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Geographic variation in responses of kelp forest communities of the California Current to recent climatic changes

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Abstract

The changing global climate is having profound effects on coastal marine ecosystems around the world. Structure, functioning, and resilience, however, can vary geographically, depending on species composition, local oceanographic forcing, and other pressures from human activities and use. Understanding ecological responses to environmental change and predicting changes in the structure and functioning of whole ecosystems require large-scale, long-term studies, yet most studies trade spatial extent for temporal duration. We address this shortfall by integrating multiple long-term kelp forest monitoring datasets to evaluate biogeographic patterns and rates of change of key functional groups (FG) along the west coast of North America. Analysis of data from 469 sites spanning Alaska, USA, to Baja California, Mexico, and 373 species (assigned to 18 FG) reveals regional variation in responses to both long-term (2006–2016) change and a recent marine heatwave (2014–2016) associated with two atmospheric and oceanographic anomalies, the "Blob" and extreme El Niño Southern Oscillation (ENSO). Canopy-forming kelps appeared most

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sensitive to warming throughout their range. Other FGs varied in their responses among trophic levels, ecoregions, and in their sensitivity to heatwaves. Changes in community structure were most evident within the southern and northern California ecoregions, while communities in the center of the range were more resilient. We report a poleward shift in abundance of some key FGs. These results reveal major, ongoing region-wide changes in productive coastal marine ecosystems in response to large-scale climate variability, and the potential loss of foundation species. In particular, our results suggest that coastal communities that are dependent on kelp forests will be more impacted in the southern portion of the California Current region, highlighting the urgency of implementing adaptive strategies to sustain livelihoods and ensure food security. The results also highlight the value of multiregional integration and coordination of monitoring programs for improving our understanding of marine ecosystems, with the goal of informing policy and resource management in the future.

KEYWORDS

biogeographic patterns, climate change effects, ecosystem functioning, ENSO, functional responses, Kelp forest communities, marine heatwaves

1 | INTRODUCTION

Kelp forests are among the most productive and species-rich marine ecosystems in the world (Mann, 1973; Schiel & Foster, 2015). As such, kelp forests generate a diversity of essential ecosystem services, including cultural, commercial, and recreational uses, seafood and materials, coastal protection, and nutrient recycling (Krumhansl et al., 2016; Smale, Burrows, Moore, O'Connor, & Hawkins, 2013). Kelps (Order Laminariales) serve as foundation species for these productive ecosystems by providing habitat and food for a great diversity of species (Carr & Reed, 2016; Darwin, 1909; Lamy et al., 2020; Schiel & Foster, 2015; Springer, Hays, & Carr, 2010; Teagle, Hawkins, Moore, & Smale, 2017). Although climate change is considered a major driver of kelp persistence and stability at global and regional scales, substantial geographic variability exists in the dynamics of kelp through time. While kelp species can exhibit high resilience to climate variability (Dayton, Tegner, Parnell, & Edwards, 1992; Edwards, 2004), major declines in the abundance of several kelp species have been documented in response to ocean warming (Díez, Muguerza, Santolaria, Ganzedo, & Gorostiaga, 2012; Ling et al., 2015; Smale, 2020; Tanaka, Taino, Haraguchi, Prendergast, & Hiraoka, 2012; Wernberg et al., 2012). A global analysis of kelp density over time revealed marked differences in the magnitude and direction of change across their geographic range, suggesting that local factors play an important role in driving patterns of kelp forest responses (i.e. distribution and abundance) to global change (Krumhansl et al., 2016). Assessing how and why responses vary geographically, identifying what regions are more vulnerable or resilient, and informing management and adaptation efforts, such as protection in marine reserves, habitat restoration efforts, and expanded biophysical monitoring and research, are urgent and critical priorities.

As a foundation species, changes in the abundance of kelp can have cascading effects on community structure and ecosystem function (Beas-Luna et al., 2014; Byrnes et al., 2011; Carr & Reed, 2016; Edwards et al., 2020; Lamy et al., 2020; Miller et al., 2018; Schiel & Foster, 2015; Vergés et al., 2016; Wernberg et al., 2012). In contrast, variability in community structure and species interactions may influence the resilience of kelps to projected warming (Eisaguirre et al., 2020; Ling et al., 2015). Building on global analyses of kelp dynamics (Krumhansl et al., 2016), a critical next step for understanding potential geographic variability in response to warming is to assess responses in the biological communities associated with these important foundation species.

Progress in understanding the responses of coastal marine communities and ecosystems to environmental change at relevant regional scales is impeded by a lack of coordinated monitoring. Long-term ecological studies provide key insights into such responses and may contribute disproportionally to our understanding of how ecosystems respond to environmental forcing and human use (Hughes et al., 2017; Reed, Washburn, et al., 2016), but they are often limited in geographic coverage. For example, our understanding of how kelp forest communities respond to climatic warming has generally been geographically limited, or limited by the number of taxa and functional groups (FG) examined, with very few exceptions (Byrnes et al., 2011; Dayton & Tegner, 1984; Dayton et al., 1992; Ebeling et al., 1985; Edwards, 2004; Schiel & Foster, 2015; exceptions: Edwards & Estes, 2006; Edwards, 2019). To assess species distributional shifts and community change in response to climate disturbances within complex coastal ecosystems, it is critical that large-scale, long-term assessments of community structure are integrated in space and time.

To date, most large geographic-scale studies have examined only the response of kelps to changing environmental conditions (e.g., Krumhansl et al., 2016; Marzinelli et al., 2015; Merzouk & Johnson, 2011; Smale & Moore, 2017; Wernberg et al., 2011), whereas very few have evaluated responses of more than two or three FGs and those that have are limited to western Australia (Wernberg et al., 2012, 2016). Here, we addressed this question for the kelp forest ecosystems of the Gulf of Alaska (GOA) and California Current large marine ecosystems. Based on results of a global meta-analysis that evaluated the rate of change in giant kelp (*Macrocystis pyrifera*) populations from 34 ecoregions over 50 years (Krumhansl et al., 2016), we predict that regional factors will play an important role in driving kelp forest responses to climate change in North America.

Along the Northeastern Pacific, from Alaska to Baja California, kelps serve as foundation species for highly diverse communities that support fisheries and recreation across three nations, Canada, the United States and Mexico. Across this large geographic range, spanning approximately 30 degrees in latitude (4,500 km), differences in species composition, community structure, and gradients in human activities and pressures (e.g., harvesting, coastal discharges) reflect marked differences in oceanographic conditions (e.g., mean ocean temperatures, magnitude and frequency of coastal upwelling, exposure to swell energy). These differences in environmental conditions and community structure are manifest in geographically distinct ecoregions (persistent geographic differences in kelp forest ecosystem structure and functioning), which may result in differences in vulnerability to climate change.

A recent sequence of strong warming events (i.e., the 2014–2016 warm temperature anomaly—the “Warm Blob”—and 2014–2016 ENSO, collectively referred to as the “Marine Heatwave”) spanned the entire range of coastal kelp forest ecosystems across the Northeastern Pacific (Di Lorenzo & Mantua, 2016; Jacox et al., 2016; Leising et al., 2015). Fortuitously, multiple independent long-term ecological studies have been established throughout North America to track changes in kelp forest community structure and function in response to environmental variability and, in some cases, the establishment of marine protected areas (MPAs). Across the entire region, declines in phytoplankton and zooplankton abundance corresponded with the anomalously warm water temperatures and reduced nutrient availability (i.e., nitrate concentrations) in the photic zone (Cavole et al., 2016; Leising et al., 2015). Warm ocean temperatures and low nutrient availability are typically correlated with reduced kelp production (Graham, Vasquez, & Buschmann, 2007; Schiel & Foster, 2015; Yorke, Hanns, Shears, Page, & Miller, 2019).

The community-wide responses to these oceanographic events and predicted declines in kelp production and abundance are complex, expected to change with time, and suggest alternative, competing outcomes for how FGs will respond to changes in kelp production and persistence. The majority of kelp production is made available to kelp forest food webs by the loss of kelp blades that litter the forest floor and are incorporated into detrital pathways (reviewed by Carr & Reed, 2016; Schiel & Foster, 2015). Thus, one likely structural and functional response of kelp forests to warming events involves rapid and persistent changes in abundance and foraging behavior of detritivores. In particular, we predicted rapid and persistent increases in sea urchins as they shift from passive detritivory to active herbivory (Beas-Luna & Ladah, 2014; Ebeling et al., 1985; Harrold & Pearse, 1987; Harrold & Reed, 1985). In contrast to a rapid and persistent decline in detritivores, we predicted initial increases and eventual declines in other herbivores, in addition to sea urchins. Numerous experimental and observational studies have described how shading by canopy-forming kelps suppresses the abundance of benthic macroalgae, which provide food and habitat for a great diversity and abundance of benthic herbivores (e.g., reviewed by Arkema, Reed, & Schroeter, 2009; Carr & Reed, 2016; Dayton, 1985; Schiel & Foster, 2015). We therefore predicted densities of herbivores to initially increase with declines of kelp density. However, with the shift from passive detritivory to active herbivory of all macroalgae by sea urchins, we predicted the abundance of herbivores to eventually decline with the development of sea urchin barrens.

We hypothesized that the responses of sessile invertebrate suspension feeders and planktivores would be more complex and time dependent. Reduction in canopy-forming kelps can impact sessile invertebrate suspension feeders and planktivores through changes in both food and space resources, and the balance of these alternative influences is not clear. Declines in the density of canopy-forming kelps are predicted to initially indirectly decrease the abundance of these two FGs due to increased competition for space with benthic macroalgae that were previously light limited under the kelp canopy (Arkema et al., 2009; Clark, Edwards, & Foster, 2004; Lamy et al., 2020). However, with increased grazing by sea urchins and reduced cover of all macroalgae, we predicted the relative abundance of sessile suspension feeders and planktivores would eventually increase. Evidence for the importance of kelp-derived particulate organic material (POM) and dissolved organic material (DOM) from kelps on the productivity and abundance of these FGs is mixed. Some studies suggest that kelp-derived organic material enhances the productivity and abundance of these groups (e.g., Bustamante & Branch, 1996; Duggins, Simenstad, & Estes, 1989; Kaehler, Pakhomov, Kalin, & Davis, 2006; Miller & Page, 2012), whereas others suggest that kelp-derived organic material is not as significant as the influx of planktonic-derived organic material (Miller et al., 2018; Miller & Page, 2012; Miller, Page, & Brzezinski, 2013; Miller, Page, & Read, 2015; Page, Reed, Brzezinski, Melack, & Dugan, 2008; Yorke, Miller, Page, & Reed, 2013). Moreover, several studies indicate reduced rates of plankton delivery across reefs in the presence of canopy-forming kelps (Bray, 1981; Gaylord et al., 2007; Jackson & Winant, 1983). Thus, we tentatively predict short-term decreases and longer term increases in suspension feeders and planktivores with reduced kelp abundance.

Predicted responses of higher trophic levels are less clear. Abundances of macroinvertivores that consume either or both sessile and mobile invertebrates are likely to exhibit mixed responses depending on the composition of these taxa in their diet. However, the predicted eventual reductions in abundance

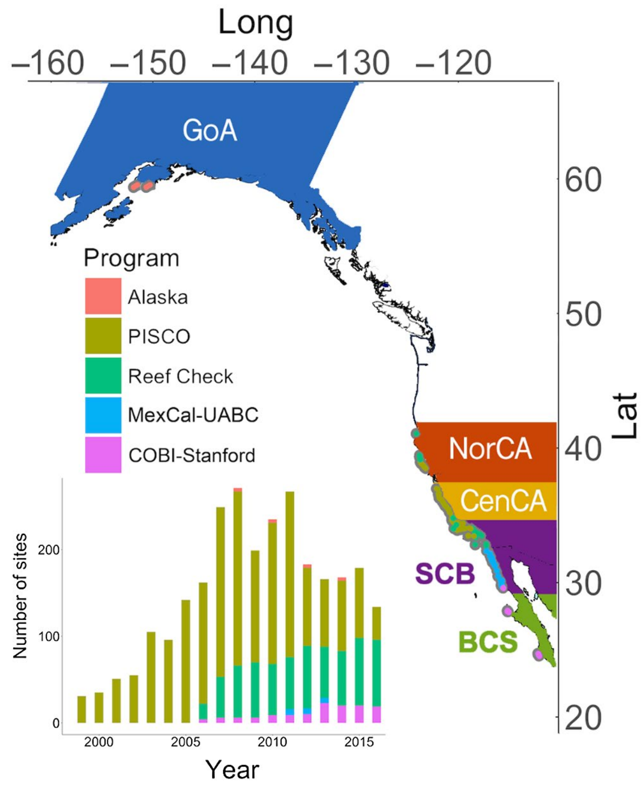

FIGURE 1 Map of the ecoregions along the west coast of United States and Mexico. GOA, Alaska; NorCA, Northern California; CenCA, Central California; SCB, Southern California and Baja Norte; BCS, Baja California Sur. The histogram shows number of sites sampled by program per year. Sampled sites are identified in the map color coded with the representative monitoring program

of sessile and mobile invertebrate detritivores, herbivores, suspension feeders, and planktivores suggest declines in their predators. Both field experiments and trophic models have detected declines in diversity of higher trophic levels with declines in kelp abundance and production (Byrnes et al., 2011). It is important to note that all FGs are likely influenced by temperature variability and extremes directly, in addition to indirect effects through changes in kelp abundance, adding further uncertainty to predicted responses.

The aim of this study was to test for predicted regional changes in kelp forest ecosystem structure and function in response to changing water temperatures over the last two decades, especially the recent, anomalous, marine heatwave. We leveraged independent datasets from Alaska, United States, to Baja California, Mexico, and information of recent warming events across the Northeastern Pacific, spanning the entire range of coastal kelp forest ecosystems in North America (Figure 1). These datasets provide a unique opportunity to assess community- and region-wide responses of these highly productive coastal ecosystems. In particular, we tested the following general predictions: (a) kelp abundance declines with increasing water temperature, and this decline is strongest at the warm edge of its range; (b) changes in abundance of kelp-associated FGs mirror changes in kelp abundance, as presented above; and (c) species ranges of kelps and associated species are shifting poleward in response to environmental change.

2 | MATERIALS AND METHODS

2.1 | Ecoregions

The geographic range of the study encompasses three well-recognized biogeographic regions that are primarily distinguished by persistent differences in ocean temperatures and species composition (Briggs, 1974; Horn, Allen, & Lea, 2006; Wilkinson et al., 2009). Southernmost, the San Diegan Province extends from the southern end of the Baja California peninsula, Mexico, north to Point Conception, United States. The Oregonian Province extends from Point Conception to the northern end of Vancouver Island, Canada. The Aleutian Province extends from Vancouver Island northward across southern Alaska and the Aleutian archipelago. These major biogeographic regions are further subdivided into distinct smaller "ecoregions," again distinguished by long-term mean sea surface temperatures (SST) and associated species assemblages (Figure 1). Within the San Diegan Province, a northern transition zone occurs within the Southern California Bight (SCB), United States, that is distinct from the Baja California Sur (BCS) ecoregion to the south. The Oregonian region includes a "Montereyan Pacific Transition" zone that is further delineated into a Central California (CenCA) ecoregion extending from Point Conception to Pigeon Point, CA, and a Northern California (NorCA) ecoregion that extends from Pigeon Point to just above Point Mendocino. There are no major subdivisions of the Aleutian Province, and it is therefore referred to here as the GOA ecoregion.

2.2 | Kelp forest monitoring programs

We combined data from five long-term monitoring programs of kelp forest ecosystems in the Northeastern Pacific (Figure 1; Table S1). All five programs collected data over time periods prior to and during the recent warming events.

Kachemak Bay Kelp Forest Monitoring began as part of the Census of Marine Life NaGISA program, a global effort to assess biodiversity on rocky shores and seagrass habitats. Currently, subtidal sites are still monitored in this ecoregion as part of the Kelp Forest Ecology class at the University of Alaska Fairbanks. Initially, sites were surveyed every year but are now surveyed every other year following the same protocol (Rigby, Iken, & Shirayama, 2007). Surveys are conducted from August to October.

The Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) is a consortium of four universities distributed along the coasts of California and Oregon. Since 1999, PISCO has conducted annual kelp forest monitoring studies with the primary goals of characterizing the geographic patterns and dynamics of community structure and the environmental and ecological processes responsible for those patterns (Caselle, Rassweiler, Hamilton, & Warner, 2015). Sites are surveyed once per year from mid-June to mid-October. Detailed descriptions of the kelp forest sampling design and protocols are available online (http://www.piscoweb.org/kelp-forest-study). The geographic range of PISCO kelp forest surveys include 371 sites, ranging from southern California to southern Oregon, though not all the sites have been surveyed for the entire time (1999–present).

Reef Check California is a citizen science non-profit organization (reefcheck.org). Since 2006, Reef Check California has monitored up to 131 sites in a given year spanning SCB to NorCA. The purpose of these long-term kelp forest studies is to engage citizens in collecting ecological data used to evaluate the effects of California's state-wide network of MPAs on kelp forest ecosystems. Sites are surveyed once per year from mid-June to mid-October. Trained volunteers use a protocol adapted from the PISCO survey methods with a reduction in taxonomic specificity. For comparisons of PISCO and Reef Check CA survey results, see Gillett et al. (2012).

Monitoring Ecosystems Across the Californias (MexCal) is based out of the Universidad Autónoma de Baja California. Since 2011, the program has conducted kelp forest ecosystem surveys at 19 sites from the US–Mexico border (Coronado Islands; 32°24′ LN) to Arrecife Sacramento (29°5′ LN), including coastal and island sites (Beas-Luna et al., 2019). Sites are surveyed once per year from August to November. The main purpose of this monitoring program has been to generate baseline information to inform the design and placement of MPAs in a transboundary context between Mexico and the United States.

COBI-Stanford University is a research consortium involving Comunidad y Biodiversidad A.C., fishing cooperatives of Baja California, Mexico, and Stanford University. The main goals of the monitoring are to assess the efficacy of MPAs established by fishing cooperatives (Fulton et al., 2018; Micheli et al., 2012; Woodson et al., 2018), to understand how kelp forest ecosystems respond to climate and oceanographic variability, and to inform management and adaptation strategies. Since 2006, the program has conducted kelp forest ecosystem monitoring at 21 sites in Isla Natividad, Isla Magdalena, and El Rosario using methods similar to Reef Check CA. Sites are surveyed once per year from July to October.

While not identical among the five programs, the sampling design and survey methods are comparable, based on depth-stratified, haphazardly distributed 30 m belt transects visually surveyed by scuba divers between 5 and 20 m water depth on rocky habitat. The main differences include the length of the programs in years, and the number of species for which information is collected. All programs quantify the density or percent cover of multiple species of conspicuous algae, invertebrates, and fishes. Details of spatial sampling design and frequency are described on each program's website or listed reference (Table S1). The taxonomic resolution was similar for all the datasets. For fish, mobile macroinvertebrates, and kelps (Laminariales), the data were collected at the species level. For colonial invertebrates, such as sponges, tunicates, and bryozoans, data were collected at the Order level. Finally, for most foliose red and brown algae, the taxonomic resolution was at the Division level and further divided based on functionally relevant morphological features of the blades (Table S2).

2.3 | Characterization of the trends in water temperature across ecoregions

We obtained composite monthly SST data for the period 2006–2016, covering the decade where all programs had sufficient data to perform analyses, from the MODIS Aqua satellite product (1.1 km resolution) available from the NOAA-ERDDAP data server (https://coastwatch.pfeg.noaa.gov/erddap/index.html). While the temperature data were coarse relative to the site spacing, they allow us to parse subregional-scale effects of temperature from long-term trends. We took the mean and maximum temperature from May to September (the timing of most surveys) of the closest 5 pixels to each survey site to evaluate the effects of temperature (warming) on FGs across the ecosystem. We also extracted the maximum temperature for the same 5 pixel window during summer months. Since mean and maximum temperature were strongly correlated with each other across the region ($R^2 = .98$, slope = 1.04), we used mean temperature for all subsequent analyses. Annual mean SSTs within each ecoregion were used to calculate annual mean anomalies from the long-term (2006–2016) mean SST for each ecoregion. We also calculated the normalized anomaly for each year within each ecoregion as the difference between the long-term mean SST divided by the long-term standard deviation.

2.4 | Characterization of the functional structure of the kelp forest communities

Along the Northeastern Pacific, four main species of kelps are the major canopy-forming and foundation species in kelp forest ecosystems. From north to south, these are the dragon kelp (*Eualaria fistulosa*), bull kelp (*Nereocystis luetkeana*), giant kelp (*Macrocystis pyrifera*), and southern sea palm (*Eisenia arborea*). Dragon kelp is abundant off the coast of Alaska, bull kelp dominates the northern latitudes from Alaska to NorCA, giant kelp is the dominant species from CenCA to Bahia Asuncion, Baja California, and *E. arborea* is dominant along the southern portion of BCS (Carr & Reed, 2016). Only a few species span the majority of the study region (e.g., the giant kelp, *M. pyrifera*; the red and purple sea urchin, *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*; and the predatory seastar, *Pisaster giganteus*). Instead, ranges of the vast majority of species associated with kelp forests are restricted to portions of the study region. These restricted ranges prevent comparison of temporal change across the entire study region at the species level. To allow for region-wide evaluation of changes in abundance and community structure, we assigned species to FGs. FG designation and species assignment were conducted by a subset of the co-authors, drawing from the literature and synthesized during two separate workshops. All taxa were grouped into 18 different FGs, primarily based on the trophic roles of each species in the community (Table S2). Information on the trophic relationships for each taxon was taken from a kelp forest species interactions database (Beas-Luna et al., 2014) and FishBase (fishbase.org). Across the initial 18 FGs, some were represented by an insufficient number of species to compare across the five ecoregions. We therefore show results of analyses of nine FGs, including the canopy-forming kelps. Several of these FGs (e.g., micro- and macroinvertivores) included many species because of the differences in species composition across such a broad study region encompassing five ecoregions. Because sea urchins play a disproportionate role in kelp forest deforestation (Estes & Duggins, 1995; Harrold & Reed, 1985; Steneck et al., 2002; Watanabe & Harrold, 1991), we removed them from the "herbivores" FG and created a separate group ("urchins"; Table S2).

2.5 | Data processing

Data integration was performed in a series of scripts in R and Rstudio (https://github.com/rbeas/ABCreef). Summary statistics (mean, standard deviation, and number of replicates) of the density (individuals per m^2 for mobile organisms and canopy kelp) and percent cover (for some algae and sessile invertebrates) for each year sampled were extracted for each program at the site scale, with each site corresponding to a reef or a stretch of the coast of ~300–500 m in length. In subsequent analyses, we only use density data because these can be more robustly transformed in a common currency across taxa (biomass), and included a majority of taxa. The integrated dataset includes 546 sites and 373 species organized into 18 FGs (Figure 1; Table S2). Data were summarized for each of the FGs for each site ($n = 12$–22 transects averaged/site × year combinations), for each of five ecoregions.

We converted density estimates to biomass, as our metric of abundance, using estimated sizes if available, or mean size of adult individuals because these were the size ranges counted in surveys (unless specifically noted). For species with estimated lengths, we used publicly available length–weight relationships from FishBase or SeaLifeBase. For species that were not available, we used values for related species.

2.6 | Statistical analyses

To evaluate how kelp forest FGs changed over the study period, and whether those changes are correlated with changing ocean temperature, we conducted four analyses. (1) We first developed predictive models of change in biomass of each FG within and among ecoregions and across all sample years (2006–2016) without temperature as an explanatory variable. (2) We then repeated this analysis with temperature as an explanatory variable and compared the directions and rate of change predicted by the models including and excluding site-level temperature. (3) To determine the extent to which rates of change identified in the predictive model with temperature might be attributed to the marine heatwave, we compared the model using all survey years (2006–2016) to a model using only the years prior to when the marine heatwave was manifest across the entire study region (2006–2013). (4) Lastly, we examined geographic shifts in FGs and changes in ecosystem structure over the study period by calculating shifts in the center of mass, range extent, and biomass of FGs using estimated instantaneous rates of change.

We tested predictions 1 and 2 using hierarchical Bayesian linear modeling to evaluate the rate of change among FGs across the entire study region, within each of the five ecoregions described above, and among sites within ecoregions, for the period 2006–2016. The model used to describe the abundance of FGs (y) through time (t) is:

$$\mu_{ijkt} = \beta_{0i} + \beta_{1i,k} + \left(\gamma_{0i} + \gamma_{1i,k}\right) x_{1ijkt}, \tag{1}$$

$$y_{ijkt} \sim \text{log normal}\left(\mu_{ijkt}, \sigma_j\right), \tag{2}$$

$$y_{ijkt} = \frac{\mathrm{FG}_{ijkt}}{max\left(\mathrm{FG}_i\right)} + 0.001, \tag{3}$$

where x is in years, β_{0i} and β_k are the intercepts, γ_{0i} and $\gamma_{i,k}$ are the slopes at ecoregional (i) and site (k) levels, respectively. The index, j, refers to the program responsible for data collection and allowed explicit incorporation of variability in program sampling protocols. y_{ijkt} is the standardized abundance of each FG within each ecoregion (i). This analysis allowed us to directly compare our results for kelp abundance with Krumhansl et al. (2016), who previously analyzed regional and global trends in kelp abundance. Results of these comparisons are available in the supplementary online material. Priors and hyperpriors were set following Krumhansl et al. (2016):

$$\left[\gamma_{0k,i}\,\gamma_{1k,i}\,\gamma_{2k,i}\right]^T \sim \mathrm{MVN}\,(0, \Sigma), \tag{4}$$

$$\Sigma = \text{diagonal}\left(\sigma_\gamma\right)\Omega, \tag{5}$$

$$\Omega = L \times L^T, \tag{6}$$

$$\gamma_{0k,i}, \gamma_{1k,i}, \beta_{0i}, \beta_{1i,k} \sim \text{uniform}\,[-\infty, \infty], \tag{7}$$

$$\sigma_j \sim \text{half}-\text{Cauchy}\left(0, \upsilon_M\right), \tag{8}$$

$$\upsilon_M \sim \text{uniform}\left[0, 3\right] \text{ or } \sim \text{half}-\text{Cauchy}\,(0, 2.5), \tag{9}$$

$$L_i \sim \text{LKJ Cholesky}\,(\upsilon = 2). \tag{10}$$

We then used a modified form of the hierarchical Bayesian linear model above (3) that incorporated temperature (x_2) to adjust for specific site level differences as:

$$\mu_{ijkt} = \beta_{0i} + \beta_{1i,k} + \left(\gamma_{0i} + \gamma_{1i,k}\right) x_{1ijkt} + \gamma_{2i,k} x_{2ijkt}. \qquad (11)$$

For temperature, we ran the model with 0 and 1 year lags to account for delayed responses to heatwaves. Time lags did not change the model predictions, so we present the non-lagged model results only. This model allowed us to incorporate site-level data that could contribute to variation in rates of change among sites. The lack of a temperature effect indicates that temperature at the site level does not preclude the potential for temperature to be a driver in regional or overall trends. We then compared the ecoregional rate of change estimates to the original model to examine if the ecoregional trends were robust to site-level differences. Priors for the site level temperature were set as:

$$\gamma_{2k,i} \sim \text{uniform}\left[-\infty, \infty\right]. \qquad (12)$$

We sampled posteriors using the no-U-turn-sampler variant of Hamilton Monte Carlo in Stan via MatlabStan. Sampling included four chains of 3,000 iterations. We ran subsampled values of the model, including burn-in for slopes moving through the samples until the subsampled values converged. A 1,000 iteration burn-in period proved sufficient for posterior convergence. From the posterior samples, we estimated the mean and 90% symmetrical credible interval for each rate. When the 90% credible interval (CI_{90}) of a specific rate did not cross zero, a significant change in the abundance of the FG is identified, equivalent to a 95% probability of decline or increase. To evaluate the extent to which observed responses were specifically attributed to the heatwave, we ran the Bayesian analysis (base model) with and without the years 2014–2016 (only 2014 for Alaska, as data are not available for 2015–2016; Figure 1). These analyses enabled us to directly assess the impacts of these extreme conditions on our estimates of long-term rates of change.

To assess geographic shifts in the distribution of FGs (see prediction 3 and analysis 4 above), we estimated the centroid of the distribution for each FG using the mean density and weighted mean latitude from all observations. This method accounts for higher numbers of observations in some ecoregions. We then combined the densities with modeled rates of change from the hierarchical Bayesian analysis to estimate the direction and magnitude of latitudinal shifts in the centroid and the extent of each distribution. These shifts are reported as centroid and range velocities where positive values indicate poleward progression and range expansion, whereas negative values indicate an equatorward progression and range contraction. For species and FGs that showed significant effects of the recent 2014–2016 warming events, we used rates of change estimated from the model that included temperature. For others, we used the original model (although no significant differences were observed when using the temperature model).

To examine changes in community structure (characterized as the relative contribution of FGs to total biomass), we compared community structure for the first and last years for which data were available across all sites (2008 and 2016). We forecast future ecosystem structure by extrapolating current trends in rates of change in abundance (year^{-1}) estimated from the hierarchical Bayesian model that did not include the temperature term out to the year 2050. We then used this total change to estimate abundance of each FG. For this analysis, the credible intervals for the rate estimates in the GOA ecoregion did not produce reliable results (negative abundances), and therefore, this ecoregion was excluded. Analyses using all slopes and only significant slopes showed no differences in results.

3 | RESULTS

3.1 | Characterization of the trends in water temperature across ecoregions

As expected, mean and maximum SST exhibited a negative poleward gradient where temperature decreased with increasing latitude (Figure S1a). However, mean SST anomaly and normalized SST anomalies were not coherent across ecoregions, with some ecoregions exhibiting anomalous increases in SST concurrent with decreases in other ecoregions (Figure S1b,c). Moreover, ecoregions differed markedly in the magnitude of variation in mean SST anomaly over the study period, with Baja Sur and Alaska exhibiting the greatest and least variation, respectively, across the ecoregions. Trends in SST anomalies among ecoregions and over time were generally consistent between the normalized and non-normalized SST anomaly approaches (Figure S1b,c), however, this difference among ecoregions in the magnitude of variation in time was dampened when normalized by ecoregion. With the exception of southern Baja California, trends in SST over time were generally consistent across ecoregions, both between the normalized and non-normalized anomalies, until the marine heatwave of 2014–2016 when all ecoregions showed strong positive anomalies (Figure S1b,c). During the heatwave, southern Baja California exhibited the highest mean positive (warm) anomaly, whereas CenCA exhibited the highest normalized mean positive (warm) anomaly. The southernmost and northernmost ecoregions exhibited additional positive anomalies: Baja California recorded positive anomalies in 2008, 2009, and 2012, while Alaska remained positive in 2016, when all the other ecoregions returned to normal temperatures.

3.2 | Response of kelp forest FGs to changes in water temperature

3.2.1 | Kelps and other macroalgae

Canopy-forming kelps declined in abundance across the entire study region, with similar rates of decline between models with and without temperature as a site-level explanatory variable (Figure 2a,b), indicative of a region-wide effect of warming. Overall, the instantaneous rate of change in kelp density across the entire study area was estimated at −0.043 year^{-1} (CI_{90}[−0.067 to −0.016]). The magnitude and direction of change in canopy kelp abundance over time

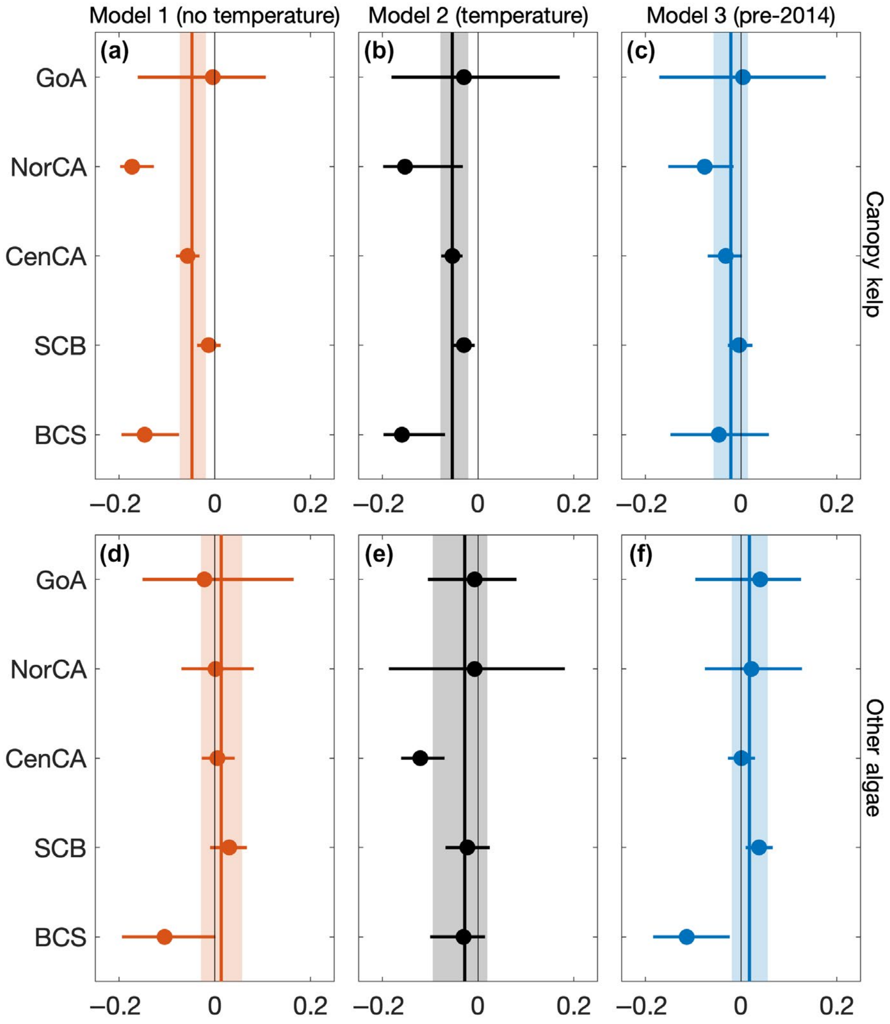

FIGURE 2 Rates of change in density of canopy kelp (a–c) and other algae (d–f) for three models (base model, model with site temperature, before marine heatwave). Rate of change (circles) and 90% credible intervals (horizontal lines) for the five ecoregions with the overall rate of change (vertical line) and 90% credible interval (shading)

differed among the ecoregions, and these differences showed no consistent latitudinal trend, regardless of the model used (Figure 2). Declines in kelp abundance were highest in the southernmost portion of the range and in the NorCA ecoregion, while declines in the central California ecoregion was smaller in magnitude, but still statistically significant, significant in southern California only in the model without temperature (Figure 2b), and not significantly different from zero in the GOA ecoregion. Removing the recent marine heatwave from the analyses significantly reduced the overall rate of change of canopy-forming kelps, suggesting that ~36% of the decline in kelp species was associated with the unprecedented recent warming event (Figure 2c). Rates of change in kelp abundance remained negative in northern and CenCA and in BCS, although the rates of change were only significantly different from zero in NorCA (Figure 2c), suggesting that other factors beyond the heatwave were responsible for kelp declines. Overall, no significant changes were observed in other macroalgal groups across the entire study region for any model (Figure 2d–f). The only exceptions to this included CenCA, which revealed a significant negative slope in the temperature model, and SCB and BCS with significant trends in the pre-heatwave models (positive and negative, respectively).

3.2.2 | Kelp-associated FG overview

There was substantial variation in the rate of change in abundance of kelp-associated FGs over the period 2006–2016 (Figure 3). Overall, FGs did not mirror the decline of kelps, with the exception of detritivores, which exhibited overall negative rates of change (except NorCA), particularly in the central and southern ecoregions (Figure 3). For all other groups, rates of change varied in magnitude and direction across ecoregions and were overall positive or not significantly different from zero (non-overlapping credible intervals; Figure 3). These trends were largely similar with and without temperature as a site-level explanatory variable. No significant differences in predicted rates of change of individual FGs across ecoregions were found when comparing these two models (Figure S2), with the exception of detritivores in NorCA and herbivores in BCS. Both of these FGs declined when site-level temperature was included in the model, matching the declines in kelp that occurred in these ecoregions (Figure S2). The marine heatwave had an effect on some rate estimates and on overall rates of change of urchins and microinvertivores (Figure 3). These effects are discussed in more detail for each FG.

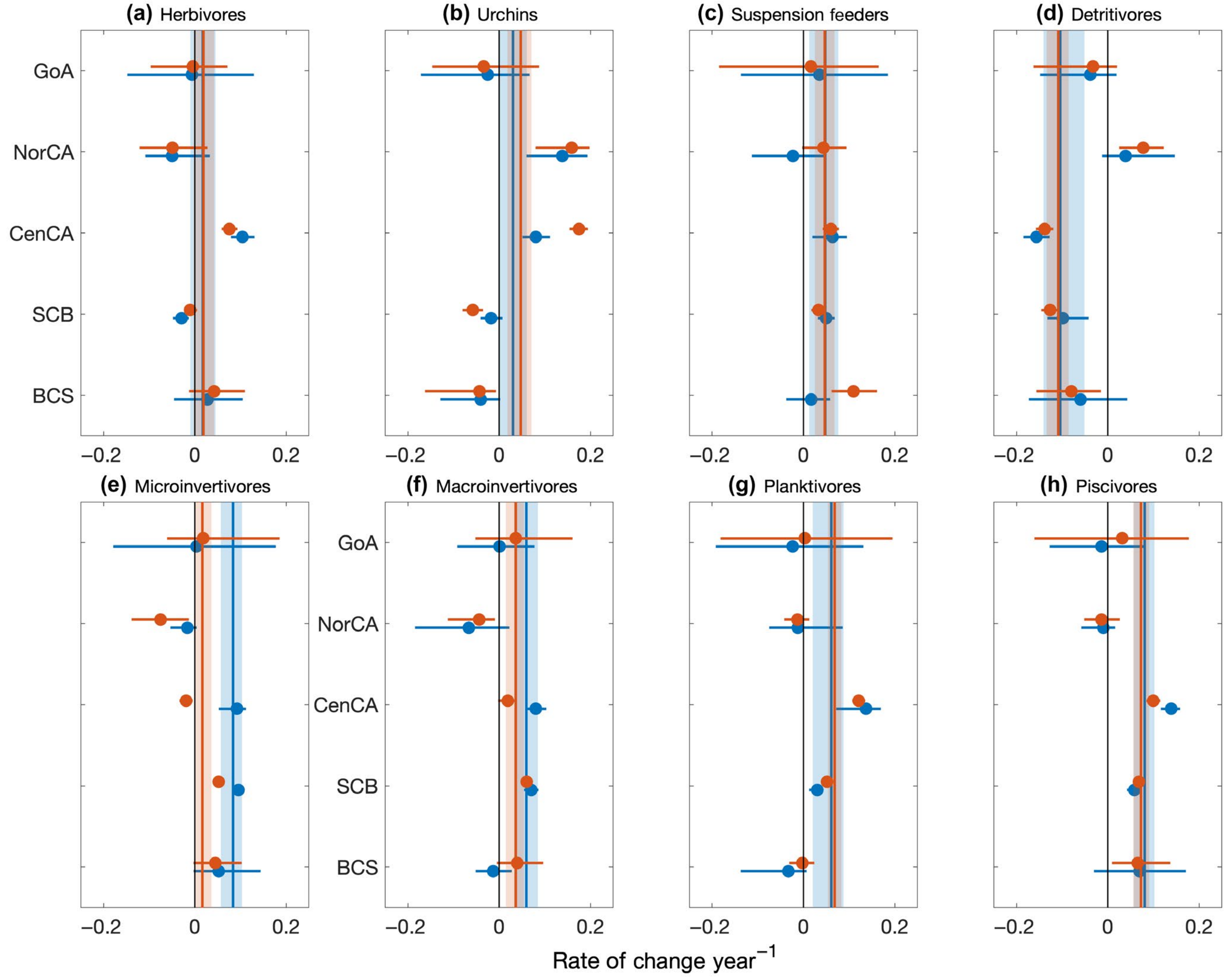

FIGURE 3 Rates of change in abundance of important functional groups (FG) over time for each ecoregion across all years, including the marine heatwave (2006–2016; red) and excluding years of the 2014–2016 marine heatwave (blue) for (a) herbivores, (b) urchins, (c) suspension feeders, (d) detritivores, (e) microinvertivores, (f) macroinvertivores, (g) planktivores, and (h) piscivores. Results are based on the model with temperature included. Rate of change (circles) and 90% credible intervals (horizontal lines) for the five ecoregions with the overall rate of change (vertical line) and 90% credible interval (shading). Note that scales are different from plot to plot. Non-overlapping credible intervals between model runs (blue vs. red) highlight regional FGs that were heavily affected by the warming event

3.2.3 | Urchins

Urchins, a key group of kelp grazers that we analyzed separately from other herbivores because of their ability to control kelp forest persistence, increased in abundance at an overall rate of 0.032 year^{-1} [CI$_{90}$: 0.003–0.050] (Figure 3b). However, analyses showed significant variation among ecoregions: urchin density increased in central and NorCA, and decreased in southern California and BCS, with no significant change at the northern limit of observations (GOA). Rates of change of urchin density were in some cases consistent with predicted patterns of change in canopy-forming kelps (declining kelp is associated with increasing urchin abundance) in northern and CenCA but not in others. For example, both kelps and urchins declined in BCS and Southern California with the marine heatwave (Figure 3b). In addition, the least amount of change in urchin density occurred in the two ecoregions that showed the least change in kelp density (GOA and Southern California). The timing of the marine heatwave was correlated with the positive rate of change of sea urchins in CenCA (Figure 3b), suggesting that the recent large changes in sea urchin abundance may be partly associated with the marine heatwave.

3.2.4 | Non-urchin herbivores

As predicted by the initial indirect positive effects of canopy-forming kelps on abundance of benthic macroalgae, herbivore abundance (excluding urchins) increased in CenCA where kelp density declined, but exhibited no significant rates of change in the other ecoregions (Figure 3a). In BCS, rates of increase were slightly higher when including the 2014–2016 marine heatwave but the rates of change were negative when site-level temperature over the entire time period (2006–2016; Figure S2) was included. The marine heatwave did not strongly influence rates of change of non-urchin herbivores in any ecoregion (Figure 3a).

3.2.5 | Remaining FGs

The marine heatwave reduced the overall rates of increase of microinvertivores, particularly in the central and southern California ecoregions (Figure 3c). In contrast, the remaining FGs—suspension feeders, macroinvertivores, planktivores, and piscivores—increased in abundance across much of the study region regardless of the effects of the marine heatwave (Figure 3). Suspension feeders increased in abundance across the entire range (Figure 3) and increased further in Baja California with the marine heatwave. Microinvertivores similarly increased in abundance, particularly in the Central and Southern California ecoregions, but decreased during the marine heatwave (Figure 3e). Macroinvertivore abundance was stable in the north, and increased in the southern ecoregions (Figure 3f). Macroinvertivore responses to the marine heatwave were mixed, with increases in Baja California and declines in CenCA. Planktivores increased in the central ecoregions (southern and CenCA), with no changes at the edges of the range (Figure 3g). These responses were consistent through the marine heatwave. Piscivores increased in the southern and central ecoregions, exhibited no change in abundance in the two northern ecoregions and did not show any significant response to the marine heatwave (Figure 3h).

3.2.6 | Geographic range and ecosystem structure shifts

We estimated changes in the geographic distributions of each FG by calculating the change in the geographic location of the centroid of the distribution and the range defined as latitudinal distance that covers 95% of total biomass. The centroids of biomass for canopy-forming kelp and detritivores have shifted to the north and their ranges have expanded (Figure 4). The centroid of biomass of urchins has similarly shifted northward, but not significantly so. In contrast, the centroid of the geographic range of all other FGs shifted to the south and contracted to various degrees. Herbivores and planktivores displayed the weakest response, while suspension feeders showed the strongest shifts (Figure 4). Higher trophic level FGs (microinvertivores, macroinvertivores, and piscivores) exhibited similar trends to one another, with relatively strong southward movement and small reductions in estimated range (Figure 4). Range velocity and center of distribution velocity are correlated ($R^2 = .78$, $p < .001$).

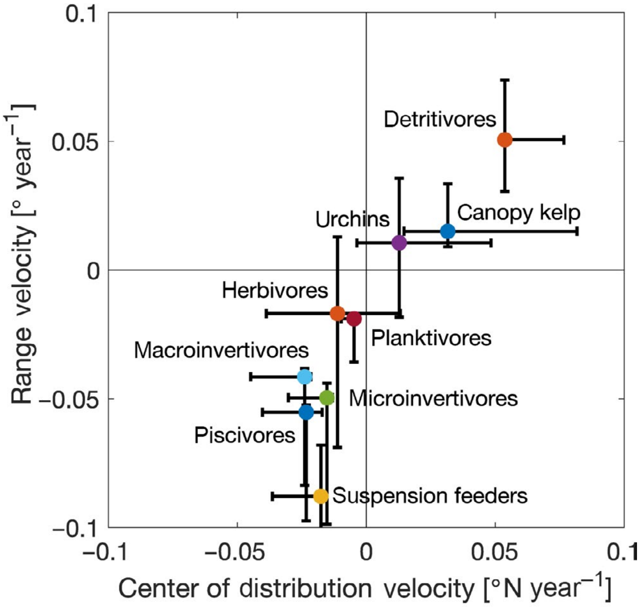

FIGURE 4 Shifts in functional group distributions as velocities based on estimated instantaneous rates of change across sites and regions. Location of center of distribution versus total range for 95% of abundance over a 10 year period. Positive values indicate poleward progression and range expansion, while negative values indicate an equatorward progression and range contraction

For kelp and associated species that are moving northward, this is likely because FGs are moving northward, but have not disappeared from their southern extent. For groups moving southward, associated contraction may be due to disappearance at the northern end of the ranges.

The results of these shifts in species abundances across their ranges may portend a dramatic shift in ecosystem structure and function over the next 20–30 years, assuming that the observed rates of change continue (Figure 5). From 2008 to 2016, the greatest change in ecosystem structure occurred in the southern ecoregions, especially off BCS, with the loss of canopy-forming kelps, and increases in the abundance of planktivores, macroinvertivores, and piscivores (Figure S3). While overall biomass is expected to decline across the range of kelp forest ecosystems (Figure 5), future community reorganization through the year 2050 is projected to be greatest in the southern (BCS) and northern (NorCA) ecoregions, but in different ways. Piscivores and invertivores are projected to increase in relative abundance to the south, while urchins and planktivores are projected to increase in relative abundance in the north (Figure 5). In contrast with the dramatic ongoing and projected ecosystem changes at the warmer edge of the range, the central ecoregions (central and southern California especially) are projected to be more resilient, with smaller ongoing and projected change in the dominant FGs (Figure 5), but with large projected increases in urchins and planktivores (Figure S3).

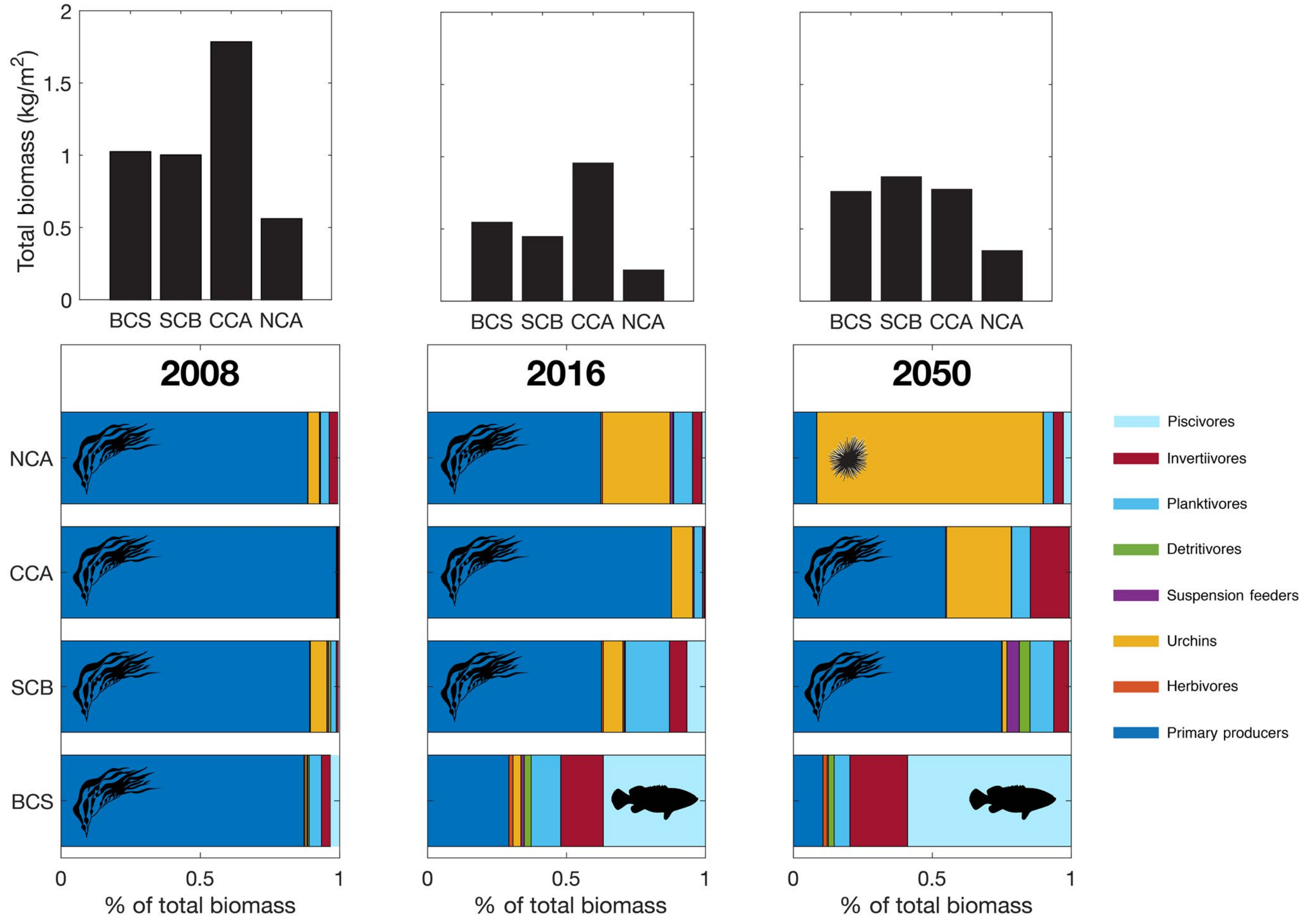

FIGURE 5 Biomass and normalized ecosystem structure before and during warming period from 2014 to 2016 shown with estimated structure based on instantaneous rates of change for the year 2050. The year 2008 is shown as baseline for before warming. Icon indicates the group with th largest biomass. Biomass density estimate is also given above each bar for each region. Gulf of Alaska is not included because of insufficient data across the functional groups (see Section 2)

4 | DISCUSSION

Results of this study contribute to the growing number of observations of structural and functional changes in coastal marine communities and ecosystems in response to changing environmental conditions (e.g., Bruno, Harley, & Burrows, 2014; Doney et al., 2012; Hoegh-Guldberg & Bruno, 2005; Poloczanska et al., 2013) and episodic marine heatwaves (e.g., Arias-Ortiz et al., 2018; Garrabou et al., 2009; Hobday et al., 2016; Hughes et al., 2017, 2018; Oliver et al., 2019; Smale et al., 2019). The period from 2014 to 2016 experienced unusual warming due to the North Pacific “Warm Blob” and the strongest positive ENSO event since 1998 (i.e., the marine heatwave; Di Lorenzo & Mantua, 2016; Jacox et al., 2016; Leising et al., 2015). While this study identified ecological responses to variation in water temperatures over the past decade across the study region, the response to the recent marine heatwave accentuated these changes, underscoring the pronounced consequences of marine heatwaves to coastal marine ecosystems. The more rapid and greater temperature change associated with marine heatwaves generates faster and more pronounced ecological responses, and the global occurrence, spatial extent, frequency, duration, and intensity of these events are increasing globally (Frölicher & Laufkötter, 2018; Holbrook et al., 2019; Oliver et al., 2019). Moreover, heatwaves are predicted to be greater with increased levels of global climate change (Frölicher & Laufkötter, 2018).

Our results, like others around the world, indicate that temperate kelp forest ecosystems appear especially vulnerable to marine heatwaves because of the pronounced effects on kelps as foundation species (sensu Dayton, 1972), which serve as major sources of primary production and physical habitat structure (e.g., Arafeh-Dalmau et al., 2020; Filbee-Dexter, Feehan, & Scheibling, 2016; Filbee-Dexter & Wernberg, 2018; Filbee-Dexter, Wernberg, Fredriksen, Norderhaug, & Pedersen, 2018; Martínez et al., 2018; Rogers-Bennett & Catton, 2019; Smale & Wernberg, 2013; Tanaka et al., 2012; Thomsen et al., 2019; Vergés et al., 2016; Wernberg et al., 2010, 2011, 2012, 2016). We found that region-wide declines in abundance of canopy-forming kelps were strongly associated with the recent marine heatwave. Overall, the instantaneous rate of change in kelp density across the entire study area (−0.043 year^{-1};

CI_{90} [−0.067 to −0.016]) is approximately 2.4 times higher than global estimates of −0.018 year^{-1} over the past 50 years (Krumhansl et al., 2016), although this was driven by two of the five ecoregions (see below).

These marked declines in kelp abundance are likely related to reduced nutrient concentrations associated with increased water temperatures (e.g., Reed, Washburn, et al., 2016), but were exacerbated by observed shifts in foraging behavior of a critically important ecosystem engineer, the purple sea urchin, *Strongylocentrotus purpuratus*, in the central and southern ecoregions. Similar to the declines in kelp, the observed increase in purple urchin densities was especially pronounced during the marine heatwave and was greatest in the NorCA and BCS ecoregions that experienced significant kelp loss, while changes in urchin densities were lowest in the Central and Southern California ecoregions that experienced the least change in kelp abundance. Increased counts of purple urchins appear attributable to three key processes. (a) In 2013, the seastar wasting disease that affected the entire study region lead to the functional extinction of the sunflower star, *Pycnopodia helianthoides*, a well-known predator of sea urchins (Harvell et al., 2019). (b) With reduced production of kelp and availability of drift, coupled with loss of a key predator, purple sea urchins shifted from passive to active foraging, denuding reefs of macroalgae, including giant kelp and bull kelp (Rogers-Bennett & Catton, 2019). (c) As reefs shifted from forests to urchin barrens, pavements of encrusting coralline algae likely facilitated settlement of purple urchins (Baskett & Salomon, 2010), exacerbating the further increase in urchin densities.

The marked variation in kelp and sea urchin trajectories across most of the ecoregions monitored in this study point to important influences of regional processes interacting with both long-term and episodic changes in ocean temperatures. For example, both kelps and urchins declined in BCS with the marine heatwave, while urchins declined and giant kelp did not change in abundance in Southern California, just to the north. Both kelps and urchins may be vulnerable to increased water temperatures at the southern end of their ranges. The extreme losses of giant kelp off Baja California, Mexico, have been noted in previous warming events (Edwards, 2004) and by others in response to the recent marine heatwave (Arafeh-Dalmau et al., 2019; Cavanaugh, Reed, Bell, Castorani, & Beas-Luna, 2019). In contrast, and similar to our results, Reed, Washburn, et al. (2016) could not attribute any change in the long-term declining trajectory of giant kelp abundance and several associated species in southern California to the same marine heatwave we evaluated. In southern ecoregions where, in contrast to our predictions, urchin counts declined, the warmer waters may be more conducive to diseases that have contributed to declines of urchin outbreaks (Behrens & Lafferty, 2004; Lafferty, 2004; Lester, Tobin, & Behrens, 2007). The greater declines of bull kelp populations in NorCA compared to patchier and less severe declines of giant kelp in CenCA could reflect the absence and presence, respectively, of the southern sea otter, *Enhydra lutris nereis*, which is a key predator on sea urchins in CenCA. Likewise, southern California also has functional redundancy in urchin predators with California sheephead and spiny lobster (Hamilton & Caselle, 2015; Selden, Gaines, Hamilton, & Warner, 2017; Tegner & Levin, 1983), especially in several MPAs, which are included in our surveys there. Thus, the persistence of kelps in our southern California survey sites may reflect the protection of key sea urchin predators and an enhanced resistance and resilience of kelp forest communities to the loss of the sunflower star (Eisaguirre et al., 2020). These are only two examples of strong environmental and ecological differences among the ecoregions of the California Current large marine ecosystem.

The direction and magnitude of responses of other FGs to the observed declines in kelp varied as a function of their direct interactions with kelp. In addition to the predicted direct responses of sea urchins, another group closely linked to kelp productivity—the detritivores—such as sea cucumbers, abalone, and some sea stars, exhibited the strongest decline of any FG, particularly in the southern portion of giant kelp's biogeographic range (Figure 3). This strong decline in the southernmost ecoregion led to the strongest poleward biogeographic shift of FGs (Figure 4). Like terrestrial forests, much of the production of kelp forests fuels detrital pathways as blades and fronds fall to the seafloor as "drift" (i.e., litter), and as the alga exudes or deteriorates to dissolved and particulate material (DOM and POM, respectively). In fact, the strength of interaction and potential responses between kelp and detritivores is masked in our study in two ways. First because we separated sea urchins from other detritivores. Secondly by recognizing the great numbers of detritvorous small crustaceans and gastropods that are major conduits of nutrients and energy from kelp to microinvertivores, which are not quantified in our and most kelp forest community surveys. That drift production is such a strong pathway is evidenced by the high densities of sea urchins and abalone that support commercial and recreational fisheries in many parts of the world. Moreover, it is the loss of drift production that triggers the switch in foraging behavior from passive detritivory to active grazing of sea urchins, and subsequent shift in states of kelp forests communities (Filbee-Dexter & Scheibling, 2014).

Microinvertivores, the most diverse group, comprising a suite of invertebrate-feeding fish and invertebrates, did not exhibit declines over the longer term, but did appear to be negatively impacted by the heatwave. Importantly, this diminished response may reflect our inability to detect change in such a speciose group because of the greater functional redundancy that would buffer overall declines in the biomass and function of that FG (e.g., Yeager, Gouhier, & Hughes, 2020). In contrast to the predicted changes in sea urchins and detritivores, the observed negligible change in the other FGs may reflect variable and lagged responses to both declining kelp abundance and reduced productivity of coastal ocean waters. For instance, while herbivores increased in abundance, in accordance with predicted greater abundance of benthic macroalgae released from competition from canopy-forming kelps, this group is likely to eventually decline in abundance where forests have shifted to urchin barrens.

All other groups exhibited either little change or increases in central and southern California. Increases in sessile suspension feeders and planktivores may reflect greater detectability in surveys due to reduced cover of macroalgae or predicted eventual increases in prey availability in the absence of canopy-forming kelps. The presence and density of kelps reduce water flow across rocky reefs and the rate of delivery of planktonic prey (Bray, 1981; Gaylord et al., 2007; Hondolero & Edwards, 2017; Jackson & Winant, 1983). Moreover, Miller et al. (2015) found no evidence from stable isotope analyses to indicate that kelp detritus is an important food source for sessile suspension-feeding invertebrates. Little change or increases in higher trophic level macroinvertivores and piscivores reflect complex dynamics of lower trophic levels, including the mixed responses of detritivores, herbivores, microinvertivores, suspension feeders, and planktivores. Many macroinvertivores, including crustaceans, octopi, and fishes, are prey for other fishes, which in turn are prey for piscivores. Dampened responses of these higher level predators may reflect the diversity of lower trophic levels characteristic of these ecosystems. As generalist predators are buffered from prey population dynamics, predators with high dietary diversity are buffered by the variable responses of different FGs to declines in kelp abundance. However, kelps are nursery habitat for many piscivorous fishes (Carr & Syms, 2006; Wernberg et al., 2016) suggesting there may be declines via different mechanisms over longer time frames.

Clear signs of tropicalization have been reported for temperate marine ecosystems (Arafeh-Dalmau et al., 2019; Horta e Costa et al., 2014; Vergés et al., 2016). In the present study, we could not focus on species thermal affinities because we grouped species into FGs. Future analyses could use the dataset we have integrated to assess responses of different taxa to warming. Despite the uncertainty of future climatic events, understanding species thermal affinities and its contribution to the changing communities will be important for improved management of marine resources.

Decoupling in the responses of FGs at the base and top of these food webs may also reflect different drivers of change. In particular, the large positive rates of change of piscivores from CenCA to BCS may reflect changes in fishing pressure and management measures. The establishment of a network of MPAs in the Northern Channel Islands (Caselle et al., 2015; Hamilton & Caselle, 2015), as well as the establishment of voluntary, community-based no-take marine reserves in Baja California (Fulton et al., 2018; Micheli et al., 2012) may have contributed to positive rates of change in species targeted by fisheries. A region-wide assessment of the effects of the regional network of MPAs is a key priority for future analyses. Moreover, the ecosystem and region-wide impacts of additional stressors associated with climate and oceanographic variability, such as hypoxia (Boch et al., 2018; Micheli et al., 2012; Woodson et al., 2018), remain to be examined. Overall, our analyses show that year-to-year variability in temperature explains little of the trends in abundance of kelp-associated FGs at higher trophic levels.

These group-specific responses have resulted in large shifts in kelp forest community structure, with a significant northward shift of the center of distributional range for kelp and associated detritivores, and southward shifts in most higher level consumer groups. If such patterns continue, there may be a spatial mismatch in FGs that develop into region-specific ecosystem structure and function that differs from that of the recent past. Overall, these results corroborate findings from Krumhansl et al. (2016) that local drivers underlie regional and subregional variation in kelps and kelp forest ecosystems, highlighting the appropriateness and need for local management actions. Understanding how ecologically and economically important species are changing their distribution is critical to design strategic management plans (Caputi et al., 2016; Cavole et al., 2016; Hodgson et al., 2018; Lonhart, Jeppesen, Beas-Luna, Crooks, & Lorda, 2019; Mills et al., 2013; Pershing et al., 2015).

Our results further highlight the importance of monitoring programs that span an entire ecosystem's range. Monitoring across the entire range of an ecosystem can provide key insights into the status and health of the ecosystem as a whole in response to global drivers, as well as responses that may be variable at regional or even local scales (Edwards, 2019). Although our geographic coverage was heterogeneous, with sampling effort heavily concentrated in southern and CenCA, we are able to discern rates of change of key FGs, and predict potential changes in ecosystem structure and function in the near future. However, our results suggest that rates of change are highest in ecoregions (BCS and NorCA), where sampling is much more sparse. Moreover, changes were less evident in the GOA where temperature remained relatively cool. Similarly, though Pfister, Berry, and Mumford (2018) detected correlations between the areal cover of canopy-forming kelps and large scale, long-term environmental forcing, forests along the coast of Washington state have been broadly persistent through 2015. This may suggest the effects of climate variability will take longer to be apparent in these more northern ecoregions.

The current positive SST anomalies and apparent re-occurrence of a “warm blob” condition over the coming years (Oliver et al., 2019) make the need for region-wide long-term monitoring ever more urgent and critical. Disconcertingly, as this need become ever more obvious, large-scale, long-term ecosystem studies have generally declined in recent years (Hughes et al., 2017). As environmental variability and extremes are expected to increase, monitoring efforts need to be able to document the geographic patterns in response. Variability in responses across sites, regions, and entire ecosystems may be missed or misinterpreted given the sparse nature of sampling. Expansion of monitoring efforts with participatory citizen science models (e.g., Fulton et al., 2018) may lessen the burden on academic and regulatory agencies, while providing needed data to assess ecological consequences of a changing climate.

In conclusion, multiregional integration of monitoring programs reveals major, ongoing region-wide change in productive kelp forest ecosystems in response to long-term and episodic warming. Results indicate that coastal communities that are dependent on kelp forest ecosystems will be more heavily impacted in the southern portion of the GOA and California Current large marine ecosystems under future climate scenarios, highlighting the urgency of implementing adaptation strategies to sustain livelihoods and ensure food security. Continued adaptation efforts, including monitoring and broad regional integration of research (Aburto-Oropeza et al., 2018), are key to enabling effective strategies for addressing the ongoing and escalating future impacts of climate change and variability on ecosystems and people in coastal regions.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available at this online repository (https://github.com/rbeas/ABCreef). As the data come from different monitoring programs with particular restrictions, the access to the repository is available upon request. Contact the corresponding author at micheli@stanford.edu to request access to the data repository.

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SUPPORTING INFORMATION

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

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