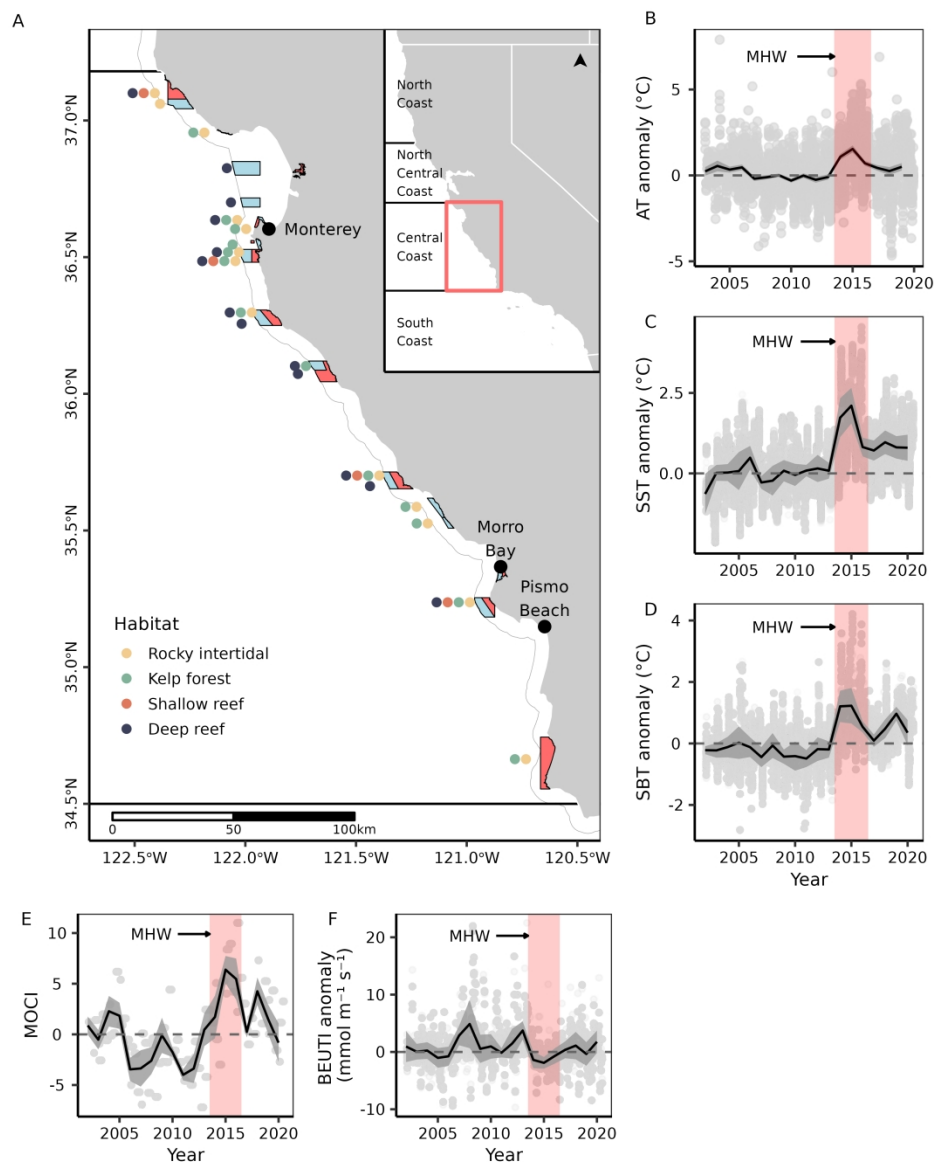


Figure 1. The (A) coverage of ecological monitoring in marine protected areas (MPAs) in California's Central Coast region and (B-F) exposure of these MPAs to five indicators of environmental conditions. In (A), points indicate which habitats were monitored both inside and outside of MPAs (i.e., points indicate data availability, not the location of sampling sites). Red polygons indicate no-take MPAs ($n = 12$, called State Marine Reserves), and blue polygons indicate partial-take MPAs ($n = 10$, called State Marine Conservation Areas; see table S1 for list of partial-take MPAs that are de facto no-take MPAs by habitat). 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). Environmental indicators include: (B) air temperature (AT), (C) sea surface temperature (SST); (D) sea bottom temperature (SBT); (E) the multivariate oceanographic climate index (MOCI); and (F) 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.

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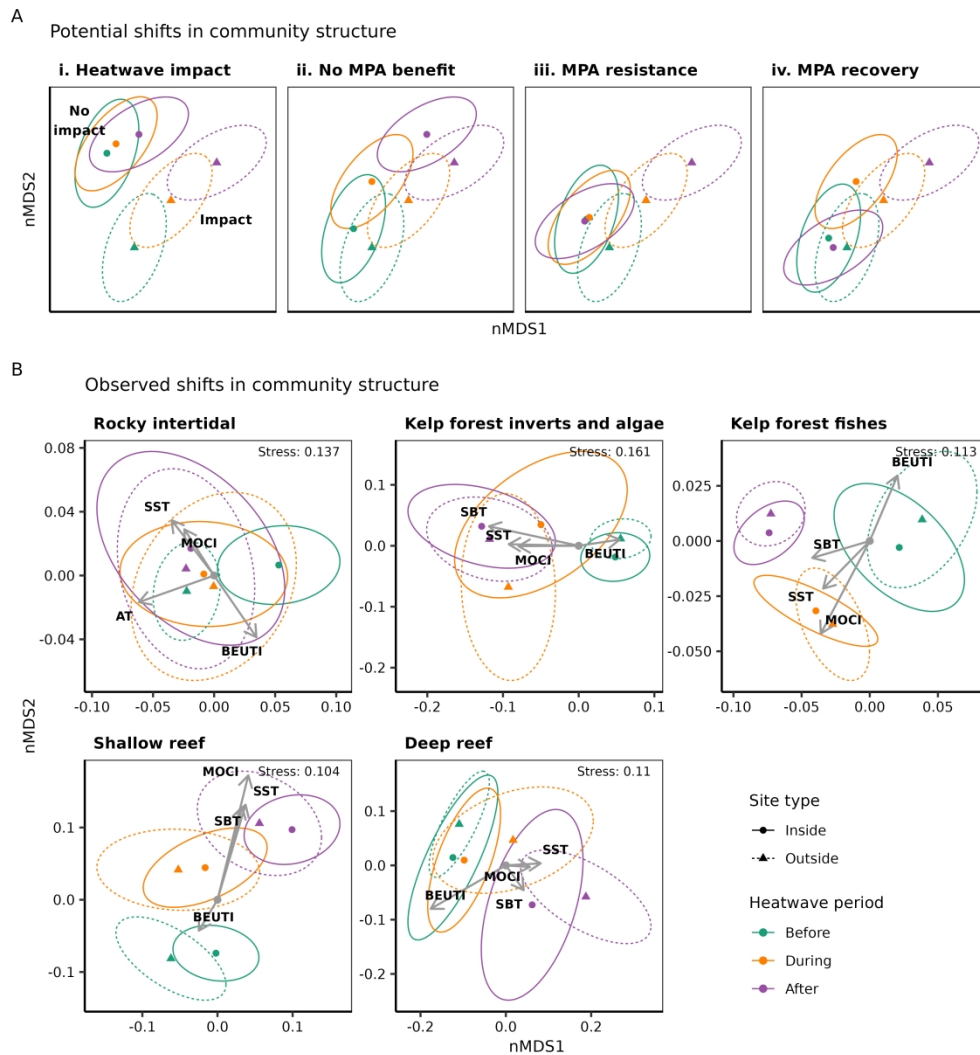


Figure 2. (A) Potential and (B) observed shifts in community structure from 2007 to 2020. Panel A illustrates a typology of potential community structure shifts: (i) “No impact”, where community structure does not shift, and “impact”, where community structure significantly shifts. Non-overlapping ellipses indicate significant differences in community structure. In this example, pre-heatwave community structure was significantly different inside (solid lines ellipses around points) vs. outside (dashed lines around triangles) MPAs; (ii) “No MPA benefit”, where communities inside MPAs respond similarly to those outside; (iii) “MPA Resistance”, where communities inside MPAs remain stable while those outside shift; and (iv) “Recovery”, where communities inside MPAs shift during the heatwave, but return to their previous state following the disturbance while communities outside of MPAs do not return. Panel B shows observed shifts in community structure before (2007-2013), during (2014-2016), and after (2017-2020) the marine heatwave inside (circles) and outside (triangles) MPAs 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 anomaly: air temperature (AT, rocky intertidal only), sea surface temperature (SST), sea bottom temperature (SBT), 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).

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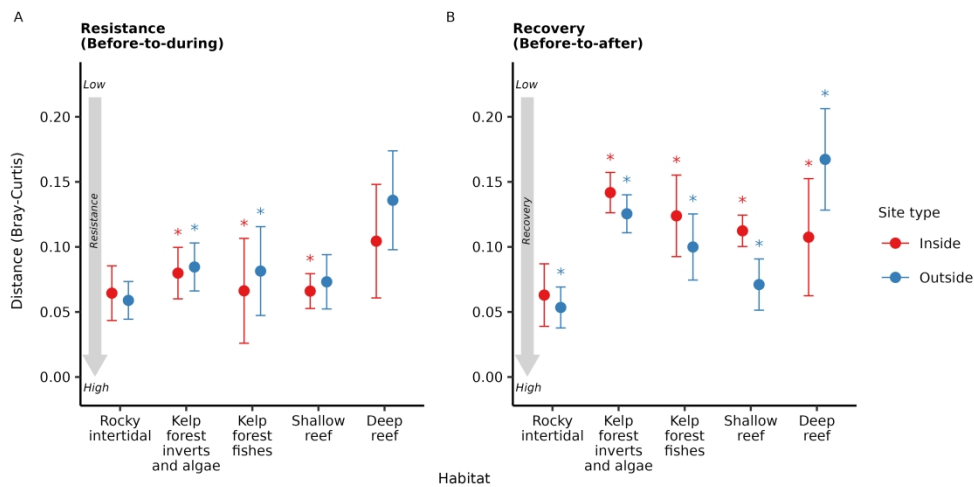


Figure 3. Community resistance (before-to-during marine heatwave comparison) and recovery (before-to-after marine heatwave comparison) as measured by multivariate distance between centroids. Each point depicts the multivariate distance between the pre-heatwave centroid (before) and the during-heatwave or the post-heatwave centroid inside (red) and outside (blue) MPAs. 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 structure between marine heatwave periods, as derived from a pairwise permutational analysis of variance (PERMANOVA). Points without asterisks indicate resistance or recovery (as measured by non-significant PERMANOVA, Table 1). Note that some communities have inherently greater interannual variability, potentially resulting from variation in sampling methodology, which can lead to larger mean multivariate distances that are not significantly different (Supplementary Appendix, Figure S9).

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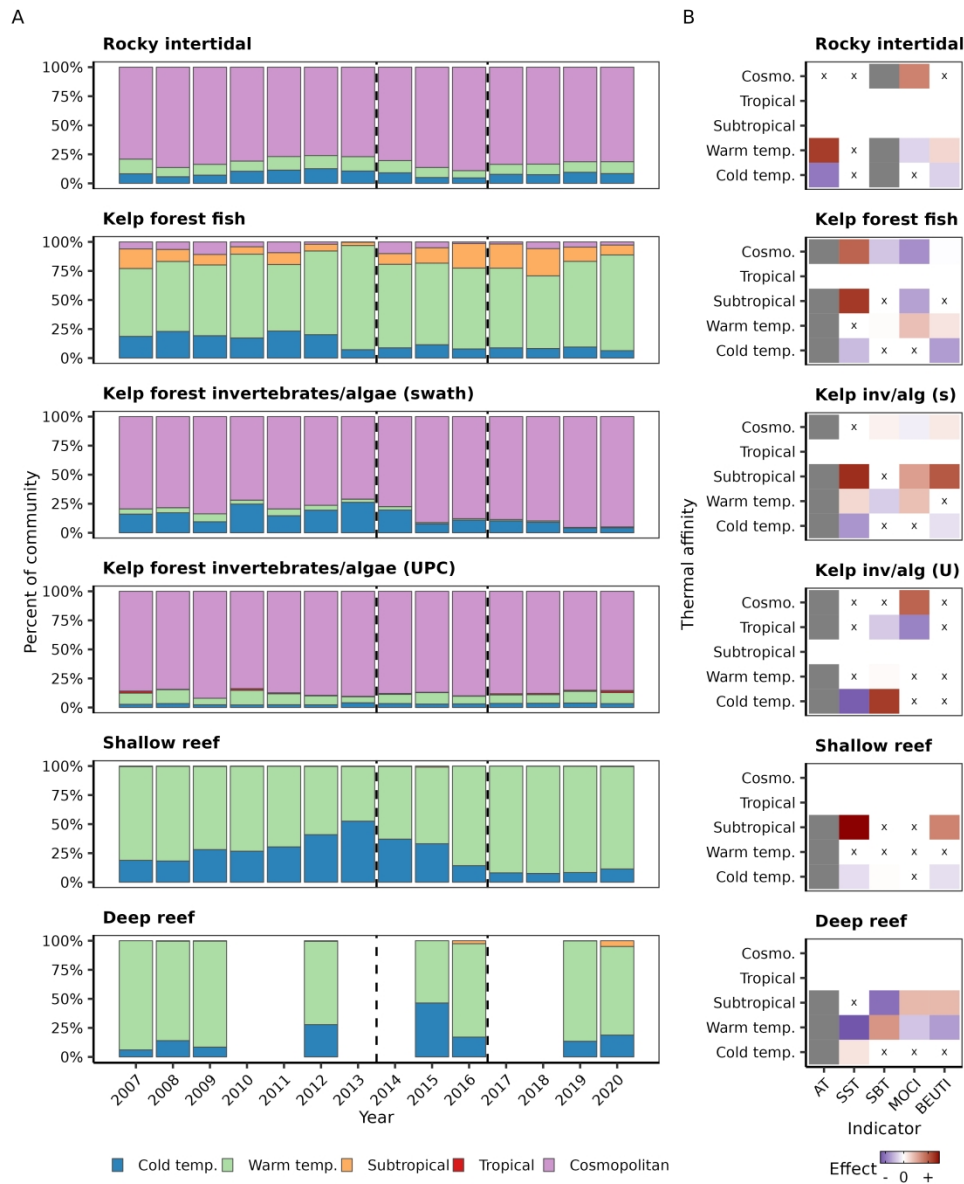


Figure 4. The (A) proportional community composition by thermal affinity groups from 2007-2020 and the (B) interactive effect of environmental anomalies (air temperature, AT, rocky intertidal only; sea surface temperature, SST; sea bottom temperature, SBT; multivariate oceanographic climate index, MOCI; 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 coefficients for all trait-oceanographic indicator interaction terms, based on multiple generalized linear-LASSO models. 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 grey squares indicate non-applicable indicators.

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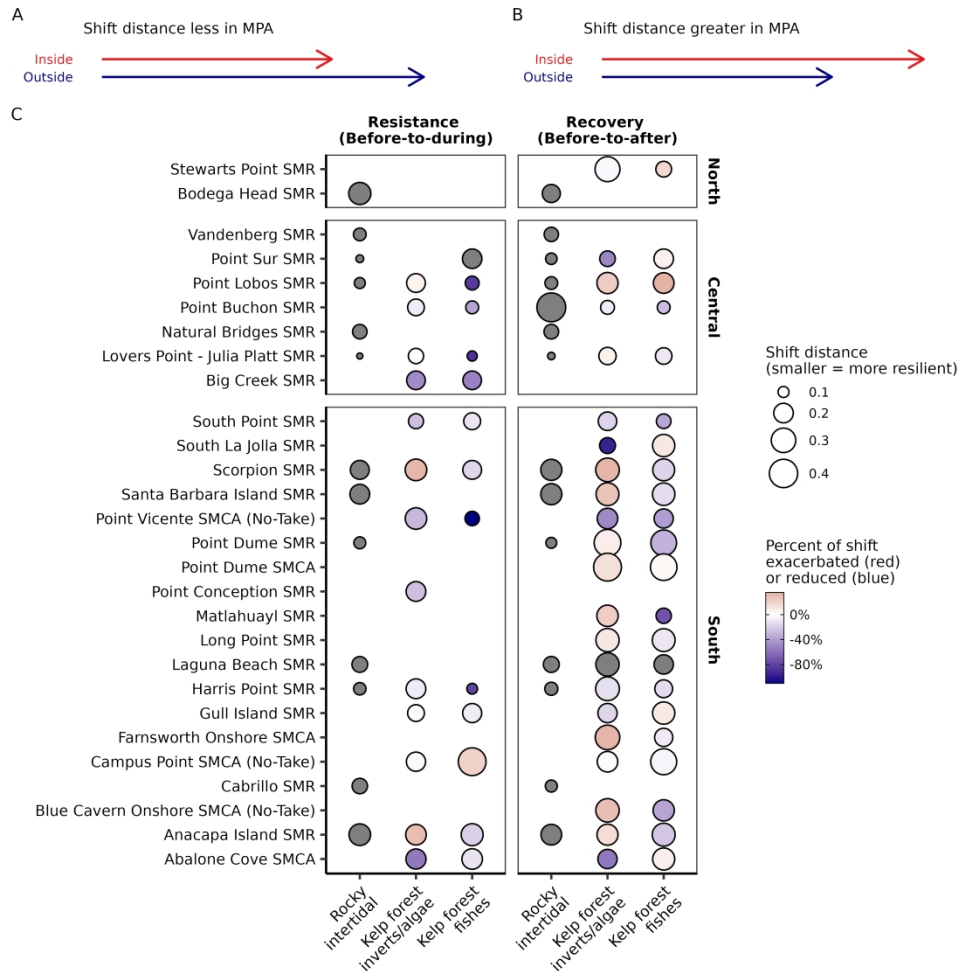


Figure 5. Conceptual schematics illustrating scenarios where (A) community structure shifts less inside a MPA than outside, thereby reducing community structure shifts, and (B) community structure shifts more inside a MPA than outside, thereby exacerbating community structure shifts relative to the outside sites. Panel C shows resistance (before-to-during marine heatwave comparison) and recovery (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 multivariate distance for resistance or recovery. Therefore, smaller points indicate MPAs that exhibited greater resistance or recovery (i.e., communities inside the MPA shifted smaller multivariate distances). Point color indicates the magnitude of the shift of community structure inside a given MPA relative to its paired outside site. Red shades indicate MPAs where the change in multivariate distance was greater than the paired outside site (i.e., shift exacerbated inside MPAs relative to outside). Blue shades indicate MPAs where the change in multivariate distance was greater in the paired outside site than inside the MPA (i.e., community structure changes were less in the MPA). Note that the rocky intertidal does not use a paired inside-outside sampling design (outside site selection is described in Supplementary Appendix, Methods) and therefore the grey points indicate MPAs without the necessary data from adjacent outside sites. Missing points indicate insufficient data to evaluate changes. SMR = State Marine Reserve (no-take MPA); SMCA = State Marine Conservation Area (partial-take MPA, with a few official and habitat-specific de facto exceptions).