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DR. RODRIGO BEAS (Orcid ID : 0000-0002-7266-3394)
DR. CHARLES A BOCH (Orcid ID : 0000-0003-1235-4941)
DR. SCOTT L HAMILTON (Orcid ID : 0000-0001-5034-4213)
DR. KRISTY JEAN KROEKER (Orcid ID : 0000-0002-5766-1999)

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

Beas-Luna, Rodrigo¹, Fiorenza Micheli^{2,3*§}, C. Brock Woodson^{4§}, Mark Carr^{5§}, Dan Malone⁵, Jorge Torre⁶, Charles Boch^{7,8}, Jennifer E. Caselle⁹, Matt Edwards¹⁰, Jan Freiwald¹¹, Scott L. Hamilton¹², Arturo Hernandez⁶, Brenda Konar¹³, Kristy J. Kroeker⁵, Julio Lorda¹, Gabriela Montaña-Moctezuma¹, Guillermo Torres¹

* corresponding author micheli@stanford.edu +1(831)655-6250, orcid: 0000-0002-6865-1438

§ should be considered joint senior authors

- ¹ Universidad Autónoma de Baja California, Ensenada, BC MX
- ² Hopkins Marine Station, Stanford University, Pacific Grove, CA USA
- ³ Stanford Center for Ocean Solutions, Stanford University, Pacific Grove, CA USA
- ⁴ College of Engineering, University of Georgia, Athens, GA USA
- ⁵ University of California, Santa Cruz, CA USA
- ⁶ Comunidad y Biodiversidad A.C., La Paz, BCS México
- ⁷ Monterey Bay Aquarium Research Institute, Moss Landing, CA USA
- ⁸ Southwest Fisheries Science Center, NOAA, San Diego, CA, USA
- ⁹ Marine Science Institute, University of California, Santa Barbara, CA USA
- ¹⁰ San Diego State University, San Diego, CA USA

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32 ¹¹ Reef Check California, Marina del Rey, CA USA

33 ¹² Moss Landing Marine Laboratories, San Jose State University, Moss Landing, CA USA

34 ¹³ University of Alaska, Fairbanks, AK USA

35

36 **Abstract**

37 The changing global climate is having profound effects on coastal marine ecosystems around the
38 world. Structure, functioning, and resilience, however, can vary geographically, depending on
39 species composition, local oceanographic forcing, and other pressures from human activities and
40 use. Understanding ecological responses to environmental change and predicting changes in the
41 structure and functioning of whole ecosystems requires large-scale, long-term studies; yet most
42 studies trade spatial extent for temporal duration. We address this shortfall by integrating
43 multiple long-term kelp forest monitoring datasets to evaluate biogeographic patterns and rates
44 of change of key functional groups (FG) along the west coast of North America. Data analysis
45 spanning 469 sites spanning Alaska, USA, to Baja California, Mexico, and 373 species (assigned
46 to 18 FG) reveal regional variation in responses to both long-term (2006-2016) change and a
47 recent marine heatwave (2014-2016) associated with two atmospheric and oceanographic
48 anomalies, the ‘Blob’ and extreme El Niño Southern Oscillation (ENSO). Canopy-forming kelps
49 appeared most sensitive to warming throughout their range. Other FGs varied in their responses
50 among trophic levels, ecoregions, and in their sensitivity to heatwaves. Changes in community
51 structure were most evident within the southern and north-central ecoregions, while
52 communities in the center of the range were more resilient. We report a poleward shift in
53 abundance of some key FGs. These results reveal major, ongoing region-wide changes in
54 productive coastal marine ecosystems in response to large-scale climate variability, and the
55 potential loss of foundation species. In particular, our results suggest that coastal communities
56 that are dependent on kelp forests will be more impacted in the southern portion of the
57 California Current region, highlighting the urgency of implementing adaptive strategies to
58 sustain livelihoods and ensure food security. The results also highlight the value of multi-
59 regional integration and coordination of monitoring programs for improving our understanding
60 of marine ecosystems, with the goal of informing policy and resource management in the future.

62 **Introduction**

63

64 Kelp forests are among the most productive and species rich marine ecosystems in the world
65 (Mann 1973, Schiel and Foster 2015). As such, kelp forests generate a diversity of essential
66 ecosystem services, including cultural, commercial, and recreational uses, seafood and materials,
67 coastal protection, and nutrient recycling (Krumhansl *et al.*, 2016; Smale *et al.*, 2013). Kelps
68 (Order Laminariales) serve as foundation species for these productive ecosystems by providing
69 habitat and food for a great diversity of species (Darwin, 1909, Springer *et al.*, 2010, Schiel and
70 Foster 2015, Carr and Reed 2016, Teagle *et al.*, 2017, Lamy *et al.*, 2020). Although climate
71 change is considered a major driver of kelp persistence and stability at global and regional
72 scales, substantial geographic variability exists in the dynamics of kelp through time. While kelp
73 species can exhibit high resilience to climate variability (Dayton *et al.*, 1992, Edwards 2004),
74 major declines in the abundance of several kelp species have been documented in response to
75 ocean warming (Diez *et al.*, 2012, Tanaka *et al.*, 2012, Wernberg *et al.*, 2013, Ling *et al.*, 2014,
76 Smale 2020). A global analysis of kelp density over time revealed marked differences in the
77 magnitude and direction of change across their geographic range, suggesting that local factors
78 play an important role in driving patterns of kelp forest responses (i.e. distribution and
79 abundance) to global change (Krumhansl *et al.*, 2016). Assessing how and why responses vary
80 geographically, identifying what regions are more vulnerable or resilient, and informing
81 management and adaptation efforts, such as protection in marine reserves, habitat restoration
82 efforts, and expanded biophysical monitoring and research, are urgent and critical priorities.,

83

84 As a foundation species, changes in the abundance of kelp can have cascading effects on
85 community structure and ecosystem function (Byrnes *et al.*, 2011, Wernberg *et al.* 2013, Beas-
86 Luna *et al.*, 2014, Carr and Reed 2016, Schiel and Foster 2015, Verges *et al.*, 2016, Miller *et al.*,
87 2018, Lamy *et al.*, 2020, Edwards *et al.*, 2020). In contrast, variability in community structure
88 and species interactions may influence the resilience of kelps to projected warming (Ling *et al.*,
89 2014, Eisaguirre *et al.*, 2020). Building on global analyses of kelp dynamics (Krumhansl *et al.*,
90 2016), a critical next step for understanding potential geographic variability in response to
91 warming is to assess responses in the biological communities associated with these important
92 foundation species.

93

94 Progress in understanding the responses of coastal marine communities and ecosystems to
95 environmental change at relevant regional scales is impeded by a lack of coordinated

96 monitoring. Long-term ecological studies provide key insights into such responses and may
97 contribute disproportionately to our understanding of how ecosystems respond to environmental
98 forcing and human use (Reed *et al.*, 2016, Hughes *et al.*, 2017), but they are often limited in
99 geographic coverage. For example, our understanding of how kelp forest communities respond
100 to climatic warming has generally been geographically limited, or limited by the number of taxa
101 and functional groups examined, with very few exceptions (Dayton and Tegner 1984, Dayton *et*
102 *al.*, 1992, Ebeling *et al.*, 1985, Edwards 2004, Schiel *et al.*, 2010, Byrnes *et al.*, 2011;
103 exceptions: Edwards and Estes 2006, Edwards 2019). To assess species distributional shifts and
104 community change in response to climate disturbances within complex coastal ecosystems, it is
105 critical that large-scale, long-term assessments of community structure are integrated in space
106 and time.

107
108 To date, most large geographic-scale studies have examined only the response of kelps to
109 changing environmental conditions (e.g., Wernberg *et al* 2011, Marzinelli *et al* 2015, Merzouk
110 and Johnson 2011, Krumhansl *et al.* 2016, Smale and Moore 2017), whereas very few have
111 evaluated responses of more than two or three functional groups and those that have are limited
112 to western Australia (Wernberg *et al.* 2013, 2016).. Here, we addressed this question for the kelp
113 forest ecosystems of the Gulf of Alaska and California Current large marine ecosystems. Based
114 on results of a global meta-analysis that evaluated the rate of change in giant kelp (*Macrocystis*
115 *pyrifera*) populations from 99 ecoregions over 50 years (Krumhansl *et al.*, 2016), we predict that
116 regional factors will play an important role in driving kelp forest responses to climate change in
117 North America.

118
119 Along the Northeastern Pacific, from Alaska to Baja California, kelps serve as foundation
120 species for highly diverse communities that support fisheries and recreation across three nations,
121 Canada, Mexico and the U.S. Across this large geographic range, spanning approximately 30
122 degrees in latitude (4,500 km), differences in species composition, community structure, and
123 gradients in human activities and pressures (e.g., harvesting, coastal discharges) reflect marked
124 differences in oceanographic conditions (e.g., mean ocean temperatures, magnitude and
125 frequency of coastal upwelling, exposure to swell energy). These differences in environmental
126 conditions and community structure are manifest in geographically distinct ecoregions
127 (persistent geographic differences in kelp forest ecosystem structure and functioning), which
128 may result in differences in vulnerability to climate change.

129

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

142
143 The community-wide responses to these oceanographic events and predicted declines in kelp
144 production and abundance are complex, expected to change with time, and suggest alternative,
145 competing outcomes for how functional groups will respond to changes in kelp production and
146 persistence. The majority of kelp production is made available to kelp forest food webs by the
147 loss of kelp blades that litter the forest floor and are incorporated into detrital pathways
148 (reviewed by Schiel and Foster 2015, Carr and Reed 2016). Thus, one likely structural and
149 functional response of kelp forests to warming events involves rapid and persistent changes in
150 abundance and foraging behavior of detritivores. In particular, we predicted rapid and persistent
151 increases in sea urchins as they shift from passive detritivory to active herbivory (Ebeling *et al.*,
152 1985, Harrold and Reed 1985, Harrold and Pearse 1987, Beas and Ladah 2014). In contrast to a
153 rapid and persistent decline in detritivores, we predicted initial increases and eventual declines in
154 other herbivores, in addition to sea urchins. Numerous experimental and observational studies
155 have described how shading by canopy-forming kelps suppresses the abundance of benthic
156 macroalgae, which provide food and habitat for a great diversity and abundance of benthic
157 herbivores (e.g., reviewed by Dayton *et al.*, 1985, Arkema *et al.*, 2009, Carr and Reed 2015,
158 Schiel and Foster 2015). We therefore predicted densities of herbivores to initially increase with
159 declines of kelp density. However, with the shift from passive detritivory to active herbivory of
160 all macroalgae by sea urchins, we predicted the abundance of herbivores to eventually decline
161 with the development of sea urchin barrens.

162

163 We hypothesized that the responses of sessile invertebrate suspension feeders and planktivores
164 would be more complex and time-dependent. Reduction in canopy-forming kelps can impact
165 sessile invertebrate suspension feeders and planktivores through changes in both food and space
166 resources, and the balance of these alternative influences is not clear. Declines in the density of
167 canopy-forming kelps are predicted to initially indirectly decrease the abundance of these two
168 functional groups due to increased competition for space with benthic macroalgae that were
169 previously light limited under the kelp canopy (Clark *et al.*, 2005, Arkema *et al.*, 2009, Miller *et*
170 *al* 2020). However, with increased grazing by sea urchins and reduced cover of all macroalgae,
171 we predicted the relative abundance of sessile suspension feeders and planktivores would
172 eventually increase. Evidence for the importance of kelp-derived particulate organic material
173 (POM) and dissolved organic material (DOM) from kelps on the productivity and abundance of
174 these functional groups is mixed. Some studies suggest that kelp-derived organic material
175 enhances the productivity and abundance of these groups (e.g., Duggins *et al.*, 1989, Bustamante
176 *et al* 1996, Kaehler *et al* 2006, Miller *et al* 2012), whereas others suggest that kelp-derived
177 organic material is not as significant as the influx of planktonic-derived organic material (Page
178 *et al* 2008, Miller and Page 2012, Miller *et al* 2013, 2018, Yorke *et al* 2013, 2015, Miller and
179 Reed 2015). Moreover, several studies indicate reduced rates of plankton delivery across reefs in
180 the presence of canopy forming kelps (Bray 1981, Jackson and Winant 1983, Gaylord *et al.*,
181 2007). Thus, we tentatively predict short-term decreases and longer-term increases in suspension
182 feeders and planktivores with reduced kelp abundance.

183
184 Predicted responses of higher trophic levels are less clear. Abundances of macroinvertebrates that
185 consume either or both sessile and mobile invertebrates are likely to exhibit mixed responses
186 depending on the composition of these taxa in their diet. However, the predicted eventual
187 reductions in abundance of sessile and mobile invertebrate detritivores, herbivores, suspension
188 feeders, and planktivores suggests declines in their predators. Both field experiments and trophic
189 models have detected declines in diversity of higher trophic levels with declines in kelp
190 abundance and production (Byrnes *et al.*, 2011). It is important to note that all functional groups
191 are likely influenced by temperature variability and extremes directly, in addition to indirect
192 effects through changes in kelp abundance, adding further uncertainty to predicted responses.

193
194 The aim of this study was to test for predicted regional changes in kelp forest ecosystem
195 structure and function in response to changing water temperatures over the last two decades,
196 especially the recent, anomalous, marine heatwave. We leveraged independent datasets from

197 Alaska, USA, to Baja California, Mexico and information of recent warming events across the
198 Northeastern Pacific, spanning the entire range of coastal kelp forest ecosystems in North
199 America (Figure 1). These datasets provide a unique opportunity to assess community- and
200 region-wide responses of these highly productive coastal ecosystems. In particular, we tested the
201 following general predictions: (1) kelp abundance declines with increasing water temperature,
202 and this decline is strongest at the warm edge of its range; (2) changes in abundance of kelp-
203 associated functional groups mirror changes in kelp abundance, as presented above; and (3)
204 species ranges of kelps and associated species are shifting poleward in response to
205 environmental change.

206

207 ***Materials and methods***

208

209 **Ecoregions**

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

226

227 **Kelp forest Monitoring programs**

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

231

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

238

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

248

249 *Reef Check California* is a citizen science non-profit organization (reefcheck.org). Since 2006,
250 Reef Check California has monitor up to 131 sites in a given year spanning southern to northern
251 California. The purpose of these long-term kelp forest studies is to engage citizens in collecting
252 ecological data used to evaluate the effects of California's state-wide network of marine
253 protected areas on kelp forest ecosystems. Sites are surveyed once per year from mid-June to
254 mid-October. Trained volunteers use a protocol adapted from the PISCO survey methods with a
255 reduction in taxonomic specificity. For comparisons of PISCO and Reef Check CA survey
256 results see Gillett *et al.* (2012) and Caselle and Cabral (2018).

257

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

265

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

274

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

287

288 **Characterization of the trends in water temperature across ecoregions**

289 We obtained composite monthly SST data for the period 2006-2016, covering the decade where
290 all programs had sufficient data to perform analyses, from the MODIS Aqua satellite product
291 (1.1 km resolution) available from the NOAA-ERDDAP data server
292 (<https://coastwatch.pfeg.noaa.gov/erddap/index.html>). While the temperature data were coarse
293 relative to the site spacing, they allow us to parse sub-regional-scale effects of temperature from
294 long term trends. We took the mean and maximum temperature from May through September
295 (the timing of most surveys) of the closest 5 pixels to each survey site to evaluate the effects of
296 temperature (warming) on functional groups across the ecosystem. We also extracted the
297 maximum temperature for the same 5 pixel window during summer months. Since mean and
298 maximum temperature were strongly correlated with each other across the region ($R^2 = 0.98$,

299 slope = 1.04), we used mean temperature for all subsequent analyses. Annual mean SSTs within
300 each ecoregion were used to calculate annual mean anomalies from the long-term (2006-2016)
301 mean SST for each ecoregion. We also calculated the normalized anomaly for each year within
302 each ecoregion as the difference between the long-term mean SST divided by the long-term
303 standard deviation.

304

305 **Characterization of the functional structure of the kelp forest communities**

306 Along the Northeastern Pacific, four main species of kelps are the major canopy-forming and
307 foundation species in kelp forest ecosystems. From north to south, these are the dragon kelp
308 (*Eualaria fistulosa*), bull kelp (*Nereocystis leutkeana*), giant kelp (*Macrocystis pyrifera*), and
309 southern sea palm (*Eisenia arborea*). Dragon kelp, is abundant off the coast of Alaska, bull
310 kelp dominates the northern latitudes from Alaska to Northern California, giant kelp is the
311 dominant species from Central California to Bahia Asuncion, Baja California, and *E. arborea* is
312 dominant along the southern portion of Baja California Sur (Carr and Reed 2015). Only a few
313 species span the majority of the study region (e.g., the giant kelp, *M. pyrifera*, the red and purple
314 sea urchin, *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*, and the predatory
315 seastar *Pisaster giganteus*). Instead, ranges of the vast majority of species associated with kelp
316 forests are restricted to portions of the study region. These restricted ranges prevent comparison
317 of temporal change across the entire study region at the species level. To allow for region-wide
318 evaluation of changes in abundance and community structure, we assigned species to functional
319 groups (FGs). FG designation and species assignment were conducted by a subset of the co-
320 authors, drawing from the literature and synthesized during two separate workshops. All taxa
321 were grouped into 18 different FGs, primarily based on the trophic roles of each species in the
322 community (Table S2). Information on the trophic relationships for each taxon was taken from a
323 kelp forest species interactions database (Beas-Luna *et al.*, 2014) and FishBase (fishbase.org).
324 Across the initial 18 FGs, some were represented by an insufficient number of species to
325 compare across the five ecoregions. We therefore show results of analyses of nine FGs,
326 including the canopy-forming kelps. Several of these FGs (e.g. micro and macroinvertivores)
327 included many species because of the differences in species composition across such a broad
328 study region encompassing five ecoregions. Because sea urchins play a disproportionate role in
329 kelp forest deforestation (Harrold and Reed 1985, Watanabe and Harrold 1991, Estes and
330 Duggins 1995, Steneck *et al.*, 2002), we removed them from the ‘herbivores’ functional group
331 and created a separate group (‘urchins’; Table S2).

332

333 **Data processing**

334 Data integration was performed in a series of scripts in R and Rstudio
335 (<https://github.com/rbeas/ABCreef>). Summary statistics (mean, standard deviation and number
336 of replicates) of the density (individuals per m² for mobile organisms and canopy kelp) and
337 percent cover (for some algae and sessile invertebrates) for each year sampled were extracted for
338 each program at the site scale, with each site corresponding to a reef or a stretch of the coast of
339 ~300-500 m in length. In subsequent analyses, we only use density data because these can be
340 more robustly transformed in a common currency across taxa (biomass), and included a majority
341 of taxa. The integrated dataset includes 546 sites and 373 species organized into 18 functional
342 groups (Fig. 1; Table S2). Data were summarized for each of the functional groups for each site
343 ($n=12-22$ transects averaged/site x year combinations), for each of five ecoregions.

344
345 We converted density estimates to biomass, as our metric of abundance, using estimated sizes if
346 available, or mean size of adult individuals because these were the size ranges counted in
347 surveys (unless specifically noted). For species with estimated lengths, we used publicly
348 available length-weight relationships from FishBase or SeaLifeBase. For species that were not
349 available, we used values for related species.

350

351 **Statistical analyses**

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

365

366 We tested predictions 1 and 2 using hierarchical Bayesian linear modeling to evaluate the rate of

367 change among functional groups across the entire study region, within each of the five
 368 ecoregions described above, and among sites within ecoregions, for the period 2006-2016. The
 369 model used to describe the abundance of functional groups (y) through time (t) is:

370

$$371 \quad \mu_{ijkt} = \beta_{0i} + \beta_{1i,k} + (\gamma_{0i} + \gamma_{1i,k})x_{1ijkt} \quad (1)$$

$$372 \quad y_{ijkt} \sim \text{lognormal}(\mu_{ijkt}, \sigma_j) \quad (2)$$

$$373 \quad y_{ijkt} = \frac{FG_{ijkt}}{\max(FG_i)} + 0.001 \quad (3)$$

374

375 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
 376 site (k) levels, respectively. The index, j , refers to the program responsible for data collection
 377 and allowed explicit incorporation of variability in program sampling protocols. y_{ijkt} is the
 378 standardized abundance of each functional group (FG) within each ecoregion (i). This analysis
 379 allowed us to directly compare our results for kelp abundance with Krumhansl *et al.* (2016), who
 380 previously analyzed regional and global trends in kelp abundance. Results of these comparisons
 381 are available in the supplementary online material. Priors and hyperpriors were set following
 382 Krumhansl *et al.* (2016):

383

$$384 \quad [\gamma_{0k,i} \ \gamma_{1k,i} \ \gamma_{2k,i}]^T \sim MVN(0, \Sigma) \quad (4)$$

$$385 \quad \Sigma = \text{diagonal}(\sigma_\gamma) \quad (5)$$

$$386 \quad \Omega = L \times L^T \quad (6)$$

$$387 \quad \gamma_{0k,i}, \gamma_{1k,i}, \beta_{0i}, \beta_{1i,k} \sim \text{uniform}[-\infty, \infty] \quad (7)$$

$$388 \quad \sigma_j \sim \text{half-Cauchy}(0, v_M) \quad (8)$$

$$389 \quad v_M \sim \text{uniform}[0, 3] \text{ or } \sim \text{half-Cauchy}(0, 2.5) \quad (9)$$

$$390 \quad L_i \sim \text{LKJ Cholesky}(v = 2) \quad (10)$$

391

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

394

$$395 \quad \mu_{ijkt} = \beta_{0i} + \beta_{1i,k} + (\gamma_{0i} + \gamma_{1i,k})x_{1ijkt} + \gamma_{2i,k}x_{2ijkt} \quad (11)$$

396

397 For temperature, we ran the model with 0 and 1 year lags to account for delayed responses to
 398 heatwaves. Time lags did not change the model predictions, so we present the non-lagged model
 399 results only. This model allowed us to incorporate site-level data that could contribute to

400 variation in rates of change among sites. The lack of a temperature effect indicates that
401 temperature at the site level does not preclude the potential for temperature to be a driver in
402 regional or overall trends. We then compared the ecoregional rate of change estimates to the
403 original model to examine if the ecoregional trends were robust to site-level differences. Priors
404 for the site level temperature were set as:

$$405 \gamma_{2k,i} \sim \text{uniform}[-\infty, \infty] \quad (12)$$

406
407
408
409 We sampled posteriors using the no-U-turn-sampler variant of Hamilton Monte Carlo in Stan via
410 MatlabStan. Sampling included 4 chains of 3,000 iterations. We ran subsampled values of the
411 model, including burn-in for slopes moving through the samples until the sub-sampled values
412 converged. A 1,000 iteration burn-in period proved sufficient for posterior convergence. From
413 the posterior samples, we estimated the mean and 90% symmetrical credible interval for each
414 rate. When the 90% credible interval (CI₉₀) of a specific rate did not cross zero, a significant
415 change in the abundance of the functional group is identified, equivalent to a 95% probability of
416 decline or increase. To evaluate the extent to which observed responses were specifically
417 attributed to the heatwave, we ran the Bayesian analysis (base model) with and without the years
418 2014-2016 (only 2014 for Alaska, as data are not available for 2015-16; Fig. 1). These analyses
419 enabled us to directly assess the impacts of these extreme conditions on our estimates of long-
420 term rates of change.

421
422 To assess geographic shifts in the distribution of functional groups (see prediction 3, and
423 analysis 4 above), we estimated the centroid of the distribution for each functional group using
424 the mean density and weighted mean latitude from all observations. This method accounts for
425 higher numbers of observations in some ecoregions. We then combined the densities with
426 modeled rates of change from the hierarchical Bayesian analysis to estimate the direction and
427 magnitude of latitudinal shifts in the centroid and the extent of each distribution. These shifts are
428 reported as centroid and range velocities where positive values indicate poleward progression
429 and range expansion, whereas negative values indicate an equatorward progression and range
430 contraction. For species and functional groups that showed significant effects of the recent 2014-
431 2016 warming events, we used rates of change estimated from the model that included
432 temperature. For others, we used the original model (although no significant differences were
433 observed when using the temperature model).

434

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

444

445

446 **Results**

447 **Characterization of the trends in water temperature across ecoregions**

448 As expected, mean and maximum sea surface temperature (SST) exhibited a negative poleward
449 gradient where temperature decreased with increasing latitude (Figure S1A). However, mean
450 SST anomaly and normalized SST anomalies were not coherent across ecoregions, with some
451 ecoregions exhibiting anomalous increases in SST concurrent with decreases in other ecoregions
452 (Figure S1B,C). Moreover, ecoregions differed markedly in the magnitude of variation in mean
453 SST anomaly over the study period, with Baja Sur and Alaska exhibiting the greatest and least
454 variation, respectively, across the ecoregions. Trends in SST anomalies among ecoregions and
455 over time were generally consistent between the normalized and non-normalized SST anomaly
456 approaches (Figure S1B,C), however, this difference among ecoregions in the magnitude of
457 variation in time was dampened when normalized by ecoregion. With the exception of southern
458 Baja California, trends in SST over time were generally consistent across ecoregions, both
459 between the normalized and non-normalized anomalies, until the marine heatwave of 2014-2016
460 when all ecoregions showed strong positive anomalies (Figure S1B,C). During the heatwave,
461 southern Baja California exhibited the highest mean positive (warm) anomaly, whereas Central
462 California exhibited the highest normalized mean positive (warm) anomaly. The southernmost
463 and northernmost ecoregions exhibited additional positive anomalies: Baja California, recorded
464 positive anomalies in 2008, 2009 and 2012, while Alaska remained positive in 2016, where all
465 the other ecoregions returned to normal temperatures.

466

467 **Response of kelp forest functional groups to changes in water temperature**

468 *Kelps* and other macroalgae– Canopy-forming kelps declined in abundance across the entire
469 study region, with similar rates of decline between models with and without temperature as a
470 site-level explanatory variable (Fig. 2A, B), indicative of a region-wide effect of warming.
471 Overall, the instantaneous rate of change in kelp density across the entire study area was
472 estimated at -0.043 yr^{-1} (CI₉₀[-0.067 to -0.016]). The magnitude and direction of change in
473 canopy kelp abundance over time differed among the ecoregions, and these differences showed
474 no consistent latitudinal trend, regardless of the model used (Fig. 2). Declines in kelp abundance
475 were highest in the southernmost portion of the range and in the northern California ecoregion,
476 while declines in the central and southern California ecoregions were smaller in magnitude, but
477 still statistically significant. Changes in kelp density were not significantly different from zero in
478 the Southern California and Gulf of Alaska ecoregions. Removing the recent marine heatwave
479 from the analyses significantly reduced the overall rate of change of canopy-forming kelps,
480 suggesting that ~36% of the decline in kelp species was associated with the unprecedented
481 recent warming event (Fig. 2C). Rates of change in kelp abundance remained negative in
482 northern and central California and in Baja California Sur, although the rates of change were
483 only significantly different from zero in northern California (Fig. 2C), suggesting that other
484 factors beyond the heatwave were responsible for kelp declines. Overall, no significant changes
485 were observed in other macroalgal groups across the entire study region for any model (Fig. 2D-
486 F). The only exceptions to this included Central California, which revealed a significant
487 negative slope in the temperature model, and SCB and BCS with significant trends in the pre-
488 heatwave models (positive and negative, respectively).

489
490 *Kelp-associated functional groups overview*- There was substantial variation in the rate of
491 change in abundance of kelp-associated functional groups over the period 2006-2016 (Fig. 3).
492 Overall, functional groups did not mirror the decline of kelps, with the exception of detritivores,
493 which exhibited overall negative rates of change (except NorCA), particularly in the central and
494 southern ecoregions (Fig. 3). For all other groups, rates of change varied in magnitude and
495 direction across ecoregions and were overall positive or not significantly different from zero
496 (non-overlapping credible intervals; Fig. 3). These trends were largely similar with and without
497 temperature as a site level explanatory variable. No significant differences in predicted rates of
498 change of individual functional groups across ecoregions were found when comparing these two
499 models (Fig. S2), with the exception of detritivores in northern California and herbivores in Baja
500 California Sur. Both of these functional groups declined when site-level temperature was
501 included in the model, matching the declines in kelp that occurred in these ecoregions (Fig. S2).

502 The marine heatwave did have an effect on some rate estimates and on overall rates of change of
503 urchins and microinvertebrates (Fig. 3). These effects are discussed in more detail for each
504 functional group.

505

506 *Urchins* - Urchins, a key group of kelp grazers that we analyzed separately from other
507 herbivores because of their ability to control kelp forest persistence, increased in abundance at
508 an overall rate of 0.032 yr^{-1} [CI₉₀: 0.003 to 0.050] (Fig. 3B). However, analyses showed
509 significant variation among ecoregions: urchin density increased in central and northern
510 California, and decreased in southern California and Baja California Sur, with no significant
511 change at the northern limit of observations (Gulf of Alaska). Rates of change of urchin density
512 were in some cases consistent with predicted patterns of change in canopy forming kelps
513 (declining kelp is associated with increasing urchin abundance) in northern and central
514 California but not in others. For example, both kelps and urchins declined in Baja California Sur
515 and Southern California with the marine heatwave (Fig. 3B). In addition, the least amount of
516 change in urchin density occurred in the two ecoregions that showed the least change in kelp
517 density (Gulf of Alaska and Southern California). The timing of the marine heatwave was
518 correlated with the positive rate of change of sea urchins in central California (Fig 3B),
519 suggesting that the recent large changes in sea urchin abundance may be partly associated with
520 the marine heatwave.

521

522 *Non-urchin herbivores* - As predicted by the initial indirect positive effects of canopy-forming
523 kelps on abundance of benthic macroalgae, herbivore abundance (excluding urchins) increased
524 in central California where kelp density declined, but exhibited no significant rates of change in
525 the other ecoregions (Fig. 3A). In Baja California Sur, rates of increase were slightly higher
526 when including the 2014-2016 marine heatwave but the rates of change were negative when site-
527 level temperature over the entire time period (2006-2016; Fig. S2) was included. The marine
528 heatwave did not strongly influence rates of change of non-urchin herbivores in any ecoregion
529 (Fig. 3A).

530

531 *Remaining functional groups* - The marine heatwave reduced the overall rates of increase of
532 microinvertebrates, particularly in the central and southern California ecoregions (Fig. 3C). In
533 contrast, the remaining functional groups – suspension feeders, macroinvertebrates, planktivores,
534 and piscivores – increased in abundance across much of the study region regardless of the effects
535 of the marine heatwave (Fig. 3). Suspension feeders increased in abundance across the entire

536 range (Fig. 3C) and increased further in Baja California with the marine heatwave.
537 Microinvertivores similarly increased in abundance, particularly in the Central and Southern
538 California ecoregions, but decreased during the marine heatwave (Fig. 3E). Macroinvertivore
539 abundance was stable in the north, and increased in the southern ecoregions (Fig. 3F).
540 Macroinvertivore responses to the marine heatwave were mixed, with increases in Baja
541 California and declines in Central California. Planktivores increased in the central ecoregions
542 (southern and central California), with no changes at the edges of the range (Fig 3G). These
543 responses were consistent through the marine heatwave. Piscivores increased in the southern and
544 central ecoregions, exhibited no change in abundance in the two northern ecoregions, and did
545 not show any significant response to the marine heatwave (Fig. 3H).

546
547 *Geographic range and ecosystem structure shifts* - We estimated changes in the geographic
548 distributions of each functional group by calculating the change in the geographic location of the
549 centroid of the distribution and the range defined as latitudinal distance that covers 95% of total
550 biomass. The centroids of biomass for canopy-forming kelp and detritivores have shifted to the
551 north and their ranges have expanded (Fig. 4). The centroid of biomass of urchins has similarly
552 shifted northward, but not significantly so. In contrast, the centroid of the geographic range of all
553 other functional groups shifted to the south and contracted to various degrees. Herbivores and
554 planktivores displayed the weakest response, while suspension feeders showed the strongest
555 shifts (Fig. 4). Higher trophic level functional groups (microinvertivores, macroinvertivores, and
556 piscivores) exhibited similar trends to one another, with relatively strong southward movement
557 and small reductions in estimated range (Fig. 4). Range velocity and center of distribution
558 velocity are correlated ($R^2=0.78$, $p<0.001$). For kelp and associated species that are moving
559 northward, this is likely because functional groups are moving northward, but have not
560 disappeared from their southern extent. For groups moving southward, associated contraction
561 may be due to disappearance at the northern end of the ranges.

562 The results of these shifts in species abundances across their ranges may portend a dramatic shift
563 in ecosystem structure and function over the next 20-30 years, assuming that the observed rates
564 of change continue (Fig. 5). From 2008 to 2016, the greatest change in ecosystem structure
565 occurred in the southern ecoregions, especially off Baja California Sur, with the loss of canopy-
566 forming kelps, and increases in the abundance of planktivores, macroinvertivores, and piscivores
567 (Fig. S3). While overall biomass is expected to decline across the range of kelp forest
568 ecosystems (Fig. 5), future community reorganization through the year 2050 is projected to be

569 greatest in the southern (Baja California Sur) and northern (Northern California) ecoregions, but
570 in different ways. Piscivores and invertivores are projected to increase in relative abundance to
571 the south, while urchins and planktivores are projected to increase in relative abundance in the
572 north (Fig. 5). In contrast with the dramatic ongoing and projected ecosystem changes at the
573 warmer edge of the range, the central ecoregions (central and southern California especially) are
574 projected to be more resilient, with smaller ongoing and projected change in the dominant
575 functional groups (Fig. 5), but with large projected increases in urchins and planktivores (Fig.
576 S3).

577 **Discussion**

578 Results of this study contribute to the growing number of observations of structural and
579 functional changes in coastal marine communities and ecosystems in response to changing
580 environmental conditions (e.g. Hoegh-Guldberg and Bruno 2005, Doney *et al.*, 2012,
581 Poloczanska *et al.*, 2013, Bruno *et al.*, 2014) and episodic marine heatwaves (e.g. Garrabou *et*
582 *al.*, 2009, Oliver *et al.*, 2017, Hughes *et al.*, 2017, 2018, Arias-Ortiz *et al.*, 2018, Hobday *et al.*,
583 2019, Smale *et al.*, 2019). The period from 2014-2016 experienced unusual warming due to the
584 North Pacific 'Warm Blob' and the strongest positive ENSO event since 1998 (i.e., the marine
585 heatwave; Leising *et al.*, 2015, Di Lorenzo and Mantua 2016, Jacox *et al.*, 2016). While this
586 study identified ecological responses to variation in water temperatures over the past decade
587 across the study region, the response to the recent marine heatwave accentuated these changes,
588 underscoring the pronounced consequences of marine heatwaves to coastal marine ecosystems.
589 The more rapid and greater temperature change associated with marine heatwaves generates
590 faster and more pronounced ecological responses, and the global occurrence, spatial extent,
591 frequency, duration and intensity of these events are increasing globally (Frölicher *et al.*, 2018,
592 Oliver *et al.*, 2018, Holbrook *et al.*, 2019). Moreover, heatwaves are predicted to be greater with
593 increased levels of global climate change (Frölicher *et al.*, 2018).

594 Our results, like others around the world, indicate that temperate kelp forest ecosystems appear
595 especially vulnerable to marine heatwaves because of the pronounced effects on kelps as
596 foundation species (*sensu* Dayton 1972), which serve as major sources of primary production
597 and physical habitat structure (e.g., Tanaka *et al* 2012, Smale and Wernberg 2013, Wernberg *et*
598 *al* 2010, 2011, 2013, 2016, Verges *et al.*, 2016, Filbee-Dexter *et al.*, 2016, 2018, Filbee-Dexter
599 and Wernberg 2018, Martinez *et al.*, 2018, Thomsen *et al.*, 2019, Rogers-Bennett and Catton
600 2019, Arafeh-Dalmau *et al.*, 2020). We found that region-wide declines in abundance of canopy-
601 forming kelps were strongly associated with the recent marine heatwave. Overall, the

602 instantaneous rate of change in kelp density across the entire study area (-0.043 yr^{-1} ; $\text{CI}_{90}[-0.067$
603 to $-0.016]$) is approximately 2.4 times higher than global estimates of -0.018 yr^{-1} over the past 50
604 years (Krumhansl *et al.*, 2016), although this was driven by two of the five ecoregions (see
605 below).

606 These marked declines in kelp abundance are likely related to reduced nutrient concentrations
607 associated with increased water temperatures (e.g., Reed *et al* 2016), but were exacerbated by
608 observed shifts in foraging behavior of a critically important ecosystem engineer, the purple sea
609 urchin, *Strongylocentrotus purpuratus*, in the central and southern ecoregions. Similar to the
610 declines in kelp, the observed increase in purple urchin densities were especially pronounced
611 during the marine heatwave and were greatest in the Northern California and Baja California Sur
612 ecoregions that experienced significant kelp loss, while changes in urchin densities were lowest
613 in the Central and Southern California ecoregions that experienced the least change in kelp
614 abundance. Increased counts of purple urchins appear attributable to three key processes. 1) In
615 2013, the seastar wasting disease that affected the entire study region lead to the functional
616 extinction of the sunflower star, *Pycnopodia helianthoides*, a well-known predator of sea urchins
617 (Harvell *et al.*, 2019). 2) With reduced production of kelp and availability of drift, coupled with
618 loss of a key predator, purple sea urchins shifted from passive to active foraging, denuding reefs
619 of macroalgae, including giant kelp and bull kelp (Rogers-Bennet and Catton 2019). 3) As reefs
620 shifted from forests to urchin barrens, pavements of encrusting coralline algae likely facilitated
621 settlement of purple urchins (Baskett and Salomon 2010), exacerbating the further increase in
622 urchin densities.

623 The marked variation in kelp and sea urchin trajectories across most of the ecoregions monitored
624 in this study point to important influences of regional processes interacting with both long-term
625 and episodic changes in ocean temperatures. For example, both kelps and urchins declined in
626 Baja California Sur with the marine heatwave, while urchins declined and giant kelp did not
627 change in abundance in Southern California, just to the north. Both kelps and urchins may be
628 vulnerable to increased water temperatures at the southern end of their ranges. The extreme
629 losses of giant kelp off Baja California, Mexico, has been noted in previous warming events
630 (Edwards 2004) and by others in response to the recent marine heatwave (Arafeh *et al.*, 2019;
631 Cavanaugh *et al* 2019). In contrast, and similar to our results, Reed *et al.* (2016) could not
632 attribute any change in the long-term declining trajectory of giant kelp abundance and several
633 associated species in southern California to the same marine heatwave we evaluated. In southern
634 ecoregions where, in contrast to our predictions, urchin counts declined, the warmer waters may

635 be more conducive to diseases that have contributed to declines of urchin outbreaks (Behrens
636 and Lafferty 2004, Lafferty 2004, Lester *et al.*, 2007). The greater declines of bull kelp
637 populations in Northern California compared to patchier and less severe declines of giant kelp in
638 central California could reflect the absence and presence, respectively, of the southern sea otter,
639 *Enhydra lutris nereis*, which is a key predator on sea urchins in central California. Likewise,
640 southern California also has functional redundancy in urchin predators with California
641 sheephead and spiny lobster (Tegner and Levin 1983, Hamilton and Caselle 2015, Selden *et al.*,
642 2018), especially in several marine protected areas, which are included in our surveys there.
643 Thus, the persistence of kelps in our southern California survey sites may reflect the protection
644 of key sea urchin predators and an enhanced resistance and resilience of kelp forest communities
645 to the loss of the sunflower star (Eisaguirre *et al.*, 2020). These are only two examples of strong
646 environmental and ecological differences among the ecoregions of the California Current large
647 marine ecosystem.

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

667

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

679 All other groups exhibited either little change or increases in central and southern California.
680 Increases in sessile suspension feeders and planktivores may reflect greater detectability in
681 surveys due to reduced cover of macroalgae or predicted eventual increases in prey availability
682 in the absence of canopy-forming kelps. The presence and density of kelps reduce water flow
683 across rocky reefs and the rate of delivery of planktonic prey (Bray 1981, Jackson and Winant
684 1983, Gaylord *et al.*, 2007, Hondolero and Edwards 2017). Moreover, Miller *et al.* (2015) found
685 no evidence from stable isotope analyses to indicate that kelp detritus is an important food
686 source for sessile suspension-feeding invertebrates. Little change or increases in higher trophic
687 level macroinvertebrates and piscivores reflect complex dynamics of lower trophic levels,
688 including the mixed responses of detritivores, herbivores, microinvertebrates, suspension feeders
689 and planktivores. Many macroinvertebrates, including crustaceans, octopi, and fishes, are prey for
690 other fishes, which in turn are prey for piscivores. Dampened responses of these higher-level
691 predators may reflect the diversity of lower trophic levels characteristic of these ecosystems. As
692 generalist predators are buffered from prey population dynamics, predators with high dietary
693 diversity are buffered by the variable responses of different functional groups to declines in kelp
694 abundance. However, kelps are nursery habitat for many piscivorous fishes (Carr and Syms
695 2006, Wernberg *et al.*, 2016) suggesting there may be declines via different mechanisms over
696 longer time frames.

697 Clear signs of tropicalization have been reported for temperate marine ecosystems (Vergés *et al.*,
698 2016, Horta e Costa *et al.*, 2014, Arafeh-Dalmau *et al.*, 2019). In the present study we could not
699 focus on species thermal affinities because we grouped species into functional groups. Future
700 analyses could use the dataset we have integrated to assess responses of different taxa to

701 warming. Despite the uncertainty of future climatic events, understanding species thermal
702 affinities and its contribution to the changing communities will be important for improved
703 management of marine resources.

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

717 These group-specific responses have resulted in large shifts in kelp forest community structure,
718 with a significant northward shift of the center of distributional range for kelp and associated
719 detritivores, and southward shifts in most higher-level consumer groups. If such patterns
720 continue, there may be a spatial mismatch in functional groups that develop into region-specific
721 ecosystem structure and function that differs from that of the recent past. Overall, these results
722 corroborate findings from Krumhansl *et al.*, (2016) that local drivers underlie regional and
723 subregional variation in kelps and kelp forest ecosystems, highlighting the appropriateness and
724 need for local management actions. Understanding how ecologically and economically
725 important species are changing their distribution is critical to design strategic management plans
726 (Mills *et al.*, 2013, Pershing *et al.*, 2015, Caputi *et al.*, 2016, Cavole *et al.*, 2016; Hodgson *et al.*,
727 2018; Lonhart *et al.*, 2019).

728 Our results further highlight the importance of monitoring programs that span an entire
729 ecosystem's range. Monitoring across the entire range of an ecosystem can provide key insights
730 into the status and health of the ecosystem as a whole in response to global drivers, as well as
731 responses that may be variable at regional or even local scales (Edwards 2019). Although our
732 geographic coverage was heterogeneous, with sampling effort heavily concentrated in southern

733 and central California, we are able to discern rates of change of key functional groups, and
734 predict potential changes in ecosystem structure and function in the near future. However, our
735 results suggest that rates of change are highest in ecoregions (Baja California Sur and Northern
736 California), where sampling is much more sparse. Moreover, changes were less evident in the
737 Gulf of Alaska where temperature remained relatively cool. Similarly, though Pfister *et al.*
738 (2018) detected correlations between the areal cover of canopy-forming kelps and large scale,
739 long-term environmental forcing, forests along the coast of Washington state have been broadly
740 persistent through 2015. This may suggest the effects of climate variability will take longer to be
741 apparent in these more northern ecoregions.

742
743
744 The current positive sea surface temperature anomalies and apparent re-occurrence of a ‘warm
745 blob’ condition over the coming years (Oliver *et al.*, 2019) make the need for region-wide long-
746 term monitoring ever more urgent and critical. Disconcertingly, as this need become ever more
747 obvious, large-scale, long-term ecosystem studies have generally declined in recent years
748 (Hughes *et al.*, 2017). As environmental variability and extremes are expected to increase,
749 monitoring efforts need to be able to document the geographic patterns in response. Variability
750 in responses across sites, regions and entire ecosystems may be missed or misinterpreted given
751 the sparse nature of sampling. Expansion of monitoring efforts with participatory citizen science
752 models (e.g. Fulton *et al.*, 2018) may lessen the burden on academic and regulatory agencies,
753 while providing needed data to assess ecological consequences of a changing climate.

754
755 In conclusion, multi-regional integration of monitoring programs reveals major, ongoing region-
756 wide change in productive kelp forest ecosystems in response to long-term and episodic
757 warming. Results indicate that coastal communities that are dependent on kelp forest ecosystems
758 will be more heavily impacted in the southern portion of the Gulf of Alaska and California
759 Current large marine ecosystems under future climate scenarios, highlighting the urgency of
760 implementing adaptation strategies to sustain livelihoods and ensure food security. Continued
761 adaptation efforts, including monitoring and broad regional integration of research (Aburto *et*
762 *al.*, 2018) are key to enabling effective strategies for addressing the ongoing and escalating
763 future impacts of climate change and variability on ecosystems and people in coastal regions.

764
765
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773
774 The data that support the findings of this study are available at this online repository
775 (<https://github.com/rbeas/ABCreef>). As the data comes from different monitoring programs with
776 particular restrictions, the access to the repository is available upon request. Contact the
777 corresponding author at micheli@stanford.edu to request access to the data repository.

779 **Literature cited**

780

781 Aburto-Oropeza, O., Johnson A.F., Agha M., Allen, E. B. Allen M. F., Arellano-González J.,
782 Arenas-Moreno D. M., Beas-Luna R. *et al.* (2018). Harnessing Cross-border Resources to
783 Confront Climate Change. *Environmental Science and Policy*, 87, 128-132. doi,
784 10.1016/j.envsci.2018.01.001

785 Arafeh-Dalmau, N., Montaña-Moctezuma, G., Martinez, J.A., Beas-Luna, R., Schoeman, D.S.
786 and Torres-Moye, G. (2019) Extreme Marine Heatwaves alter kelp forest community near its
787 equatorward distribution limit. *Frontiers in Marine Science*, 6, 499. doi,
788 10.3389/fmars.2019.00499

789 Arafeh-Dalmau, N., Schoeman, D., Montaña-Moctezuma, G., Micheli, F., Rogers-Bennett, L.,
790 Olguin-Jacobson, C., Possingham, H.P. (2020) Marine heatwaves threaten kelp forests. *Science*
791 *Letters*, 367. doi, 10.1126/science.aba5244

792

793 Arias-Ortiz, A., Serrano, O., Masqué, P., Lavery, P.S., Mueller, U., Kendrick, G.A., Rozaimi,
794 M., Esteban, A., Fourqurean, J.W., Marbà, N. and Mateo, M.A. (2018). A marine heatwave
795 drives massive losses from the world's largest seagrass carbon stocks. *Nature Climate Change*,
796 8(4), 338. doi, 10.1038/s41558-018-0096-y

797 Arnqvist, G. and Wooster, D. (1995) Meta-analysis, synthesizing research findings in ecology
798 and evolution. *Trends in Ecology and Evolution*, 10, 236–240. doi, 10.1016/S0169-
799 5347(00)89073-4

800 Baskett, M.L. and Salomon, A.K. (2010). Recruitment facilitation can drive alternative states on
801 temperate reefs. *Ecology*, 91(6), 1763-1773. doi, [jstor.org/stable/25680416](https://doi.org/10.1093/ecology/91/6/1763)

802 Beas-Luna, R. and Ladah, L.B. (2014). Latitudinal, seasonal, and small-scale spatial differences
803 of the giant kelp, *Macrocystis pyrifera*, and an herbivore at their southern range limit in the
804 northern hemisphere. *Botanica Marina*, 57, 73–83. doi, 10.1515/bot-2013-0114

805 Beas-Luna, R., Novak, M., Carr, M.H., Tinker, M.T., Black, A., Caselle, J.E., Hoban, M.,
806 Malone, D., Iles, A., (2014). An Online Database for Informing Ecological Network Models,
807 <http://kelpforest.ucsc.edu>. *PLoS ONE*, 9, e109356. doi, 10.1371/journal.pone.0109356

808 Beas-Luna, R., Malpica-Cruz, L., Montaña-Moctezuma, G., Zepeda-Domínguez, J.A., Vaca-
809 Rodríguez, J., Abadía-Cardoso, A. (2019). Bosques de macroalgas en arrecifes templados, in,
810 Paz-Pellat, F., Hernandez-Ayon, J.M., Sosa-Avalos, R., Velazquez-Rodriguez, A.S. (Eds.),
811 Estado Del Ciclo Del Carbono Agenda Azul Y Verde. Texcoco, Estado de Mexico, pp. 1–24.

812 Behrens, M.D., and Lafferty, K.D. (2004). Effects of marine reserves and urchin disease on
813 southern California rocky reef communities. *Marine Ecology Progress Series*, 279, 129–139.
814 doi, 10.3354/meps279129

815 Boch, C.A., Micheli, F., AlNajjar, M., Monismith, S.G., Beers, J.M., Bonilla, J.C., Espinoza,
816 A.M., Vazquez-Vera, L., Woodson, C.B. (2018). Local oceanographic variability influences the
817 performance of juvenile abalone under climate change. *Scientific Reports*, 1–12. doi,
818 10.1038/s41598-018-23746-z

819 Bray, R. N. (1981). Influence of water currents and zooplankton densities on daily foraging
820 movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish. *U.S. Fishery*
821 *Bulletin*, 78, 829– 841.

822 Briggs, J. C. (1974). *Marine zoogeography*. McGraw Hill, New York, New York.

823 Bruno J. F., Harley, C. Burrows, M.T. (2014) *Climate change and marine communities*. *Marine*
824 *Community Ecology and Conservation*, p. 566. Sinauer Associates Incorporated.

825 Bustamante, R. H., and G. M. Branch. (1996). The dependence of intertidal consumers on kelp-
826 derived organic matter on the west coast of South Africa. *Journal of Experimental Marine*
827 *Biology and Ecology*, 196, 1-28. doi, 10.1016/0022-0981(95)00093-3

828 Byrnes, J. E., D. C. Reed, B. J. Cardinale, K. C. Cavanaugh, S. J. Holbrook, and R. J. Schmitt.
829 (2011). Climate driven increases in storm frequency simplify kelp forest food webs. *Global*
830 *Change Biology*, 17, 2513– 2524. doi, 10.1111/j.1365-2486.2011.02409.x

831 Caputi, N., Kangas, M., Denham, A., Feng, M., Pearce, A., Hetzel, Y., Chandrapavan, A.
832 (2016). Management adaptation of invertebrate fisheries to an extreme marine heat wave event
833 at a global warming hot spot. *Ecology and Evolution*, 6, 3583–3593. doi, 10.1002/ece3.2137

834 Carr, M.H. and Syms, C. (2006) Chapter 15, Recruitment. pp. 411-427 In, Allen, L.G., D.J.
835 Pondella II, and M.H. Horn (eds.) *The Ecology of Marine Fishes, California and Adjacent*
836 *Waters*. University of California Press, Berkeley, California, USA.

- 837 Carr, M.H. and Reed, D.C. (2016). Chapter 17, Shallow Rocky Reefs and Kelp Forests. Pages
838 311-336 in, H. Mooney and E. Zavaleta (eds) *Ecosystems of California*. Berkeley, University
839 of California Press.
- 840 Caselle, J.E., Rassweiler, A., Hamilton, S.L., Warner, R.R. (2015). Recovery trajectories of kelp
841 forest animals are rapid yet spatially variable across a network of temperate marine protected
842 areas. *Scientific Reports*, 5, 948. doi, 10.1038/srep14102
- 843 Cavanaugh, K.C., Reed, D.C., Bell, T.W., Castorani, M.C.N., Beas-Luna, R. (2019). Spatial
844 Variability in the Resistance and Resilience of Giant Kelp in Southern and Baja California to a
845 Multiyear Heatwave. *Frontiers in Marine Science*, 6, 49. doi, 10.3389/fmars.2019.00413
- 846 Cavole, L., Demko, A., Diner, R., Giddings, A., Koester, I., Pagniello, C., Paulsen, M.-L.,
847 Ramirez-Valdez, A., Schwenck, S., Yen, N., Zill, M., Franks, P., (2016). Biological Impacts of
848 the 2013–2015 Warm-Water Anomaly in the Northeast Pacific, Winners, Losers, and the Future.
849 *Oceanography*, 29(2),1-9. doi, 10.5670/oceanog.2016.32
- 850 Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B. and Thomas, C.D. (2011). Rapid Range Shifts
851 of Species Associated with High Levels of Climate Warming. *Science*, 333, 1024-1026. doi,
852 10.1126/science.1206432
- 853 Clark, R.P., Edwards M.S., and Foster M.S. (2004). Effects of shade from multiple kelp
854 canopies on an understory algal assemblage. *Marine Ecology Progress Series*, 267, 107-119. doi,
855 10.3354/meps267107
- 856 Clarke, K.R., Somerfield, P.J., Airoidi, L. and Warwick, R.M. (2006) Exploring interactions by
857 second-stage community analyses. *Journal of Experimental Marine Biology and Ecology*, 338,
858 179–192. doi, /10.1016/j.jembe.2006.06.019
- 859 Darwin C. (909). *The voyage of the Beagle*. New York, NY, PF Collier & Son.
- 860 Dayton P.K., Tegner M.J. (1984). Catastrophic storms, el Niño, and patch stability in a southern
861 California kelp community. *Science*, 224(4646), 283–285. doi, 10.1126/science.224.4646.283
- 862 Dayton, P.K., Tegner, M.J., Parnell, P.E. and Edwards, P.B. (1992) Temporal and spatial
863 patterns of disturbance and recovery in a kelp forest community. *Ecological Monographs*, 62,
864 421–445. doi, 10.2307/2937118

- 865 Dayton, P.K. (1972). Toward an understanding of community resilience and the potential effects
866 of enrichments to the benthos at McMurdo Sound, Antarctica. Pages 81–95 in Parker, B.C., ed.
867 Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press
- 868 Di Lorenzo, E., Mantua, N. (2016). Multi-year persistence of the 2014/15 North Pacific marine
869 heatwave. *Nature Climate Change*, 6, 1042–1047. doi, 10.1038/nclimate3082
- 870 Díez, I., Muguerza, N., Santolaria, A., Ganzedo, U., Gorostiaga, J.M. (2012). Seaweed
871 assemblage changes in the eastern Cantabrian Sea and their potential relationship to climate
872 change. *Estuarine, Coastal and Shelf Science*, 99, 108–120. doi, 10.1016/j.ecss.2011.12.027
- 873 Doney, S.C., Fabry, V.J., Feely, R.A., Kleypas, J.A., (2009). Ocean Acidification, The Other
874 CO₂ Problem. *Annual Review of Marine Science*, 1, 169–192. doi,
875 10.1146/annurev.marine.010908.163834
- 876 Doney, S.C., Rosenberg, A.A., Alexander, M., Chavez, F., Harvell, D.C., Hoffman, G., Orbach,
877 M. and Ruckelshaus, M. (2014) Oceans and marine resources. (eds J.M. Melillo, T.C. Richmond
878 and G.W. Yohe), pp. 557–578. U.S. Global Change Research Program.
- 879 Doney, S.C., Ruckelshaus, M., Duffy, J.E., Barry, J.P. and Chan, F. (2012) Climate change
880 impacts on marine ecosystems. *Annual Review of Marine Science*, 4, 11–37. doi,
881 10.1146/annurev-marine-041911-111611
- 882 Duggins D.O., Simenstad C.A., Estes J.A. (1989). Magnification of secondary production by
883 kelp detritus in coastal marine ecosystems. *Science*, 245, 170-173. doi,
884 10.1126/science.245.4914.170
- 885 Ebeling, A. W., Laur D. R., and Rowley R. J. (1985). Severe storm disturbances and reversal of
886 community structure in a southern California kelp forest. *Marine Biology*, 84, 287– 294. doi,
887 10.1007/BF00392498.pdf
- 888 Edwards, M.S. (2004) Estimating scale-dependency in disturbance impacts, El Niños and giant
889 kelp forests in the northeast Pacific. *Oecologia* 138(3),436–447. doi, 10.1007/s00442-003- 1452-
890 8
- 891 Edwards, M.S. (2019) Comparing the impacts of four ENSO events on giant kelp (*Macrocystis*
892 *pyrifera*) in the northeast Pacific Ocean. *Algae*, 34, 141-151. doi, 10.4490/algae.2019.34.5.4

- 893 Edwards, M.S., Konar B., Kim J.H., Gabara S., Sullaway G., McHugh T., Spector M., Small S.
894 (2020). Marine deforestation leads to widespread loss of ecosystem function. PLoS ONE, 15(3),
895 e0226173. doi, 10.1371/journal.pone.0226173
- 896 Eisaguirre, J.H., Eisaguirre, J.M., Davis, K., Carlson, P.M., Gaines, S.D., Caselle, J.E. (2020).
897 Trophic redundancy and predator size-class structure drive differences in kelp forest ecosystem
898 dynamics. Ecology, 101(5), e02993. doi, 10.1002/ecy.2993
- 899
- 900 Estes, J.A. and Duggins, D.O. (1995). Sea Otters and Kelp Forests in Alaska, Generality and
901 Variation in a Community Ecological Paradigm. Ecological Monographs, 65, 75–100. doi,
902 10.2307/2937159
- 903 Filbee-Dexter, K. and Scheibling, R. E. (2014). Sea urchin barrens as alternative stable states of
904 collapsed kelp ecosystems. Marine Ecology Progress Series, 495:1-25. doi, 10.3354/meps10573
- 905 Filbee-Dexter, K. and Wernberg, T. (2018). Rise of turfs, A new battlefield for globally
906 declining kelp forests. Bio Science, 68, 64-76. doi, 10.1093/biosci/bix147
- 907 Filbee-Dexter, K., Feehan, C.J. and Scheibling, R.E. (2016). Large-scale degradation of a kelp
908 ecosystem in an ocean warming hotspot. Marine Ecology Progress Series, 543, 141-152. doi,
909 10.3354/meps11554
- 910 Filbee-Dexter, K., Wernberg, T., Fredriksen, S., Norderhaug, K.M. and Pedersen, M.F. (2018).
911 Arctic kelp forests, Diversity, resilience and future. Global and Planetary Change, 62(2), 64-76.
912 doi, 10.1016/j.gloplacha.2018.09.005
- 913 Frölicher, T.L. and Laufkötter, C. (2018). Emerging risks from marine heat waves. Nature
914 Communications, 9, 443. doi, 10.1038/s41467-018-03163-6
- 915 Fulton, S., Hernández-Velasco, A. Suarez-Castillo, A., Fernández-Rivera Melo, M., Rojo, M.,
916 Sáenz-Arroyo, A., Hudson Weaver, A., Cudney-Bueno, R., Micheli, F. and Torre, J. (2018).
917 From fishing fish to fishing data, The role of artisanal fishers in conservation and resource
918 management in Mexico. In, Salas S., Barragán-Paladines M., Chuenpagdee R. (eds) Viability
919 and Sustainability of Small-Scale Fisheries in Latin America and The Caribbean. MARE
920 Publication Series, vol 19. Springer, Cham. doi, 10.1007/978-3-319-76078-0_7
- 921 Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M., Diaz, D.,
922 Harmelin, J.G., Gambi, M.C., Kersting, D.K., Ledoux, J.B., Lejeusne, C., Linares, C., Marschal,

923 C., Pérez, T., Ribes, M., Romano, J.C., Serrano, E., Teixidó, N., Torrents, O., Zabala, M.,
924 Zuberer, F., Cerrano, C. (2009). Mass mortality in Northwestern Mediterranean rocky benthic
925 communities, effects of the 2003 heat wave. *Global Change Biology*, 15, 1090–1103. doi,
926 10.1111/j.1365-2486.2008.01823.x

927 Gaylord, B., Rosman, J.H., Reed, D.C., Koseff, J.R., Fram, J., MacIntyre, S. and Mardian, B.
928 (2007). Spatial patterns of flow and their modification within and around a giant kelp forest.
929 *Limnology and Oceanography*, 52, 1838–1852. doi, 10.4319/lo.2007.52.5.1838

930 Graham, M.H., Vasquez J.A., and Buschmann, A.H. (2007). Global ecology of the giant kelp
931 *Macrocystis*. From ecotypes to ecosystems. *Oceanography and Marine Biology, An Annual*
932 *Review*, 45, 39– 88.

933 Greene, C. (2016). North America’s Iconic Marine Species at Risk Due to Unprecedented Ocean
934 Warming. *Oceanography*, 29(3), 14–17. doi, 10.5670/oceanog.2016.67.

935 Hamilton, S.L. and Caselle, J. E. (2015). Exploitation and recovery of a sea urchin predator has
936 implications for the resilience of southern California kelp forests. *Proceedings of the Royal*
937 *Society of London B*, 282, 20141817. doi, 10.1098/rspb.2014.1817.

938 Harley, C., Anderson, K.M. and Demes, K.W. (2012). Effects of climate change on global
939 seaweed communities. *Journal of Phycology*, 48, 1064–1078.

940 Harrold, C., Reed, D.C. (1985). Food Availability, Sea Urchin Grazing, and Kelp Forest
941 Community Structure. *Ecology*, 66, 1160–1169. doi, 10.2307/1939168

942 Harrold, C. and Pearse J.S. (1987). The ecological role of echinoderms in kelp forests. Pages
943 137– 233 in M. Jangoux and J. M. Lawrence, editors. *Echinoderm studies*, Volume 2. A. A.
944 Balkema Press, Rotterdam, The Netherlands.

945 Harvell, C.D., Montecino-Latorre, D., Caldwell, J.M., Burt, J.M., Bosley, K., Keller, A., Heron,
946 S.F., Salomon, A.K., Lee, L., Pontier, O. and Pattengill-Semmens, C. (2019). Disease epidemic
947 and a marine heat wave are associated with the continental-scale collapse of a pivotal predator
948 (*Pycnopodia helianthoides*). *Science advances*, 5(1), p.eaau7042. doi, 10.1126/sciadv.aau7042

949 Hodgson, E.E. Kaplan I., Marshall K., Leonard J., Essington T., Busch S., Fulton, E., Harvey,
950 C., Hermann, A., McElhany, P. (2018). Consequences of spatially variable ocean acidification in
951 the California Current, Lower pH drives strongest declines in benthic species in southern regions

952 while greatest economic impacts occur in northern regions. *Ecological Modelling*, 383, 106-117.
953 doi, 10.1016/j.ecolmodel.2018.05.018

954 Hoegh-Guldberg, O. and Bruno, J.F. (2005). The impact of climate change on the worlds marine
955 ecosystems. *Science*, 308, 541. doi, 10.1126/science.1189930

956 Holbrook, N.J., Scannell, H.A., Gupta, A.S., Benthuyssen, J.A., Feng, M., Oliver, E.C.,
957 Alexander, L.V., Burrows, M.T., Donat, M.G., Hobday, A.J. and Moore, P.J. (2019). A global
958 assessment of marine heatwaves and their drivers. *Nature communications*, 10, 2624. doi,
959 10.1038/s41467-019-10206-z

960 Hondolero, A.K., Edwards, M.S. (2017). Physical and biological characteristics of kelp forests
961 in Kachemak Bay, Alaska. MS Thesis. San Diego State University. Horn, M.H., L.G. Allen, and
962 R.N. Lea. (2006). Chapter 1, Biogeography. pp. 3-25 In, Allen, L.G., D.J. Pondella II, and M.H.
963 Horn (eds.) *The Ecology of Marine Fishes, California and Adjacent Waters*. University of
964 California Press, Berkeley, California, USA.

965 Horta e Costa, B., Assis, J., Franco, G., Erzini, K., Henriques, M., Gonçalves, E. J., Caselle J.E.
966 (2014). Tropicalization of fish assemblages in temperate biogeographic transition zones. *Marine*
967 *Ecology Progress Series*, 504, 241–252. doi, 10.3354/meps10749.

968 Hughes, B.B., Beas-Luna, R., Barner, A.K., Brewitt, K., Brumbaugh, D.R., Cerny-Chipman,
969 E.B., Close, S.L., Coblenz, K.E., de Nesnera, K.L., Drobitch, S.T., Figurski, J.D., Focht, B.,
970 Friedman, M., Freiwald, J., Heady, K.K., Heady, W.N., Hettinger, A., Johnson, A., Karr, K.A.,
971 Mahoney, B., Moritsch, M.M., Osterback, A.-M.K., Reimer, J., Robinson, J., Rohrer, T., Rose,
972 J.M., Sabal, M., Segui, L.M., Shen, C., Sullivan, J., Zuercher, R., Raimondi, P.T., Menge, B.A.,
973 Grorud-Colvert, K., Novak, M. and Carr, M.H. (2017) Long-Term Studies Contribute
974 Disproportionately to Ecology and Policy. *BioScience*, 67, 1–11. doi, 10.1093/biosci/bix072

975 Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Dietzel, A., Eakin, C.M., Heron, S.F.,
976 Hoey, A.S., Hoogenboom, M.O., Liu, G., McWilliam, M.J., Pears, R.J., Pratchett, M.S.,
977 Skirving, W.J., Stella, J.S. and Torda, G. (2018). Global warming transforms coral reef
978 assemblages. *Nature*, 556, 492–496. doi, 10.1038/s41586-018-0041-2

979 Jackson, G.A. and Winant, C.D. (1983). Effect of a kelp forest on coastal currents. *Continental*
980 *Shelf Research*, 2(1), 75-80. doi, 10.1016/0278-4343(83)90023-7

981 Jacox, M.G., Hazen, E.L., Zaba, K.D., Rudnick, D.L., Edwards, C.A., Moore, A.M., Bograd,
982 S.J., (2016). Impacts of the 2015–2016 El Niño on the California Current System, Early
983 assessment and comparison to past events. *Geophysical Research Letters*, 43, 7072–7080. doi,
984 10.1002/2016GL069716

985 Johnson, C.R., Banks, S.C., Barrett, N.S., Cazassus, F., Dunstan, P.K., Edgar, G.J., Frusher,
986 S.D., Gardner, C., Haddon, M., Helidoniotis, F., Hill, K.L., Holbrook, N.J., Hosie, G.W., Last,
987 P.R., Ling, S.D., Melbourne-Thomas, J., Miller, K., Pecl, G.T., Richardson, A.J., Ridgway,
988 K.R., Rintoul, S.R., Ritz, D.A., Ross, D.J., Sanderson, J.C., Shepherd, S.A., Slotwinski, A.,
989 Swadling, K.M. and Taw, N. (2011). Climate change cascades, Shifts in oceanography, species'
990 ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental*
991 *Marine Biology and Ecology*, 400, 17–32. doi, 10.1016/j.jembe.2011.02.032

992 Kaehler, S., Pakhomov E. A., Kalin R. M. and Davis S. (2006). Trophic importance of kelp-
993 derived suspended particulate matter in a through-flow sub-Antarctic system. *Marine Ecology*
994 *Progress Series*, 316, 17-22. doi, 10.3354/meps316017

995 Krumhansl, K.A., Okamoto, D.K., Rassweiler, A., Novak, M., Bolton, J.J., Cavanaugh, K.C.,
996 Connell, S.D., Johnson, C.R., Konar, B., Ling, S.D., Micheli, F., Norderhaug, K.M., Pérez-
997 Matus, A., Sousa-Pinto, I., Reed, D.C., Salomon, A.K., Shears, N.T., Wernberg, T., Anderson,
998 R.J., Barrett, N.S., Buschmann, A.H., Carr, M.H., Caselle, J.E., Derrien-Courtel, S., Edgar, G.J.,
999 Edwards, M., Estes, J.A., Goodwin, C., Kenner, M.C., Kushner, D.J., Moy, F.E., Nunn, J.,
1000 Steneck, R.S., Vásquez, J., Watson, J., Witman, J.D. and Byrnes, J.E.K. (2016). Global patterns
1001 of kelp forest change over the past half-century *Proceedings of the National Academy of*
1002 *Sciences of the United States of America*, 113, 13785–13790. doi, 10.1073/pnas.1606102113

1003 Lafferty, K.D. (2004). Fishing for lobsters indirectly increases epidemics in sea urchins.
1004 *Ecological Applications*, 14, 1566–1573. doi., 10.1890/03-5088

1005 Lamy, T., Koenigs, C., Holbrook, S.J., Miller, R.J., Stier, A.C. and Reed, D.C. (2020).
1006 Foundation species promote community stability by increasing diversity in a giant kelp forest.
1007 *Ecology*, p.e02987. doi, 10.1002/ecy.2987

1008 Leising, A.W., Schroeder, I.D., Bograd, S.J., Abell, J., Durazo, R., Gaxiola-Castro G.,
1009 Bjorkstedt, E.P., Field, J., Sakuma, K., Robertson, R.R. and Goericke R. (2015) State of the
1010 California Current 2014-15, Impacts of the warm water "Blob". *California Cooperative Oceanic*
1011 *Fisheries Investigations Reports*, 56, 31-68.

- 1012 Lester, S.E., Tobin, E.D. and Behrens, M.D., (2007). Disease dynamics and the potential role of
1013 thermal stress in the sea urchin, *Strongylocentrotus purpuratus*. Canadian Journal of Fisheries
1014 and Aquatic Sciences, 64(2), 314-323. doi, 10.1139/f07-010
- 1015 Ling, S.D., Scheibling, R.E., Rassweiler, A., Johnson, C.R., Shears, N., Connell, S.D., Salomon,
1016 A.K., Norderhaug, K.M., Perez-Matus, A., Hernandez, J.C., Clemente, S., Blamey, L.K., Hereu,
1017 B., Ballesteros, E., Sala, E., Garrabou, J., Cebrian, E., Zabala, M., Fujita, D., Johnson, L.E.,
1018 (2015). Global regime shift dynamics of catastrophic sea urchin overgrazing. Philosophical
1019 Transitions Royal Society B, 370, 20130269. doi, 10.1098/rstb.2013.0269
- 1020 Lonhart, S.I., Jeppesen, R., Beas-Luna, R., Crooks, J.A. and Lorda, J. (2019). Shifts in the
1021 distribution and abundance of coastal marine species along the eastern Pacific Ocean during
1022 marine heatwaves from 2013 to 2018. Marine Biodiversity Records. 12, 1151. doi,
1023 10.1186/s41200-019-0171-8
- 1024 Lowe, C.B., Kellis, M., Siepel, A., Raney, B.J., Clamp, M., Salama, S.R., Kingsley, D.M.,
1025 Lindblad-Toh, K. and Haussler, D. (2011). Three Periods of Regulatory Innovation During
1026 Vertebrate Evolution. Science, 333, 1019–1024. doi, 10.1126/science.1202702
- 1027 Mann, K.H. (1973) Seaweeds, their productivity and strategy for growth. Science, 182, 975-981.
- 1028 Martínez, B., Radford, B., Thomsen, M.S., Connell, S.D., Carreño, F., Bradshaw, C.J., Fordham,
1029 D.A., Russell, B.D., Gurgel, C.F.D. and Wernberg, T. (2018). Distribution models predict large
1030 contractions of habitat-forming seaweeds in response to ocean warming. Diversity and
1031 Distributions, 24(10), 1350-1366.
- 1032 Micheli, F., A. Saenz, Greenley, A., Vazquez, L., Espinoza, A., Rossetto, M., De Leo, G. (2012).
1033 Evidence that marine reserves enhance resilience to climatic impacts. PLoS ONE, 7(7), e40832.
1034 doi, 10.1371/journal.pone.0040832.
- 1035 Miller, R.J., Lafferty, K.D., Thomas, L., Kui L., Rassweiler A., and Reed, D.C. (2018). Giant
1036 kelp, *Macrocystis pyrifera*, increases faunal diversity through physical engineering Proc. R. Soc.
1037 B, 285, 20172571. doi, 10.1098/rspb.2017.2571
- 1038 Miller R. and Page H. (2012). Kelp as a trophic resource for marine suspension feeders, a review
1039 of isotope-based evidence. Marine Biology, 159, 1391–1402. doi,10.1007/s00227-012-1929-2

- 1040 Miller, R., Page, H. and Reed, D. (2015). Trophic versus structural effects of a marine
1041 foundation species, giant kelp (*Macrocystis pyrifera*). *Oecologia*, 179, 1199–1209. doi,
1042 10.1007/s00442-015-3441-0
- 1043 Miller, R., Page, H., Brzezinski, M. (2013). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of particulate organic matter in the
1044 Santa Barbara Channel, drivers and implications for trophic inference. *Marine Ecology Progress*
1045 *Series*, 474, 53–66. doi, 10.3354/meps10098
- 1046 Mills, K.E., Pershing, A.J., Brown, C.J. and Chen, Y. (2013). Fisheries management in a
1047 changing climate, lessons from the 2012 ocean heat wave in the Northwest Atlantic.
1048 *Oceanography*, 191-195. doi, 10.2307/24862052
- 1049 Moy, F.E. and Christie, H. (2012). Large-scale shift from sugar kelp (*Saccharina latissima*) to
1050 ephemeral algae along the south and west coast of Norway. *Marine Biology Resources* 8,309-
1051 321. doi, 10.1080/17451000.2011.637561
- 1052 Oliver E.J.C., Burrows M.T., Do.nat M.G., Sen Gupta A., Alexander L.V., Perkins-Kirkpatrick
1053 S.E., Benthuyssen J., Hobday A.J., Holbrook N.J., Moore P.J., Thomsen M.S., Wernberg T.,
1054 Smale D.A. (2019). Projected marine heatwaves in the 21st century and the potential for
1055 ecological impact. *Frontiers in Marine Science*, 6, 734. doi, 10.3389/fmars.2019.00734
- 1056 Page H.M., Reed D.C., Brzezinski M.A., Melack J.M., Dugan J.E. (2008) Assessing the
1057 importance of land and marine sources of organic matter to kelp forest food webs. *Marine*
1058 *Ecology Progress Series*, 360, 47–62. doi, 10.3354/meps07382
- 1059 Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Le Bris, A., Mills, K.E., Nye
1060 J.A., Record, N.R., Scannell, H.A., Scott, J.D., Sherwood, G.D. and Thomas A.C. (2015). Slow
1061 adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery.
1062 *Science*, 350, 809–812. doi, 10.1126/science.aac9819
- 1063 Pessarrodona, A., Moore, P.J., Sayer, M.D.J. and Smale D.A. (2018). Carbon assimilation and
1064 transfer through kelp forests in the NE Atlantic is diminished under a warmer ocean climate.
1065 *Global Change Biology*, 24, 4386-4398. doi, 10.1111/gcb.14303
- 1066 Pfister, C.A., Berry, H.D. and Mumford, T. (2018). The dynamics of kelp forests in the
1067 Northeast Pacific Ocean and the relationship with environmental drivers. *Journal of Ecology*,
1068 106(4), 1520-1533. doi, 10.1111/1365-2745.12908

- 1069 Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L., (2013). Marine taxa track local climate
1070 velocities. *Science*, 341,1239-1242. doi,10.1126/science.1239373 doi, 10.1126/science.1239352
- 1071 Poloczanska, E.S. and Burrows, M.T. (2016) Responses of marine organisms to climate change
1072 across oceans. *Frontiers in Marine Science* 3(28),1-21 doi, 10.3389/fmars.2016.00062
- 1073 Poloczanska, E.S., Brown, C.J. and Sydeman, W.J. (2013) Global imprint of climate change on
1074 marine life. *Nature Climate Change*, 3, 919–925. doi, 10.1038/nclimate1958
- 1075 Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J.,
1076 Brander, K., Bruno, J.F., Buckley, L.B., Michael T. Burrows, Duarte C.M, Halpern B.S, Holding
1077 J., Kappel C. V., O’Connor M. I., Pandolfi J. M., Parmesan C., Schwing F., Thompson S. A. &
1078 Richardson A.J. (2013). Global imprint of climate change on marine life. *Nature Climate*
1079 *Change*, 3, 919–925. doi, 10.1038/nclimate1958
- 1080 Reed, D., Washburn, L., Rassweiler, A., Miller, R., Bell, T., Harrer, S., (2016). Extreme
1081 warming challenges sentinel status of kelp forests as indicators of climate change. *Nature*
1082 *Communications*, 7, 1496. doi, 10.1038/ncomms13757
- 1083 Reed, D.C., Rassweiler, A.R., Miller, R.J., Page, H.M. and Holbrook S.J. (2016) The value of a
1084 broad temporal and spatial perspective in understanding dynamics of kelp forest ecosystems.
1085 *Marine and Freshwater Research*, 67, 14–11. doi, 10.1071/MF14158
- 1086 Rigby, P.R., Iken, K. and Shirayama, Y. eds., (2007). Sampling biodiversity in coastal
1087 communities, NaGISA protocols for seagrass and macroalgal habitats. Kyoto University , Press,
1088 Japan. 147pp.
- 1089 Rogers-Bennett, L. and Catton, C.A. (2019). Marine heat wave and multiple stressors tip bull
1090 kelp forest to sea urchin barrens. *Scientific reports*, 9(1), 1-9. doi, 10.1038/s41598-019-51114-y
- 1091 Schiel, D.R. and Foster, M.S. (2015) *The Biology and Ecology of Giant Kelp Forests*. Univ of
1092 California Press.
- 1093 Smale, D.A., Burrows, M.T., Moore, P.J., O’Connor, N. and Hawkins S.J. (2013). Threats and
1094 knowledge gaps for ecosystem services provided by kelp forests, a northeast Atlantic
1095 perspective. *Ecology and Evolution*, 3, 4016–4038. doi, 10.1002/ece3.774

1096 Smale, D.A., and Wernberg T. (2013). Extreme climatic event drives range contraction of a
1097 habitat-forming species. *Proceedings of the Royal Society B*, 280, 20122829. doi,
1098 10.1098/rspb.2012.2829

1099 Smale, D.A. and P.J. Moore. (2017). Variability in kelp forest structure along a latitudinal
1100 gradient in ocean temperature. *Journal of Experimental Marine Biology and Ecology*, 486,255-
1101 264. doi, 10.1016/j.jembe.2016.10.023

1102 Smale, D.A. (2020). Impacts of ocean warming on kelp forest ecosystems. *New Phytologist*,
1103 225, 1447–1454. doi, 10.1111/nph.16107

1104 Smale, D.A., Wernberg, T., Oliver, E.C.J., Thomsen, M., Harvey, B.P., Straub, S.C., Burrows,
1105 M.T., Alexander, L.V., Benthuyssen, J.A., Donat, M.G., Feng, M., Hobday, A.J., Holbrook, N.J.,
1106 Perkins-Kirkpatrick, S.E., Scannell, H.A., Gupta, Sen, A., Payne, B.L. and Moore, P.J. (2019).
1107 Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature*
1108 *Climate Change*, 9, 306–312. doi, 10.1038/s41558-019-0412-1

1109 Springer, Y.P., Hays, C.G. and Carr, M.H. (2010). Toward ecosystem-based management of
1110 marine macroalgae—The bull kelp, *Nereocystis luetkeana*. *Oceanography and Marine Biology*,
1111 *An Annual Review* 48,1-42. doi, 10.1201/EBK1439821169-c1

1112 Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A.,
1113 TEGNER, M.J. (2003). Kelp forest ecosystems, biodiversity, stability, resilience and future.
1114 *Environmental Conservation*, 29, 436–459. doi, 10.1017/S0376892902000322

1115 Tanaka, K., Taino, S., Haraguchi, H., Prendergast, G., Hiraoka, M., (2012). Warming off
1116 southwestern Japan linked to distributional shifts of subtidal canopy-forming seaweeds. *Ecology*
1117 *and Evolution*, 2,2854–2865. doi, 10.1002/ece3.391

1118 Teagle, H., Hawkins, S.J., Moore, P.J. and Smale, D.A. (2017). The role of kelp species as
1119 biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology*
1120 *and Ecology*, 492, 1–18. doi, 10.1016/j.jembe.2017.01.017

1121 Thomsen, M.S., Mondardini, L., Alestra, T., Gerrity, S., Tait, L., South, P., Lilley, S. and Schiel,
1122 D. (2019). Local extinction of bull kelp (*Durvillaea* spp.) due to a marine heatwave. *Frontiers in*
1123 *Marine Science*, 6, 84. doi, 10.3389/fmars.2019.00084

- 1124 Vergés, A., Doropoulos, C., Malcolm, H.A., Skye, M., Garcia-Pizá, M., Marzinelli, E.M.,
1125 Campbell, A.H., Ballesteros, E., Hoey, A.S., Vila-Concejo, A., Bozec, Y.-M. and Steinberg,
1126 P.D. (2016). Long-term empirical evidence of ocean warming leading to tropicalization of fish
1127 communities, increased herbivory, and loss of kelp. *Proceedings of the National Academy of*
1128 *Sciences*, 113, 13791–13796. doi, 10.1073/pnas.1610725113
- 1129 Watanabe, J.M. and Harrold, C. (1991). Destructive grazing by sea urchins *Strongylocentrotus*
1130 *spp.* in a central California kelp forest, potential roles of recruitment, depth, and predation.
1131 *Marine Ecology Progress Series*, 71,125–141. doi, 10.3354/meps071125
- 1132 Wernberg, T., Bennett, S., Babcock, R. C., de Bettignies, T., Cure, K., Depczynski, M.,
1133 Depczynski M., Dufois F., Fromont J., Fulton C.J., Hovey R., Harvey E., Holmes T.H., Kendrick
1134 G.A., Radford B., Santana-Garcon, J., Saunders B.J., Smale D.A., Thomsen A.S., Tuckett C.A.,
1135 Tuya F., Vanderiklif M.A., Wilson S. (2016). Climate-driven regime shift of a temperate marine
1136 ecosystem. *Science*, 353(6295),169–172. doi, 10.1126/science.aad8745
- 1137 Wernberg, T., Russell, B., Thomsen, M. S., Gurgel, F. G., Bradshaw, C. J. A., Poloczanska, E.
1138 S. (2011). Seaweeds in retreat from ocean warming. *Current Biology*, 21, 1–5. doi,
1139 10.1016/j.cub.2011.09.028
- 1140 Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett,
1141 S. and Rousseaux, C.S. (2012). An extreme climatic event alters marine ecosystem structure in a
1142 global biodiversity hotspot. *Nature Climate Change*, 3, 78–82. doi, 10.1038/nclimate1627
- 1143 Wernberg, T., Thomsen, M.S., Tuya, F., Kendrick, G.A., Sather P.A., and Toohy B.D. (2010)
1144 Decreasing Resilience of Kelp Beds Along a Latitudinal Temperature Gradient, Potential
1145 Implications for a Warmer Future. *Ecology Letters*, 13(6), 685–94. doi, 10.1111/j.1461-
1146 0248.2010.01466.x
- 1147 Wilkinson, T.A., Wiken, E. J., Bezaury-Creel, T.F., Hourigan, T., Agardy, H., Herrmann, L.,
1148 Janishevski, C., Madden, L., Morgan, L and Padilla, M. (2009). *Marine Ecoregions of North*
1149 *America*. Commission of Environmental Cooperation. Montreal, Canada. 200 pp.
- 1150 Woodson, C.B., Micheli, F., Boch, C., Al-Najjar, M., Espinoza, A., Hernandez, A., Vázquez-
1151 Vera, L., Saenz-Arroyo, A., Monismith, S.G., Torre, J. (2018). Harnessing marine microclimates
1152 for climate change adaptation and marine conservation. *Conservation Letters*, 12, e12609. doi,
1153 10.1111/conl.12609

- 1154 Yeager, M.E., Gouhier, T.C. and Hughes, A.R. (2020). Predicting the stability of multitrophic
1155 communities in a variable world. *Ecology*, p.e02992. doi, 10.1002/ecy.2992
- 1156 Yorke, C., Miller, R., Page, H., Reed D. (2013). Importance of kelp detritus as a component of
1157 suspended particulate organic matter in giant kelp *Macrocystis pyrifera* forests. *Marine Ecology*
1158 *Progress Series*, 493, 113–125. doi, 10.3354/meps10502
- 1159 Yorke, C.E., Page, H.M. and Miller R. J. (2019). Sea urchins mediate the availability of kelp
1160 detritus to benthic consumers 286. *Proceedings of the Royal Society B*. doi,
1161 10.1098/rspb.2019.0846
- 1162 Yorke, C.E., Hanns, B., Shears, N., Page, H.M., Miller, R.J. (2019). Living kelp versus plankton
1163 as food sources for suspension feeders. *Marine Ecology Progress Series*, 614,21-33. doi,
1164 10.3354/meps12906

1166 **FIGURE LEGEND**

1167

1168 Figure 1. Map of the ecoregions along the west coast of United States and Mexico. AK=
1169 Alaska, NorCA= Northern California, CenCA= Central California, SCB= Southern
1170 California and Baja Norte, and BCS= Baja California Sur. The histogram shows
1171 number of sites sampled by program per year. Sampled sites are identified in the
1172 map color-coded with the representative monitoring program.

1173

1174 Figure 2. Rates of change in density of canopy kelp (A-C) and other algae (D-F) for 3
1175 models (Base Model, Model with site temperature, before marine heatwave). Rate
1176 of change (circles) and 90% credible intervals (horizontal lines) for the five
1177 ecoregions with the overall rate of change (vertical line) and 90% credible interval
1178 (shading).

1179

1180 Figure 3. Rates of change in abundance of important functional groups over time for each
1181 ecoregion across all years, including the marine heatwave (2006-2016; red) and
1182 excluding years of the 2014-2016 marine heatwave (blue) for (A) herbivores, (B)
1183 urchins, (C) suspension feeders, (D) detritivores, (E) microinvertebrates, (F)
1184 macroinvertebrates, (G) planktivores, and (H) piscivores. Results are based on the
1185 model with temperature included. Rate of change (circles) and 90% credible
1186 intervals (horizontal lines) for the five ecoregions with the overall rate of change
1187 (vertical line) and 90% credible interval (shading). Note that scales are different
1188 from plot to plot. Non-overlapping credible intervals between model runs (blue vs.
1189 red) highlight regional functional groups that were heavily affected by the warming
1190 event.

1191

1192 Figure 4. Shifts in functional group distributions as velocities based on estimated
1193 instantaneous rates of change across sites and regions. Location of center of
1194 distribution versus total range for 95% of abundance over a 10-year period. Size of
1195 circle indicates number of observations. Positive values indicate poleward
1196 progression and range expansion, while negative values indicate an equatorward
1197 progression and range contraction.

1198

1199 Figure 5. Biomass and normalized ecosystem structure before and during warming period
1200 from 2014-2016 shown with estimated structure based on instantaneous rates of
1201 change for year 2050. 2008 shown as baseline for before warming. Icon indicates
1202 group with largest biomass. Biomass density estimate also given above each bar for
1203 each region. GOA is not included because of insufficient data across the functional
1204 groups (see Methods).

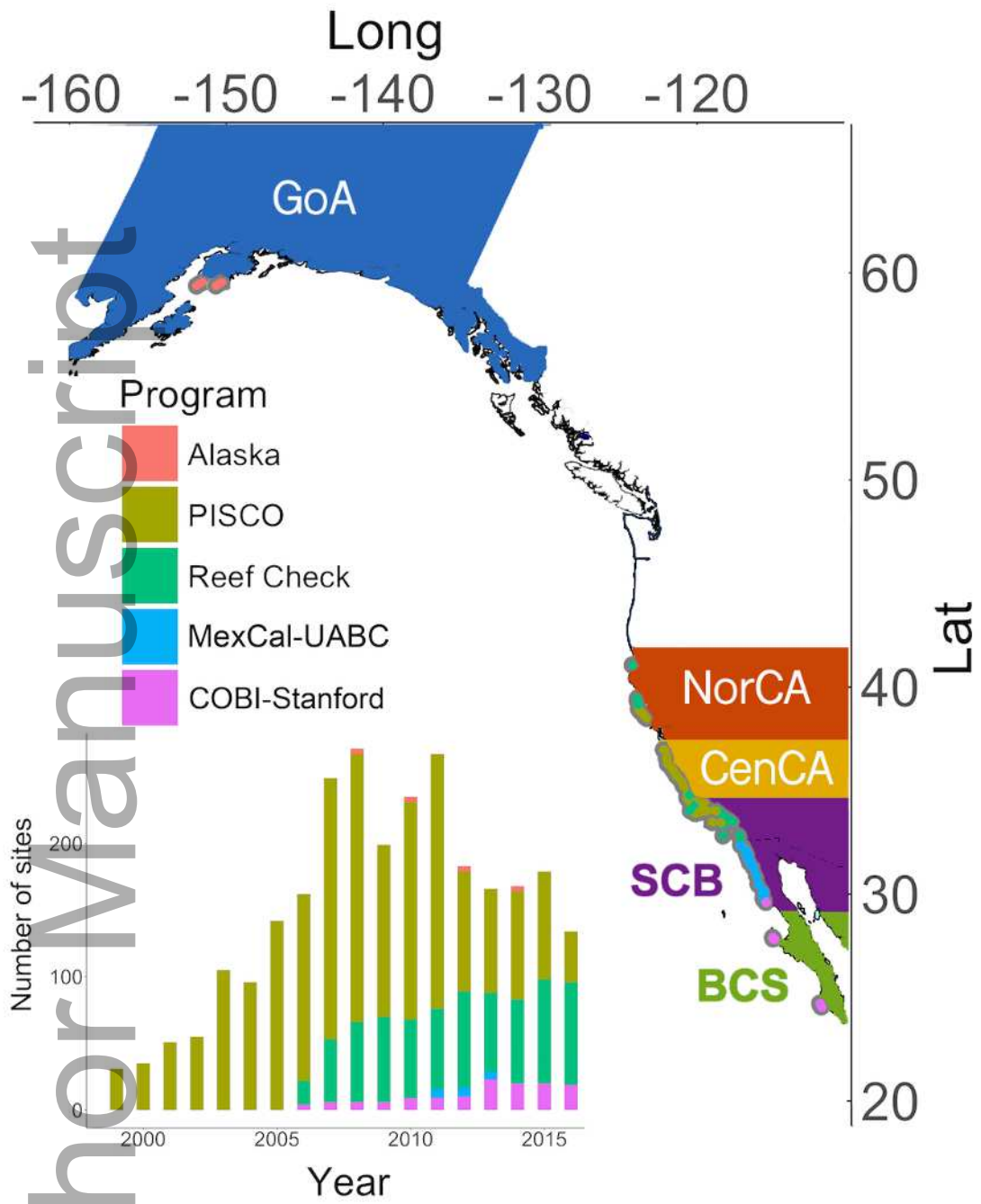
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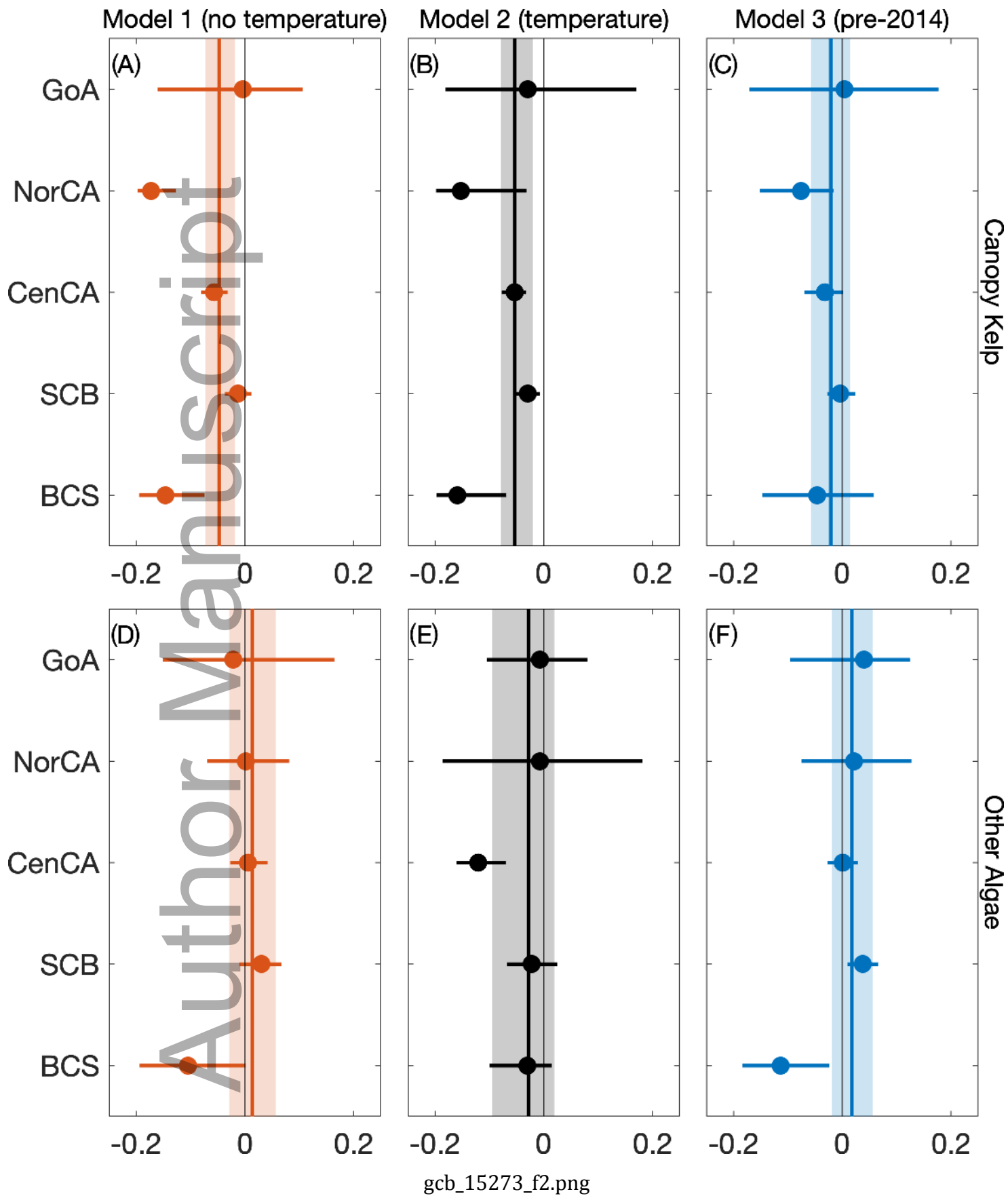
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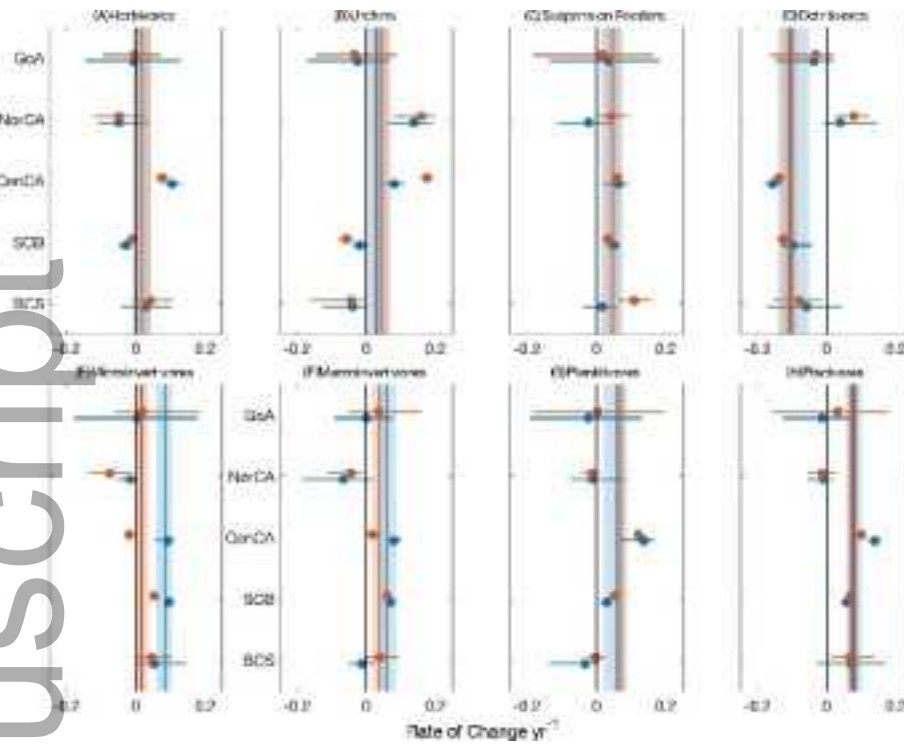
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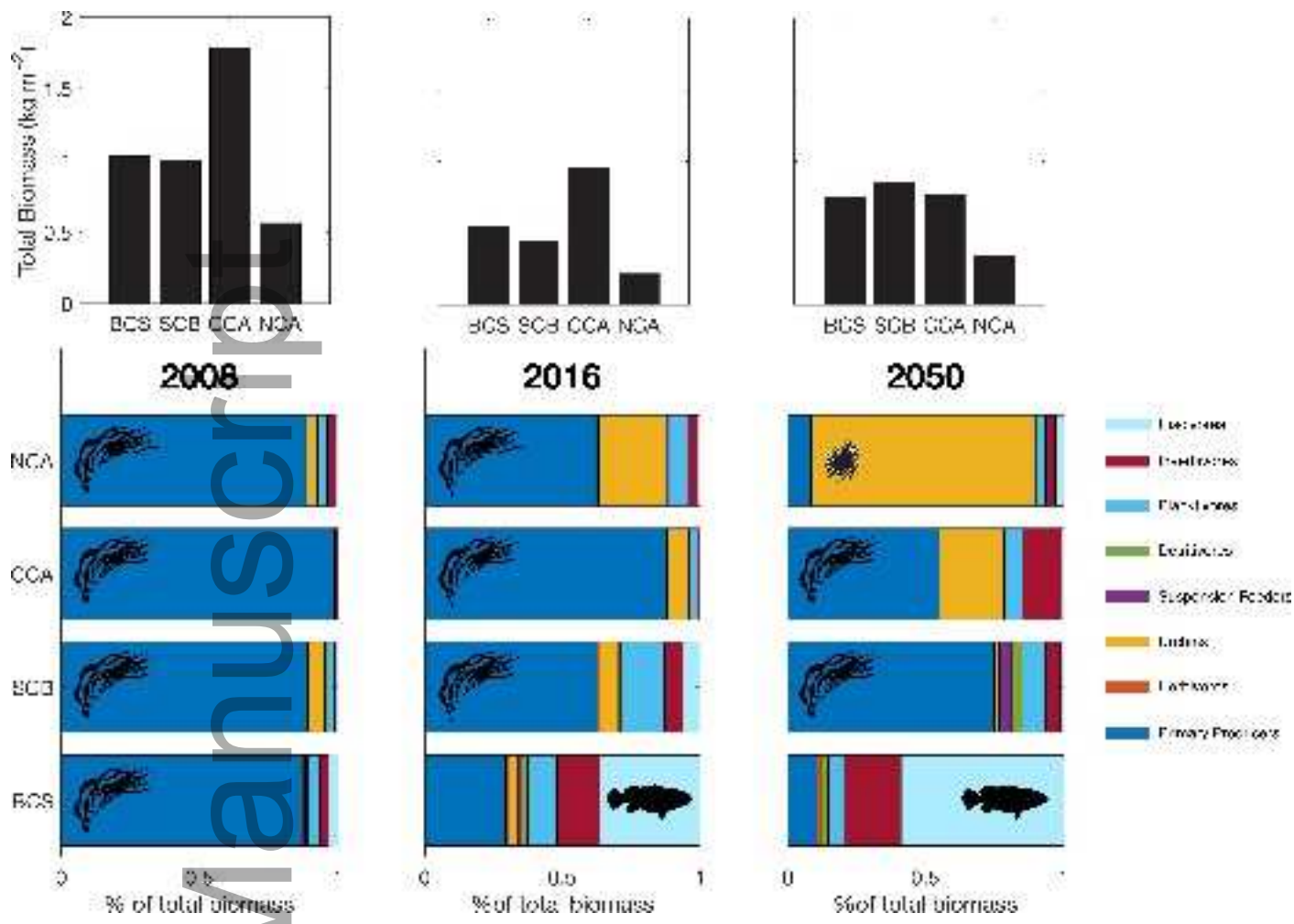


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