Received: 1 June 2023 | Revised: 6 December 2023 | Accepted: 7 February 2024

DOI: 10.1002/ecy.4288

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

A marine heatwave changes the stabilizing effects of biodiversity in kelp forests

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Funding information
National Natural Science Foundation of China, Grant/Award Numbers: 31988102, 32122053; NSF, Grant/Award Numbers: 1714195, 2023474, 2023523, 2023555, 2140335; National Science Foundation of USA (NSF); NASA, Grant/Award Number: 80NSSC22K0169

Handling Editor: Matthew E. Bracken

Abstract

Biodiversity can stabilize ecological communities through biological insurance, but climate and other environmental changes may disrupt this process via simultaneous ecosystem destabilization and biodiversity loss. While changes to diversity–stability relationships (DSRs) and the underlying mechanisms have been extensively explored in terrestrial plant communities, this topic remains largely unexplored in benthic marine ecosystems that comprise diverse assemblages of producers and consumers. By analyzing two decades of kelp forest biodiversity survey data, we discovered changes in diversity, stability, and their relationships at multiple scales (biological organizational levels, spatial scales, and functional groups) that were linked with the most severe marine heatwave ever documented in the North Pacific Ocean. Moreover, changes in the strength of DSRs during/after the heatwave were more apparent among functional groups than both biological organizational levels (population vs. ecosystem levels) and spatial scales (local vs. broad scales). Specifically, the strength of DSRs decreased for fishes, increased for mobile invertebrates and understory algae, and were unchanged for sessile invertebrates during/after the heatwave. Our findings suggest that biodiversity plays a key role in stabilizing marine ecosystems, but the resilience of DSRs to adverse climate impacts primarily depends on the functional identities of ecological communities.

https://doi.org/10.1002/ecy.4288

KEYWORDS
asynchrony, biological insurance, climate, diversity–stability relationships, kelp forest, long-term ecological research, stability

INTRODUCTION

Ecologists have long recognized that biodiversity loss can cause reductions in the temporal stability of community and ecosystem properties (Ives & Carpenter, 2007; Loreau et al., 2021; May, 1973; McCann, 2000; McNaughton, 1977; Pimm, 1984; Tilman et al., 2014). One important property is total community biomass, the "stability" of which is usually measured as the ratio between the temporal mean to the temporal SD (Donohue et al., 2016; Hector et al., 2010; Isbell et al., 2015; Pennekamp et al., 2018; Tilman et al., 2006). The mechanisms underpinning diversity–stability relationships (DSRs) have been the focus of much ecological theory (Tilman et al., 2014). The *species insurance theory* predicts that more diverse communities have greater stability due to locally asynchronous responses of different species to environmental fluctuations, leading to compensatory dynamics (Lehman & Tilman, 2000; Yachi & Loreau, 1999). At broader scales (e.g., landscape), the spatial insurance theory predicts that species turnover across space (i.e., β diversity) provides insurance effects to regional (γ) stability (i.e., the stability of aggregated local [α] communities within a region) by promoting spatial asynchrony (Loreau et al., 2003, 2021; Wang & Loreau, 2016). Although there is an extensive theoretical foundation and numerous terrestrial studies on plants (Craven et al., 2018; Hautier et al., 2014; Liang et al., 2022), the application of these theories to aquatic and marine ecosystems remains a topic of considerable debate (Hodapp et al., 2023; Lamy et al., 2019; Thorson et al., 2018). This gap is especially apparent in understanding the stabilizing effects of biodiversity in nature, particularly in the capacity of a diversity of benthic producers and consumers to buffer against drastic environmental fluctuations from local to landscape scales.

Relative to terrestrial ecosystems, benthic marine ecosystems typically have longer food chains, indicative of a highly diverse system characterized by more complex biotic interactions (McCauley et al., 2015). Generally, such systems are more directly influenced by environmental changes at broader spatial scales, such as fluctuations in ocean hydrodynamics (currents, waves), light availability, and temperature (Miller et al., 2018). For instance, a marine heatwave (prolonged anomalously warm water; Hobday et al., 2016) triggered unprecedented shifts across trophic levels in the North Pacific Ocean from 2014 to 2016 (Di Lorenzo & Mantua, 2016), the impacts of which showed considerable spatial variability in impacts to kelp forest ecosystems (Cavanaugh et al., 2019). Consequently, the ecological niches of species—defined by characteristics such as trophic level or mobility—are key to determining population responses to extreme events (Reed et al., 2016; Rogers-Bennett & Catton, 2019), which in turn could critically influence ecosystem stability. Terrestrial plant studies have indicated that biodiversity can stabilize community biomass dynamics by increasing species insurance, thereby enhancing ecosystem resistance against extreme environmental changes (Isbell et al., 2015). However, DSRs and their response to environmental change are understudied in marine systems, which are characterized by relatively greater biocomplexity and diverse communities of producers and consumers of varying mobility. It remains unresolved how diversity stabilizes marine ecosystems, especially in the face of spatially widespread and accelerating environmental changes (Frölicher et al., 2018; Oliver et al., 2018).

Recent studies utilized Before-After Control-Impact (BACI) designs (Underwood, 1994) to elucidate how disturbances, such as sudden environmental changes, can affect the spatial and temporal variabilities of populations and ecosystems (Benkwitt et al., 2020; Donovan et al., 2021; Rassweiler et al., 2021; Reed et al., 2016). Drawing on the theoretical underpinnings of DSR at hierarchical spatial and temporal scales (Wang & Loreau, 2014, 2016), we further expand on this by outlining various scenarios illustrating how acute environmental changes can rapidly impact population dynamics and, consequently, affect ecosystem stability across multiple scales (Figure 1). At the local (α) scale (Figure 1A), a decrease in α stability can be attributed to a combination of (1) a direct decrease in population-level stability (the weighted mean of local population-level stability across species [Thibaut & Connolly, 2013; Wang et al., 2019]) and/or (2) a decrease in species asynchrony (e.g., reduced compensatory dynamics among species within local communities). At broader spatial scales, any decrease in α stability will propagate to γ stability (Figure 1B[3]) and, thus, decrease γ stability (Wang et al., 2019; Wang & Loreau, 2014, 2016). If environmental changes further decrease spatial asynchrony (i.e., reductions in compensatory dynamics among different local communities), γ stability may decrease even more (Figure 1B[4]). However, most

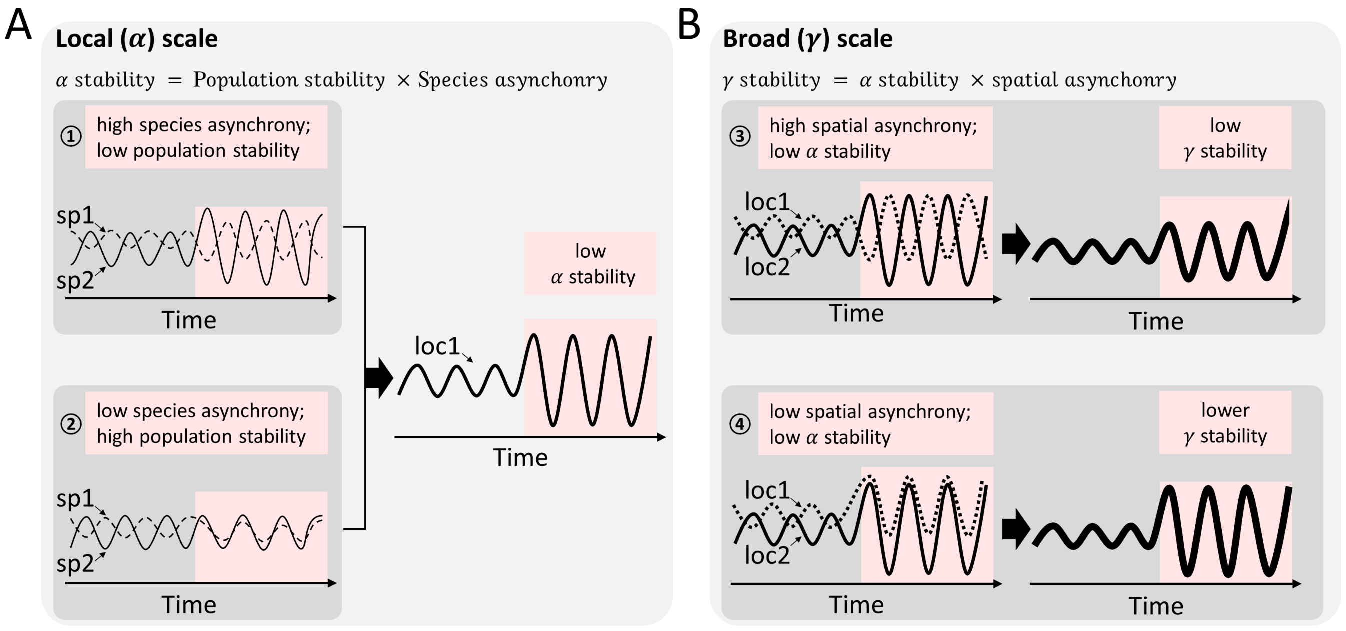

FIGURE 1 Conceptual diagram illustrating how climate extremes can reduce ecosystem stability at multiple spatial scales. (A) At the local (α) scale, climate extremes may decrease both population-level stability (①) and species asynchrony (②) due to rapid and extreme changes in environmental conditions that affect the dynamics of multiple species in a similar way, both resulting in a decrease in α stability. (B) At the broader (γ) spatial scale, such effects on α stability propagate to γ stability. If climate extremes also cause low (③) or high (④) spatial asynchrony among local communities, γ stability may decrease to various degrees. The periods of exposure to a climate extreme event are shaded in red. Different species are denoted by "sp" and different locations by "loc."

empirical studies focus on sampling and, comparing stability at a single scale, are based in terrestrial ecosystems and/or concentrate solely on one type of organism, such as plants (Loreau et al., 2021; Tilman et al., 2014). Thus, there is an incomplete understanding of how DSRs and ecosystem stability respond to extreme environmental changes (Cardinale et al., 2012; Gonzalez et al., 2020; Isbell et al., 2017).

Furthermore, such reductions in stability are likely associated with how biodiversity responds to drastic environmental changes across multiple scales (Hautier et al., 2020; Liang et al., 2021). For instance, environmental shifts can expose species to conditions beyond their physiological limits, leading to expansions of their niche breath and fostering positive interspecific interactions (He et al., 2013). This, in turn, indirectly strengthens biodiversity effects on ecosystem stability through compensatory dynamics at the local scale (Hong et al., 2022; see also Figure 2A). At broader spatial scales, such environmental changes may induce biotic homogenization, characterized by regional species declines outpacing local ones (Blowes et al., 2019). This further results in a synchronization of spatial population dynamics by reducing spatial species turnover (e.g., β diversity), potentially decreasing broader-scale (γ) ecosystem stability. As such,

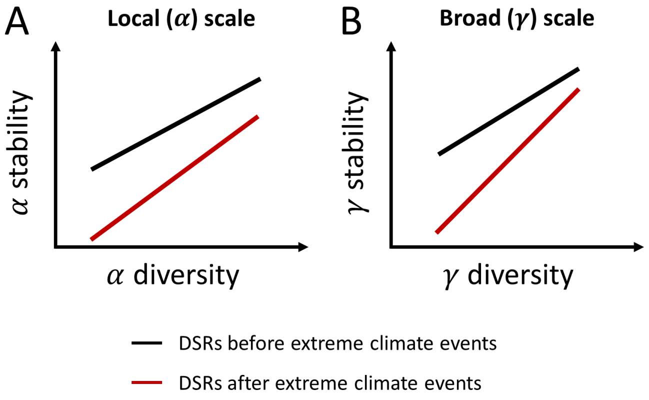

FIGURE 2 Hypothetical changes in diversity–stability relationships (DSRs) at multiple spatial scales before and after an extreme climate event. (A) After an extreme climate event, the strength of DSRs may be increased at the local (α) scale due to an increased facilitation among species. (B) These changes in DSRs can propagate to the broader (γ) spatial scale. With an amplified relationship between spatial asynchrony and β diversity, which are additional partitioning products scaling DSRs from local to broader spatial scales, the strength of the DSRs might experience further buffering at the broader (γ) spatial scale. Black and red lines indicate DSRs before and after extreme climate events, respectively. Information about alternative hypotheses is provided in Appendix S1: Figure S1.

maintaining or strengthening the relationship between spatial asynchrony and β diversity in the face of environmental changes could serve as a spatial buffer, preserving γ stability (Wang et al., 2021). Considering the spatial variability observed in marine ecosystem responses to drastic environmental changes, such as heatwaves (Cavanaugh et al., 2019), it may be anticipated that an asynchronization of spatial population dynamics may alleviate the negative impacts of such events on ecosystem stability (e.g., spatial insurance), potentially mitigating declines in γ stability (Figure 1B[3]). If positive DSRs are amplified at the local scale following environmental changes (Figure 2A; see also Appendix S1: Figure S1 for alternative hypotheses), a spatial asynchrony–β-diversity relationship could counterbalance these DSRs at a broader (γ) scale (Figure 2B). Further, if this relationship is itself amplified by such changes, the spatial insurance effect might be even more pronounced. Although this possibility has been investigated in various studies (Catano et al., 2020; Hautier et al., 2020; Liang et al., 2021, 2022; Patrick et al., 2021; Qiao et al., 2022; Wang et al., 2021), the debate continues (Wilcox et al., 2017; Yang et al., 2022; Zhang et al., 2019), particularly in marine ecosystems (Hodapp et al., 2023; Lamy et al., 2019; Thorson et al., 2018). The consistency and applicability of these theories and the extent to which DSRs apply to marine organisms at the seascape scale (ones to tens of kilometers) remain under discussion. Therefore, understanding changes in the strength of DSR is crucial to determining the mechanisms governing the dynamics of climate-driven ecosystems across scales.

Here, we used a long-term survey of kelp forest communities in the Santa Barbara Channel (California, USA) to assess scale-dependent changes in the magnitude of DSRs following a particularly extreme marine heatwave. Giant kelp forests are among the most productive ecosystems (Castorani et al., 2021; Pace & Lovett, 2013; Pessarrodona et al., 2022), support diverse communities (Castorani et al., 2018; Miller et al., 2018), and provide numerous ecosystem services worldwide (Graham et al., 2007; Schiel & Foster, 2015). However, the kelp forests are also increasingly threatened by environmental changes (Krumhansl et al., 2016), including marine heatwaves (Arafeh-Dalmau et al., 2021; Cavanaugh et al., 2019; McPherson et al., 2021; Smale, 2020). In 2014–2016, the largest marine heatwave on record swept the North Pacific Ocean (Di Lorenzo & Mantua, 2016). Within sites studied by the Santa Barbara Coastal Long Term Ecological Research (SBC LTER) project (Appendix S1: Figure S2), reef bottom water temperatures remained above the 16-year (2004–2020) average after the heatwave (2014–2020) (Figure 3). Marine population dynamics changed in response to this heatwave (Appendix S1: Figures S3–S5), offering a unique opportunity to explore the impact of marine heatwaves in a diverse benthic marine community (Donovan et al., 2021; Rassweiler et al., 2021; Reed et al., 2016; Rogers-Bennett & Catton, 2019). To take advantage of this natural extreme event, we used a BACI approach to test how biodiversity, stability, and their relationships shifted before versus during/after the heatwave.

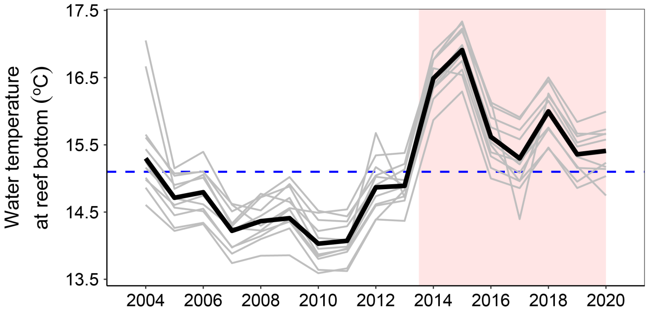

FIGURE 3 Reef bottom water temperature at Santa Barbara Coastal Long Term Ecological Research sites. Plot shows time series of mean bottom water temperature between 2004 and 2020. The thick dark line represents the average bottom water temperature across all sites, while the thin gray lines depict the temperature at each individual site. A blue dashed line marks the overall mean bottom temperature for the entire 2004–2020 period. Red shading shows the during/after heatwave period (2014–2020).

Kelp forest community dynamics have been recorded for over two decades (since 2001) by the SBC LTER project. Briefly, divers nondestructively estimate the biomass of >220 taxa of macroalgae, mobile and sessile invertebrates, and fishes at two to eight fixed 80-m^2 transects at each of 11 kelp forest sites (Santa Barbara Coastal LTER, et al., 2021). From these data we computed biomass-based diversity, stability indices, and their relationships across spatial scales among these functional groups between the periods before (2007–2013) and during/after (2014–2020) the heatwave. We calculated site-level (γ) stability and partitioned it into transect-level (α) stability (weighted mean of stability at the transect level within each site) and β stability (spatial asynchrony among transects within each site). We then partitioned α stability into population-level stability (weighted mean of stability at the population level) and species asynchrony (Figure 1). Simultaneously, we calculated γ and α diversity metrics, from which we multiplicatively computed β diversity as $\beta = \gamma/\alpha$. Our analysis addressed two key questions: (1) How does the marine heatwave affect the strength of DSRs across four functional groups (understory algae, sessile invertebrates, mobile invertebrates, and fishes)? (2) Do the impacts of the heatwave on DSRs, as they extend from local to broader spatial scales, vary among functional groups? We hypothesized that the strength of DSRs would be altered during and after (vs. before) the marine heatwave because of the heatwave's profound disruptions on both population abundances and biodiversity, directly and indirectly (Figure 2A and Appendix S1: Figure S1). We anticipated that these effects would extend from local to broader spatial scales (Figure 2B).

MATERIALS AND METHODS

Study area and data sets

Annual surveys of biomass for kelp forest organisms were performed by the SBC LTER in July/August of each year between 2000 and 2021 (Santa Barbara Coastal LTER, et al., 2021). At each of 11 sites, two to eight permanently located 40×2 m transects were established (Appendix S1: Figure S2). Within each transect, the density and size of benthic species were nondestructively measured and later converted to biomass using species-specific allometric relationships (Lamy et al., 2019; Reed et al., 2016). Divers recorded 227 unique taxa across four functional groups: fishes (66 taxa), sessile invertebrates (69 taxa), mobile invertebrates (33 taxa), and understory macroalgae (58 taxa). We use the term "species" but acknowledge that some taxa were identified to higher taxonomic levels (e.g., genus; see the data deposited by Reed et al., [2021] for a complete list of taxa).

Diversity

We regarded 11 sites as communities at the large spatial scale (i.e., γ scale), which encompassed 44 transects as local communities at the local spatial scale (i.e., α scale). We used the number of taxa to calculate richness, the simplest and most common diversity metric. We counted taxa richness at the local transect (α_{rich}) and broader site (γ_{rich}) scales, as well as multiplicative beta diversity ($\beta_{\mathrm{rich}} = \gamma_{\mathrm{rich}}/\alpha_{\mathrm{rich}}$). We also used the inverse of the Simpson index (see below) according to biomass-based metrics, which has been recognized as the effective number of species based on the probability of interspecific encounter (Chase & Knight, 2013). By integrating the number of species and their biomass, this diversity index is more robust to the effect of rare species than taxa richness and can provide a more scale-independent measure of potential biodiversity effects in terms of examining the DSRs (Seabloom et al., 2021). At the local scale, we calculated the Simpson index: $\phi_l = \sum_i^S p_{il}^2$, where p_{il} denotes the relative biomass of species i of the local community l and S is the number of species in the local community l at the transect level. $\alpha_{1/\mathrm{simp}} = 1/\sum_{l=1}^{n}\omega_l\phi_l$, where ω_l represents the weight ratio of the total biomass of the local community l to that of the aggregate community (i.e., aggregation of two or multiple transects) at the site level. At the broader spatial scale, we similarly defined γ diversity as the inverse of the Simpson index: $\gamma_{1/\mathrm{simp}} = 1/\sum_i p_{i.}^2$, where $p_{i.} = \sum_{l=1}^{n}\omega_l p_{il}$ is the relative biomass of species i in the aggregate community at the site level. β diversity was computed as follows: $\beta_{1/\mathrm{simp}} = \gamma_{1/\mathrm{simp}}/\alpha_{1/\mathrm{simp}}$.

Stability

We defined community stability at both the α scale ($N_{\mathrm{transect}} = 44$) and the γ scale ($N_{\mathrm{site}} = 11$). At the local transect (α) scale, α stability can be partitioned into the weighted average of local population stability across species and local communities (i.e., population stability) and species asynchrony (Loreau & de Mazancourt, 2008; Thibaut & Connolly, 2013). At the broader site (γ) scale, γ stability also can be mathematically partitioned into the weighted average of local (α) stability and spatial asynchrony (Wang & Loreau, 2014, 2016). In light of this framework, species asynchrony is the ratio of α stability to population stability while spatial asynchrony is the ratio of γ stability to α stability. Thus, γ stability is the aggregated product of population stability, species asynchrony, and spatial asynchrony. The mathematical formulas for these definitions are as follows:

$$\text{Population stability} = \frac{\sum_{i,k}\mu_{i,k}}{\sum_{i,k}\sqrt{\nu_{ii,kk}}}, \tag{1}$$

$$\alpha\,\text{stability} = \frac{\sum_{i,k}\mu_{i,k}}{\sum_{k}\sqrt{\sum_{i,j}\nu_{ij,kk}}}, \tag{2}$$

$$\gamma\,\text{stability} = \frac{\sum_{i,k}\mu_{i,k}}{\sqrt{\sum_{i,j,k,l}\nu_{ij,kl}.}}, \tag{3}$$

$$\text{Species asynchrony} = \frac{\sum_{i,k}\sqrt{\nu_{ii,kk}}}{\sum_{k}\sqrt{\sum_{i,j}\nu_{ij,kk}}}, \tag{4}$$

$$\text{Spatial asynchrony} = \frac{\sum_{k}\sqrt{\sum_{i,j}\nu_{ij,kk}}}{\sqrt{\sum_{i,j,k,l}\nu_{ij,kl}}}, \tag{5}$$

where $\mu_{i,k}$ is the temporal mean of the biomass of species i in local community k, and $\nu_{ij,kl}$ denotes the covariance between species i in local community k and species j in local community l. Calculations of the stability and asynchrony indices were based on recent studies (Liang et al., 2021; 2022; Wang et al., 2019).

Data analysis

To determine whether changes in diversity, stability, and their relationships were associated with the marine heatwave, we compared kelp forest biodiversity data before (2007–2013) and during/after (2014–2020) the heatwave at all sites. This BACI approach has been widely used in many works to discern community changes attributable to sudden, severe disturbances like extreme temperature anomalies (Benkwitt et al., 2020; Reed et al., 2016; Rogers-Bennett & Catton, 2019). Moreover, large-scale, long-term experimental in situ temperature manipulation is not feasible in this system. While recognizing the limitations of a BACI approach to study a "natural experiment," particularly that further correlation analyses does not equate to causation, this approach provides valuable insights into the temporal dynamics of ecosystem responses to environmental change.

To assess changes in diversity and stability between the periods before versus during/after the heatwave, we first calculated the indices of diversity and stability among functional groups at local transect and broader site scales between these two periods, respectively. For comparable measurement time intervals, we separated the time interval into two 7-year windows before (2007–2013) versus during/after (2014–2020) the heatwave (Appendix S1: Figures S6–S9 and Tables S1–S3). We then ran two types of models to compare changes in these variables of each functional group before versus during/after the heatwave at the transect and site scales. Specifically, we used linear mixed-effects models with "sites" as a random factor at the local scale ($N_{\text{transect}} = 44$) using the R package nlme (Pinheiro et al., 2022). We used simple linear models at the broader spatial scale ($N_{\text{site}} = 11$). To determine the influence on our results by the duration of measurements of diversity and stability, we repeated our analyses with temporal intervals of 3 years (2011–2013 vs. 2014–2016), 4 years (2010–2013 vs. 2014–2017), 5 years (2009–2013 vs. 2014–2018), and 6 years (2008–2013 vs. 2014–2019). These results were broadly consistent with our initial findings using the 7-year interval, indicating a robustness to our results (Appendix S1: Tables S2–S11).

To investigate changes in DSRs between the periods before versus during/after the heatwave, we compared the strength of DSRs (e.g., significance level: p-values; slope: regression coefficients; and R^2: explained variance in linear models) before (2007–2013) versus during/after (2014–2020) the heatwave in the 7-year interval window. In these linear models, the response variables were stability and asynchrony metrics and the fixed predictor variables were diversity metrics at multiple scales for fishes, sessile invertebrates, mobile invertebrates, and understory algae. Specifically, α diversity was used for analyzing α stability, population stability, and species asynchrony at the local scale ($N_{\text{transect}} = 44$); β diversity was used for analyzing β stability (spatial asynchrony); γ diversity was used for analyzing γ stability at the broader spatial scales ($N_{\text{site}} = 11$). We also used analysis of covariance (ANCOVA) to compare changes in DSR slopes before versus after the heatwave. Our analysis comparing the temporal window of measurement demonstrated constant results (Appendix S1: Figures S10–S12 and Tables S4–S12).

To facilitate the comparison of effect sizes, we log-transformed all variables. We ensured the normality of model residuals using histograms and quantile–quantile plots. Likewise, we ensured the homogeneity of variance by plotting normalized model residuals against model predictions and individual predictors. All analyses were carried out in R version 4.2.3 (R Development Core Team, 2023).

RESULTS

Changes in diversity and stability

Changes in kelp forest diversity before versus during/after the heatwave varied among functional groups and spatial scales (Figure 4A; Appendix S1: Figures S4, S5, and Table S1). At the local (transect) scale, fish richness (α_{rich}, number of taxa) decreased by 21% (Appendix S1: Figure S6A; $F_{1,76} = 10.78$, $p = 0.002$) and fish diversity ($\alpha_{1/\text{simp}}$, effective number of species) decreased by 15% (Appendix S1: Figure S7A; $F_{1,76} = 8.31$, $p = 0.005$). Mobile invertebrate richness (α_{rich}) decreased by 16% ($F_{1,76} = 6.58$, $p = 0.012$), but diversity did not change ($F_{1,76} = 2.58$, $p = 0.113$). Understory algal diversity ($\alpha_{1/\text{simp}}$) increased by 20% ($F_{1,76} = 6.76$, $p = 0.011$), but richness did not change ($F_{1,76} = 0.97$, $p = 0.328$). Neither local richness ($F_{1,76} = 0.21$, $p = 0.648$) nor diversity ($F_{1,76} = 0.27$, $p = 0.604$) changed for sessile invertebrates. At the broader (site) scale, we did not detect changes in β richness, γ richness, or the diversity of any functional groups during/after the heatwave (Figure 4A; Appendix S1: Figures S6B,C, S7B,C, and Table S1; $p > 0.05$ in all cases).

Changes in stability before versus during/after the heatwave also varied among functional groups

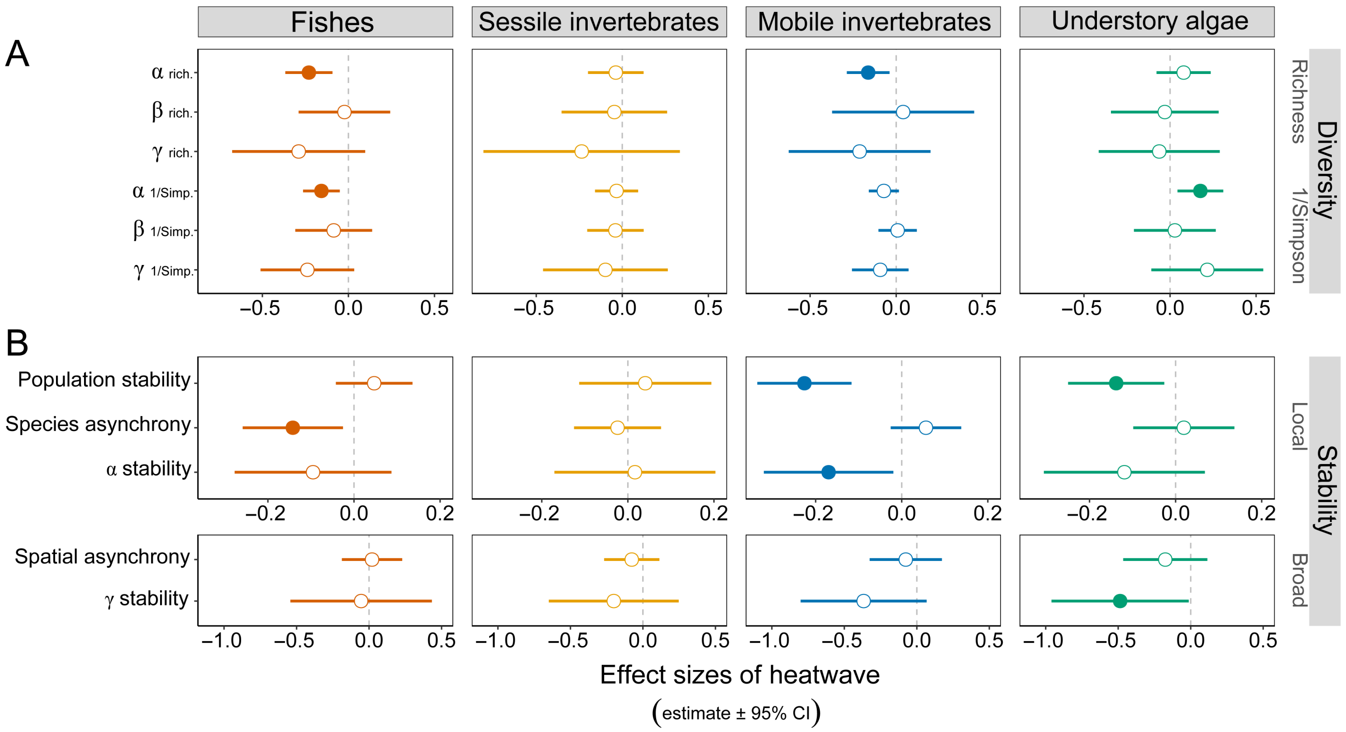

FIGURE 4 Changes in kelp forest biodiversity and stability at multiple spatial scales before versus during/after marine heatwave. Points and error bars are the standardized effect sizes and their 95% confidential intervals, respectively. Positive/negative effect sizes indicate higher/lower diversity or stability, respectively, during/after the heatwave compared to before the heatwave. Filled points indicate significant effects ($p \leq 0.05$). Sample sizes were 44 and 11 for the indices at local scales (i.e., α diversity [α_{rich} and $\alpha_{1/\text{simp}}$], population-level stability, species asynchrony, and α stability) and at broader spatial scales (i.e., β diversity [β_{rich} and $\beta_{1/\text{simp}}$], γ diversity [γ_{rich} and $\gamma_{1/\text{simp}}$], spatial asynchrony, and γ stability), respectively. Details and results of the sensitivity analysis can be found in Appendix S1: Figures S6 to S8, Tables S1 and S2.

(Figure 4B; Appendix S1: Figure S8 and Table S2). At the local scale, population-level stability decreased by 23% for mobile invertebrates ($F_{1,76} = 16.42$, $p = 0.0001$) and decreased by 17% for understory algae ($F_{1,76} = 5.87$, $p = 0.018$). Local population stability did not change for sessile invertebrates ($F_{1,76} = 0.27$, $p = 0.607$) or fishes ($F_{1,76} = 1.07$, $p = 0.305$). Community-level stability (α stability) of mobile invertebrates decreased by 19% ($F_{1,76} = 4.90$, $p = 0.030$) but did not change for any other groups ($p > 0.05$ in all cases). The species asynchrony of fishes decreased by 15% ($F_{1,76} = 5.72$, $p = 0.019$) but did not change in other groups ($p > 0.05$ in all cases). At the broader among-site scale, spatial asynchrony and γ stability did not change for any functional groups ($p > 0.05$ in all cases), except for marginal decreases in understory algae (46% decrease, $F_{1,20} = 4.07$, $p = 0.057$) and mobile invertebrates (39% decrease, $F_{1,20} = 2.74$, $p = 0.114$).

Our results on stability focus on a 7-year duration before versus during/after the heatwave (2007–2013 vs. 2014–2020) but were robust to the duration over which stability was calculated, including 3-year (2010–2013 vs. 2014–2016), 4-year (2009–2013 vs. 2014–2017), 5-year (2009–2013 vs. 2014–2018), and 6-year (2008–2013 vs. 2014–2019) durations (Appendix S1: Tables S2). By concentrating on α stability and its two key components—the temporal mean and SD of biomass—we observed that the magnitude of changes in these variables tended to vary among functional groups and also depended on the duration of observation. Notably, both the temporal mean and SD of biomass for mobile invertebrates decreased following the heatwave (Appendix S1: Figure S9 and Table S3).

Changes in DSRs

For fishes, stability indices (Figure 5A; Appendix S1: Figures S10–S12) were positively related to biodiversity regardless of the diversity metric used (richness or diversity expressed as an effective number of species). This held true at the population level (Appendix S1: Table S4; α_{rich}: $F_{1,42} = 29.47$, $p < 0.0001$; $\alpha_{1/\text{simp}}$: $F_{1,42} = 27.60$, $p < 0.0001$), local community level (α_{rich}: $F_{1,42} = 22.80$, $p < 0.0001$; $\alpha_{1/\text{simp}}$: $F_{1,42} = 22.67$, $p < 0.0001$), and broader site level (Appendix S1: Table S5; γ_{rich}: $F_{1,9} = 5.88$, $p = 0.038$; $\gamma_{1/\text{simp}}$; $F_{1,9} = 11.43$, $p = 0.008$). Fish species asynchrony was also positively related to α richness

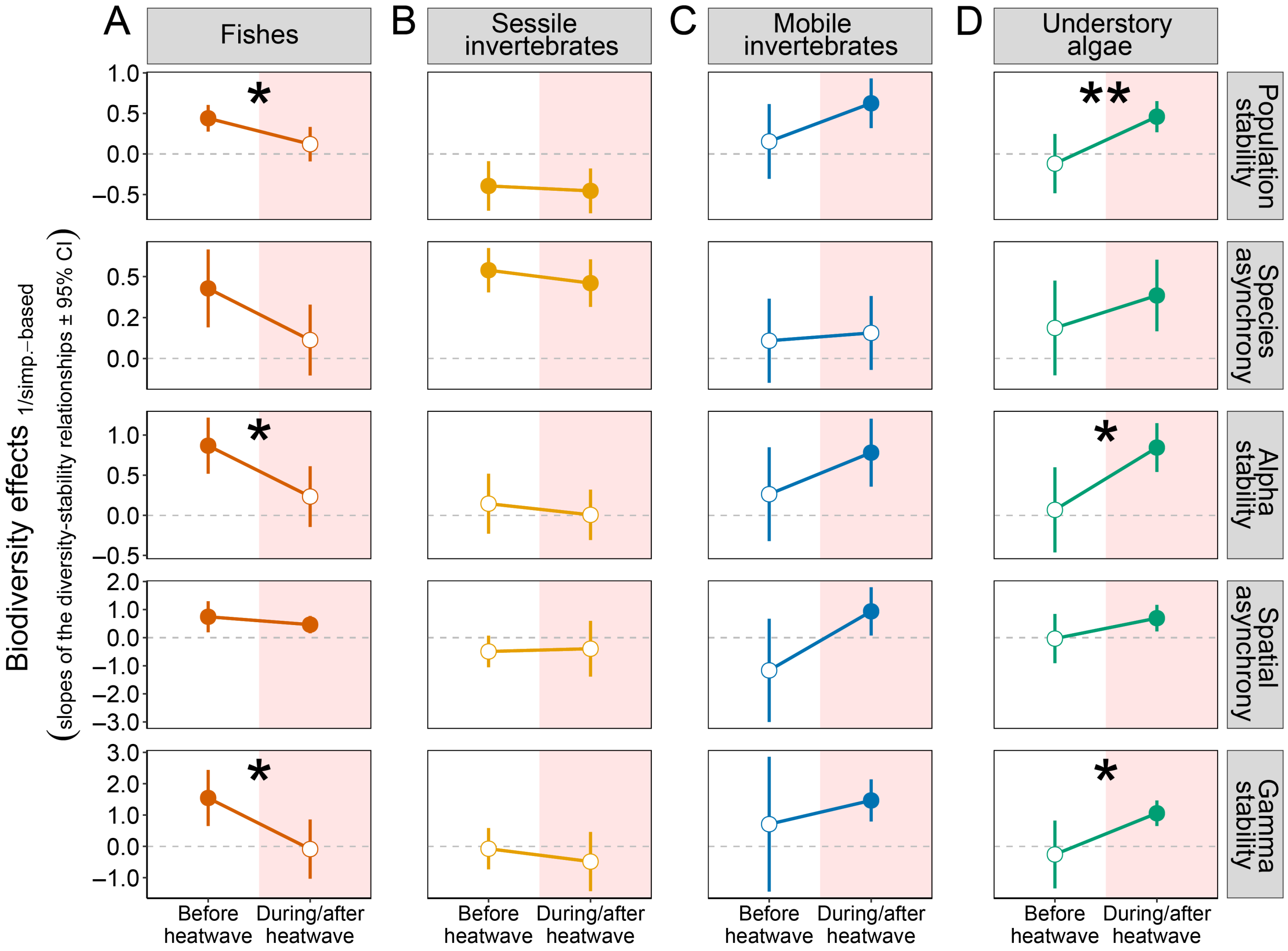

FIGURE 5 Changes in diversity–stability relationships (DSRs) across multiple scales of kelp forest before versus during/after the heatwave. Shown are the standardized magnitude of DSR slopes (simple linear models between stability and diversity) for fishes, sessile invertebrates, mobile invertebrates, and understory algae before (2007–2013) versus during/after (2014–2020) the marine heatwave. The diversity indices used here are based on the inverse of the Simpson index. In the models, α diversity is the explanatory variable for analyzing α stability, population stability, and species asynchrony at the local scale ($N_{\text{transect}} = 44$); β diversity was used for analyzing β stability (spatial asynchrony); γ diversity was employed for explaining changes in γ stability at the broader spatial scales ($N_{\text{site}} = 11$). Points and error bars are the standardized effect sizes of DSRs and their 95% confidential intervals. Filled points indicate slopes significantly greater than zero ($p \leq 0.05$). Asterisks show the significance of pairwise differences between slopes before versus during/after: *$p \leq 0.05$ and **$p \leq 0.001$. Information about the model fit, the DSR of each functional group, and further sensitivity analysis are provided in Appendix S1: Figures S11 to S12 and Tables S4 to S11.

($F_{1,42} = 11.07$, $p = 0.002$) and α diversity ($F_{1,42} = 12.45$, $p = 0.001$), while spatial asynchrony was positively related to β diversity based on $\gamma_{1/\text{simp}}/\alpha_{1/\text{simp}}$ ($F_{1,9} = 6.96$, $p = 0.027$) but negatively related to β diversity based on $\gamma_{\text{rich}}/\alpha_{\text{rich}}$ ($F_{1,9} = 16.02$, $p = 0.003$). However, these significant relationships consistently switched to nonsignificant trends during/after the heatwave.

For sessile invertebrates, population stability was negatively related to α diversity (e.g., $\alpha_{1/\text{simp}}$) both before and during/after the heatwave (Figure 5B; $F_{1,42} = 6.42$, $p = 0.015$ and $F_{1,42} = 10.44$, $p = 0.002$, respectively). On the other hand, for both time periods there were positive relationships between species asynchrony and α_{rich} (Appendix S1: Figure S10 and Table S6; $F_{1,42} = 11.37$, $p = 0.002$ and $F_{1,42} = 8.41$, $p = 0.006$, respectively) and species asynchrony and $\alpha_{1/\text{simp}}$ (Appendix S1: Figures S11 and S12, and Table S6; $F_{1,42} = 61.16$, $p < 0.0001$ and $F_{1,42} = 38.72$, $p < 0.0001$, respectively). We did not detect significant relationships between community stability and diversity at local or broader spatial scales, nor a relationship between spatial asynchrony and β diversity (Appendix S1: Figure S12 and Table S7; $p > 0.05$ in all cases). Changes in these slopes were not significant during/after the heatwave ($p > 0.05$ in all cases).

For mobile invertebrates and understory algae, changes in DSRs before versus during/after the heatwave varied based on the diversity metric used (Figure 5C,D; Appendix S1: Figures S10–S12 and Tables S8–S11). For richness, positive DSRs were unchanged during/after the heatwave (Appendix S1: Figure S10C,D; $p > 0.05$ in all cases). However, DSRs based on the effective number of species (1/Simpson) tended to switch from neutral (i.e., nonsignificant slope, $p > 0.05$) to positive ($p < 0.05$) during/after the heatwave for both functional groups (Figure 5C,D). For understory algae, the DSR slopes for population stability ($F_{1,42} = 22.17$, $p < 0.0001$), α stability ($F_{1,42} = 29.60$, $p < 0.0001$), and γ stability ($F_{1,9} = 26.00$, $p = 0.001$) significantly increased during/after the heatwave (Figure 5D; Appendix S1: Tables S10 and S11).

In summary, DSRs changed before versus during/after the heatwave, but the magnitude of DSR responses associated with the heatwave varied among functional groups. As with trends for stability, changes in DSRs before versus during/after the heatwave were robust to changes in the temporal interval, including 3-year (2010–2013 vs. 2014–2016), 4-year (2009–2013 vs. 2014–2017), 5-year (2009–2013 vs. 2014–2018), 6-year (2008–2013 vs. 2014–2019), and 7-year (2007–2013 vs. 2014–2020) durations (Appendix S1: Tables S4–S11). Additionally, the relationship between stability and its two components, temporal mean and SD, held robustly before and during/after the heatwave (Appendix S1: Table S12).

DISCUSSION

Kelp forests—among the most productive ecosystems on Earth (Castorani et al., 2021; Pace & Lovett, 2013; Pessarrodona et al., 2022)—are experiencing increasingly dramatic environmental changes, particularly from ocean warming (Di Lorenzo & Mantua, 2016; Smale, 2020). In the North Pacific Ocean, reef communities experienced substantial changes in response to the largest marine heatwave on record (Arafeh-Dalmau et al., 2021; Cavanaugh et al., 2019; McPherson et al., 2021; Rassweiler et al., 2021; Rogers-Bennett & Catton, 2019; but see Reed et al., 2016). Our analyses shed new light on the effects of marine heatwaves on DSRs in kelp forests. Our study unravels the complex mechanisms underpinning DSRs, leading to two primary insights. First, aligning with numerous terrestrial plant studies, our findings corroborate the stabilizing influence of biodiversity in kelp forests at multiple scales (Lamy et al., 2019, 2020). Here, "scale" encompasses spatial dimensions (local and broader scales), levels of biological organization (species and community), and marine functional groups, including understory algae, sessile and mobile invertebrates, and fishes (Figures 4 and 5). Second, the positive DSRs underwent a shift in correspondence with the marine heatwave and its aftermath. Notably, changes in DSR strength during and after the heatwave (vs. before) were more pronounced among functional groups than across organizational levels (population vs. community) or spatial scales (local vs. broader). Specifically, we observed a decrease in DSR strength for fishes, an increase for mobile invertebrates and understory algae, and no change for sessile invertebrates (Figures 4 and 5). Our study underscores the critical role of biodiversity in maintaining ecosystem stability across multiple scales within a diverse marine ecosystem, despite the growing intensity and duration of climate change impacts (Frölicher et al., 2018; Oliver et al., 2018).

Differences in heatwave-associated changes in DSRs among functional groups may be intricately related to variations in life-history traits and their adaptability to thermal stress. Although definitive conclusions are constrained by the limited information on species-specific traits (Kinlan & Gaines, 2003; Reed et al., 2000), our observations offer several insights. First, a notable distinction among kelp forest functional groups lies in the mobility of their adult life stages. Our study revealed that the previously positive DSRs for fishes dissipated during and after the marine heatwave (Figure 5A). In contrast, the DSRs for sessile invertebrates remained unchanged (Figure 5B). This contrast may imply a higher resilience of sessile invertebrates to the thermal stress induced by the heatwave. The mobility of fishes might have contributed to their observed response; they may have relocated to more thermally suitable habitats outside of our study area, thereby manifesting as a destabilizing effect following the heatwave. This movement could be a behavioral thermoregulation strategy, indicating a complex interplay between mobility and environmental stress adaptation (He et al., 2013). Second, shifts in the dynamics of resource competition can profoundly influence DSRs, as predicted by theoretical studies (Lehman & Tilman, 2000; Loreau & de Mazancourt, 2008; Thibaut & Connolly, 2013). The heatwave's adverse impact, particularly on large understory species such as the dominant stalked kelp (*Pterygophora californica*), may have facilitated the opening of ecological niches and the reduction of competition, thereby altering community structure and function. The decrease in this dominant alga may have enhanced the availability of bottom light and benthic space, favoring other algae or invertebrates less affected by the warming (Castorani et al., 2018; Reed et al., 2016). A reduction in competition or, potentially, an increase in facilitation may have amplified DSRs observed among understory algae following the heatwave (Figure 5D). While our study was not designed to differentiate among these particular mechanisms, our observations underscore the multifaceted species' responses to environmental stressors and the potential shifts in biotic interactions and highlight the importance of considering species-specific traits within the broader ecological context. Further research into the traits and adaptive strategies of marine organisms is essential for a more comprehensive understanding of ecosystem resilience and stability in the face of escalating climatic changes.

Furthermore, our findings indicate that the post-heatwave alterations in DSRs extended from population to local communities and, further, to broader spatial scales. These alterations manifested with notably varied magnitudes across different functional groups. In the case of fishes, we found that the positive DSRs at the population level diminished during and after the heatwave, with this effect subsequently cascading to local communities and then to broader spatial scales (Figure 5A). Conversely, among understory algae, the emergence of positive DSRs at the population level and their subsequent propagation from local communities to broader scales became apparent only during/after the heatwave (Figure 5D). Our study specifically indicates that increased biodiversity can enhance both population-level stability and asynchrony, thereby contributing to heightened local (α) stability across these groups. This finding contrasts with recent meta-analyses suggesting that increasing biodiversity primarily promotes α stability by bolstering population stability rather than species asynchrony (Xu et al., 2021). In a previous investigation of SBC LTER kelp forest biodiversity data, Lamy et al. (2020) found positive DSRs for both population stability and species asynchrony among understory algae and sessile invertebrates, aligning with our findings. Although our in-depth analysis of DSRs encompassed a broader range of marine organisms, we underscore the need for more research that differentiates among functional groups, beyond our relatively coarse groupings, and investigates their particular responses to extreme environmental change.

At the broader spatial scale, our analysis further supports the existence of positive β DSRs—that is, a positive relationship between spatial asynchrony and β diversity—because this relationship was consistently found for fish communities both before and during/after the heatwave and for mobile invertebrates and understory algae only during/after the heatwave (Figure 5). Although we found variability in β DSRs among these functional groups, our findings support the importance of the spatial insurance theory (i.e., the positive relationship between spatial asynchrony and β diversity) in kelp forests (Figure 2B). In line with research on DSRs in terrestrial ecosystems and examining the spatial insurance theory across various organisms, such as birds (Catano et al., 2020), grasslands (Hautier et al., 2020; Liang et al., 2021; Wang et al., 2021), forests (Qiao et al., 2022), and mixed vegetations (Liang et al., 2022), our findings offer insights into marine species' responses to severe environmental shifts and their role in stabilizing ecosystem stability at broader spatial scales. Furthermore, despite our use of moving window sensitivity analysis, the study's spatial extent was relatively confined for aquatic ecosystems (within sites). In addition to considering spatial variations in the response of marine organisms to heatwaves (Cavanaugh et al., 2019), further research at larger spatial extents is essential to fully generalize the spatial insurance theory in the sea.

The increasing frequency and severity of marine heatwaves pose a significant threat to kelp forests and coastal ecosystems in general (Frölicher et al., 2018; Oliver et al., 2018; Smale, 2020). While our study sheds light on climate-associated changes in the stabilizing effects of biodiversity across various scales, a comprehensive understanding of how valuable coastal ecosystems respond to marine heatwaves remains a pressing need. Future studies should help unravel how trophic interactions within complex food webs respond to anomalous warming. Understanding top-down and bottom-up cascading effects is vital for a comprehensive grasp of biodiversity and ecosystem dynamics (Arimitsu et al., 2021). Kelp forests may be an ideal system to explore this idea, as they have served as a model ecosystem for testing theory on trophic cascades (Estes et al., 1998) and foundation species (Castorani et al., 2018; Miller et al., 2018). Changes in marine ecosystem stability may be linked to shifts in the stability of foundational species, such as giant kelp (Lamy et al., 2020; but see also Appendix S1: Figure S13). Our investigation into the impact of a marine heatwave on kelp forest ecosystems provides a framework for future research aimed at quantifying the effects of climate extremes on DSRs across scales.

AUTHOR CONTRIBUTIONS

M. L. conceived the idea, analyzed the data, and wrote the paper, with substantial input from all authors.

ACKNOWLEDGMENTS

This study is supported by the data sets from the Santa Barbara Coastal Long Term Ecology Research funded by the U.S. National Science Foundation (NSF). M. L. and M. C. N. C. were supported by NSF Award 2023555. K. C. C. was supported by NSF Award 2140335; T. W. B. was supported by NSF Award 2023523 and NASA Award 80NSSC22K0169; D. C. R. was supported by NSF Awards 2023474 and 1714195. S. W. was supported by the National Natural Science Foundation of China (Award 31988102 and 32122053). We thank A. Adeboje, L. E. Brideau, N. J. Coombs, M. R. Cornish, K. Emery, S. Hardison, E. Kadiyala, V. Karatayev, L. W. Sheppard, R. S. Smith, K. N. Tedford, and J. Walter for discussions that improved this study. M. E. S. Bracken and one anonymous reviewer provided comments that improved this manuscript. We are grateful to numerous scientists and staff members at SBC LTER who collected and managed the data.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data from Santa Barbara Coastal LTER et al. (2021) were utilized for this research; these data are available from the Environmental Data Initiative at https://doi.org/10.6073/pasta/f1cf070648d7654ada052835afb2cfe9. Additional data and code (Liang et al., 2023) are available in Zenodo at https://doi.org/10.5281/zenodo.10271527.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Liang, Maowei, Thomas Lamy, Daniel C. Reuman, Shaopeng Wang, Tom W. Bell, Kyle C. Cavanaugh, and Max C. N. Castorani. 2024. "A Marine Heatwave Changes the Stabilizing Effects of Biodiversity in Kelp Forests." *Ecology* e4288. https://doi.org/10.1002/ecy.4288