

Variable exposure to multiple climate stressors across the California marine protected area network and policy implications

S. L. Hamilton^{1,2,*}, E. G. Kennedy^{1,3}, M. Zulian^{1,3}, T. M. Hill^{1,3}, B. Gaylord^{1,4}, E. Sanford^{1,4}, A. M. Ricart^{5,6}, M. Ward⁷, A. K. Spalding^{8,9}, and K. Kroeker¹⁰

¹Bodega Marine Laboratory—University of California, Davis, CA 95616, USA

²Oregon Kelp Alliance, Port Orford, OR 97465, USA

³Department of Earth and Planetary Sciences, University of California, Davis, CA 95616, USA

⁴Department of Evolution and Ecology, University of California, Davis, CA 95616, USA

⁵Bigelow Laboratory for Ocean Sciences, East Boothbay, ME 04544, USA

⁶Institut de Ciències del Mar (ICM-CSIC), Barcelona 08003, Spain

⁷San Diego State University, San Diego, CA 92182, USA

⁸Oregon State University, Corvallis, OR 97331, USA

⁹Smithsonian Tropical Research Institute, Panama City 0843-03092, Panama

¹⁰University of California, Santa Cruz, CA 95064, USA

*Corresponding author: tel:1-540-292-4313; e-mail: sahamilton@ucdavis.edu.

The efficacy of marine protected areas (MPAs) may be reduced when climate change disrupts the ecosystems and human communities around which they are designed. The effects of ocean warming on MPA functioning have received attention but less is known about how multiple climatic stressors may influence MPAs efficacy. Using a novel dataset incorporating 8.8 million oceanographic observations, we assess exposure to potentially stressful temperatures, dissolved oxygen concentrations, and pH levels across the California MPA network. This dataset covers more than two-thirds of California's 124 MPAs and multiple biogeographic domains. However, spatial-temporal and methodological patchiness constrains the extent to which systematic evaluation of exposure is possible across the network. Across a set of nine well-monitored MPAs, the most frequently observed combination of stressful conditions was hypoxic conditions (<140 $\mu\text{mol/kg}$) co-occurring with low pH (<7.75). Conversely, MPAs exposed most frequently to anomalously warm conditions were less likely to experience hypoxia and low pH, although exposure to hypoxia varied throughout the 2014–2016 marine heatwaves. Finally, we found that the spatial patterns of exposure to hypoxia and low pH across the MPA network remained stable across years. This multiple stressor analysis both confirms and challenges prior hypotheses regarding MPA efficacy under global environmental change.

Keywords: acidification, climate change, dissolved oxygen, hypoxia, marine heatwave, multiple stressors, pH, temperature.

Introduction

Marine protected areas (MPAs) are a common conservation and stewardship tool globally and currently occupy 5.9% of the world's oceans (*sensu* Grorud-Colvert *et al.*, 2021). However, it is unclear whether the social and ecological effectiveness of MPAs may change as climate change modifies the physical, chemical, and biological processes within protected areas (e.g. Roberts *et al.*, 2017; Bruno *et al.*, 2018; Bates *et al.*, 2019), and affects human communities that are dependent on associated marine resources (e.g. Cinner *et al.*, 2012). While theory suggests MPAs could increase ecosystem, and potentially social, resilience to global climate change (e.g. Roberts *et al.*, 2017), evidence substantiating these predictions remains sparse (Micheli *et al.*, 2012; Bates *et al.*, 2019; Eisaguirre *et al.*, 2020; Freedman *et al.*, 2020). The resulting knowledge gap leaves managers, scientists, and the public unsure of the value of MPAs amid changing environmental conditions.

In response, MPA science and literature have increasingly considered how to design, implement, and manage spatial protections in a way that takes climate change into consideration

or even increases the resilience of protected ecosystems to climate change, sometimes referred to as “climate-smart MPAs” (e.g. Arafeh-Dalmau *et al.*, 2021; Queirós *et al.*, 2021; Brito-Morales *et al.*, 2022). An expanding body of literature has identified strategies for creating climate-smart MPAs, including locating MPAs within climate change refugia (Woodson *et al.*, 2019; Arafeh-Dalmau *et al.*, 2021; Brito-Morales *et al.*, 2022), creating MPA networks that spread risk across space (Carr *et al.*, 2017; Fredston-Hermann *et al.*, 2018), and siting MPAs at leading edges of key species ranges (Fredston-Hermann *et al.*, 2018). MPA efficacy in the face of climate change also hinges upon social, cultural, and policy considerations, and to date even less is known about how climate-smart MPAs might be designed to also support human communities associated with MPAs or how, in turn, climate impacts on human communities might affect MPA effectiveness (Ban *et al.*, 2011; Grorud-Colvert *et al.*, 2021; Schmidt *et al.*, 2022).

The climate-smart MPA literature often focuses on how changing temperature regimes will influence the future of MPAs (e.g. Arafeh-Dalmau *et al.*, 2021; Brito-Morales *et*

Received: 26 January 2023; Revised: 24 May 2023; Accepted: 10 July 2023

© The Author(s) 2023. Published by Oxford University Press on behalf of International Council for the Exploration of the Sea. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

al., 2022). This attention follows the known effects of long-term warming, increased thermal variability, and marine heatwaves (MHWs) on population stability, species persistence, and ecosystem trajectories under climate change (e.g. Sunday *et al.*, 2015; Sanford *et al.*, 2019; Fredston *et al.*, 2021). While temperature undoubtedly plays a crucial role in structuring biological responses to climate change, other, less-often measured parameters also do so. Parameters such as dissolved oxygen (DO), salinity, and pH often stand out as crucial factors governing biological responses to climate change when they are well measured and paired with biological observations (Kroeker *et al.*, 2013; Gunderson *et al.*, 2016; McHenry *et al.*, 2019; Sampaio *et al.*, 2021). For instance, deoxygenation of coastal waters is driving decreases in the vertical distribution of rocky reef fish in southern California (Meyer-Gutbrod *et al.*, 2021). Additionally, Dungeness crab movement and foraging ecology in estuaries is shaped by crab avoidance of low salinity waters (McGaw and McMahon, 1996; Curtis and McGaw, 2008, 2012). Further, interactions between temperature and other potential stressors can be significantly different from the effects of temperature alone. Temperature–pH interactions often modify the impacts of changing seawater chemistry on marine calcifiers (Byrne and Przeslawski, 2013; Przeslawski *et al.*, 2015). Moreover, organismal oxygen demand, an important energetic consideration in many taxa, increases with temperature due to the thermodynamics of biochemical and cellular processes (Somero *et al.*, 2016; Howard *et al.*, 2020).

Despite the recognized potential for interactions among multiple stressors to structure ecological responses to climate change inside MPAs (Crain *et al.*, 2008; Gunderson *et al.*, 2016; Somero *et al.*, 2016; Bruno *et al.*, 2018), relatively few studies regarding climate-smart MPAs explicitly consider the implications of combined stressors. The studies that do consider multiple stressors often focus on either small-spatial scales, such as individual sites or MPAs (e.g. Woodson *et al.*, 2019) or analyses based on modelled environmental parameters rather than direct observations (e.g. Bruno *et al.*, 2018; Queirós *et al.*, 2021). Empirical studies investigating the impacts of multiple climate stressors on MPAs over broader spatial scales have remained elusive. Contemporary evaluations of biophysical MPA outcomes in a changing climate, therefore, lack crucial context for assessing how temperature interacts with additional stressors over larger regional scales.

The California MPA network in the United States is one of the oldest, largest, and best studied in the world (Gleason *et al.*, 2013; Murray and Hee, 2019). In 2022, California began conducting a decadal management review of the 124 MPAs in the network (CDFW, 2022). Because this evaluation will assess how California's network met its goals over the years 2010–2020, this process will have to assess how the MPAs performed over the unusual and highly variable environmental conditions of 2010–2020. For instance, the record-breaking series of MHWs over 2014–2016 impacted the entire state throughout those years and was associated with die-offs of foundation species (e.g. McPherson *et al.*, 2021), exacerbation of novel disease outbreaks (e.g. Hamilton *et al.*, 2021), shifts in species distributions (e.g. Sanford *et al.*, 2019; Freedman *et al.*, 2020), and many more disruptions of marine life (e.g. Cavole *et al.*, 2016; McCabe *et al.*, 2016; Piatt *et al.*, 2020). Although researchers have thoroughly described the direct temperature effects of the 2014–2016 MHWs (Bond *et al.*, 2015; Di Lorenzo and Mantua, 2016; Gentemann *et al.*,

2017), the interactions between these heatwaves and other stressors, and their impacts on MPAs, are poorly resolved. Even less is known about the social outcomes of these changes within MPAs; but we can readily assume that coastal communities dependent on marine resources will also face threats from changing ocean conditions and their impacts on MPAs (Gurney *et al.*, 2014; Whitney and Ban, 2019; Schmidt *et al.*, 2022).

As one of the world's major upwelling systems, the California Current routinely transports waters with low pH and low DO into nearshore habitats (Feely *et al.*, 2008; Chavez and Messié, 2009; Chan *et al.*, 2017; Cheresh and Fiechter, 2020; Low *et al.*, 2021). Whether by themselves or in combination with temperature stress, low pH and hypoxia are well documented to affect biological processes in the California Current (McClatchie *et al.*, 2010; Hofmann *et al.*, 2014; Keller *et al.*, 2017; Howard *et al.*, 2020; Bednaršek *et al.*, 2021a). While individual studies have assessed the impacts of various combinations of temperature, pH, and DO stress on organisms in the California Current (e.g. Kroeker *et al.*, 2016; Meyer-Gutbrod *et al.*, 2021; Donham *et al.*, 2022), no one has conducted a quantitative, MPA network-wide assessment of organisms' exposure to these stressors to our knowledge. Here, we assessed how California's 124 MPAs experienced different combinations of hypoxia, low pH, and unusually warm temperatures from 2010 to 2020. Our analysis employs a novel dataset incorporating >65 publicly available oceanographic datasets covering the target area and time. Using this dataset we asked:

- What is the spatial and temporal coverage of publicly available temperature, DO, and pH data across the MPA network?
- How did MPAs differ in their exposure to potentially biologically stressful temperature, DO, and pH conditions?
- Did exposure to low DO in MPAs change during the 2014–2016 MHWs?
- Did the spatial patterns of relative exposure to low DO and low pH persist across MPAs over 2018–2020?

Methods

Oceanographic dataset

The dataset used for this analysis is available through the National Center for Environmental Information (Kennedy *et al.*, 2023a) and is fully described in Kennedy *et al.* (2023b), although we utilize a subset of the full dataset that was collected prior to September 2022. The 65 publicly available oceanographic datasets included in this study include ~8.8 million observations from State waters spanning California (Supplementary Table S1). This dataset is primarily composed of high-accuracy measurements of temperature, DO, pH, and related carbonate chemistry parameters derived from discrete water samples, autonomous moored sensors, and handheld sensors. Nearshore and open ocean observations dominate the dataset alongside a limited number of estuarine datasets. Each set of observations integrated into this larger dataset was re-framed into a common data format that associated each observation with a sampling date, time, depth, location, and data source. Any observations that included paired carbonate system observations were used to constrain the full carbonate system using the R package “seacarb” and constants recom-

mended by Dickson *et al.* (2007) according to sample temperature and salinity (Gattuso *et al.* 2022).

Additionally, all observations were independently evaluated for quality and flagged as “good”, “not evaluated”, and “suspect” upon integration in the dataset. This was done using a combination of instrument type, property–property plots, time-series plots, comparison between sensor and discrete samples data (where applicable), and notes from the data collector. For complete details on dataset creation, formatting, and quality control, see Kennedy *et al.* (2023b). For the current study, we filtered the dataset to include only surface observations (≤ 30 m depth) taken from the study period (2010–2020) to reflect the largely shallow, coastal nature of most of the MPAs in the California network. For portions of the dataset that recorded multiple observations of a single metric at a single site per day, we aggregated to a daily mean value. After filtering and aggregating in this way, 161176 daily mean oceanographic observations of temperature, DO, and pH in California coastal waters were available for further analysis.

Associating data points with individual MPAs

To assess data availability across the study period, we identified the number of temperature, DO, and pH observations collected within each MPA. We focused our analysis on State-designated MPAs in oceans and estuaries, excluding the San Francisco Bay, resulting in 124 MPAs. We identified the MPAs’ spatial boundaries using a shapefile provided by the State of California (Marine Region GIS, 2019). We identified observations within 10 km of the edge of each MPA by creating a distance matrix for the distance between each data point and each of the MPAs. We classified each MPA as either estuarine or oceanic and only characterized each MPA using oceanographic observations from the same category. We then identified the number of observations for each parameter available by season and year for each MPA, partitioning measurements according to spring (March–May), summer (June–August), fall (September–November), and winter (December–February) seasons of each year from 2010 to 2020.

Assessing MPA exposure to simultaneous temperature, DO, and pH stress

We examined the exposure of MPAs to potential stressors using two different combinations of parameters: (1) DO and temperature and (2) DO, temperature, and pH. To quantify how often potentially stressful conditions were present in MPAs, we developed heuristic criteria of pH, DO, and temperature conditions that could be anticipated to impose physiological stress on diverse marine species. Because marine taxa tend to exhibit a narrower range of thresholds for pH and DO stress than for temperature, we identified threshold values for low pH and hypoxia that are most often associated with sublethal impacts to animal fitness in the literature: 7.75 for pH (Bednaršek *et al.*, 2021a, 2021b) and 140 $\mu\text{mol/kg}$ for DO (Vaquer-Sunyer and Duarte, 2008). In contrast, because biological responses to temperature are less conserved across taxa and more sensitive to acclimatization and local adaptation (Osovitz and Hofmann, 2005; Somero, 2005), we used temperature anomalies to reflect potentially stressful thermal conditions (Hobday *et al.*, 2016).

To examine MPA exposure to simultaneous temperature and DO stress, we identified MPAs that had 50+ paired temperature and DO measurements either within the MPA

boundaries or within 10 km of the MPA. We further restricted our analysis to MPAs representing different biogeographic regions in California and had observations available in various seasons to minimize seasonal bias when comparing MPA exposure. This approach resulted in the inclusion of 19 MPAs for analysis, although for visualization purposes only 9 MPAs with 350+ paired temperature and DO measurements are shown in Figure 2 (see Supplementary Figure S1 for all MPAs).

To investigate MPA exposure to stressful temperature, DO, and pH conditions, we used similar criteria to those used for the temperature and DO analysis (above), but limited our analysis to those MPAs that had high frequency (daily–weekly), continuous (minimum of a 6-month period) simultaneous monitoring of temperature, DO, and pH. We identified nine MPAs that met these criteria, which had on average 1–2 years of consistent multiple stressor monitoring. These MPAs were primarily sampled over the 2018–2020 time period, except for Kashtayit State Marine Conservation Area (SMCA), which was sampled in 2015–2016, and over multiple seasons, which should limit temporal biases between MPAs (see Supplementary Table S2 for details).

To quantify the frequency of exposure to stressful conditions, we calculated the percentage of pH observations ≤ 7.75 and DO observations ≤ 140 $\mu\text{mol/kg}$. To quantify temperature stress, we set the threshold as surpassing the 90th percentile of a 25–30 year temperature climatology because this metric is used in the definition of MHWs (Hobday *et al.*, 2016). In order to calculate temperature anomalies in MPAs between 2010 and 2020, we needed to first establish a baseline of long-term temperature in or near each MPA. To do this, we used time series of daily temperature data from ~1990 to 2020 available for each MPA (Supplementary Table S2). We determined the mean daily difference between the temperatures in the MPA focal dataset and the long-term temperature dataset and adjusted temperatures in the long-term temperature dataset by this mean difference. This adjusted daily long-term mean temperature was then subtracted from the measured temperature in the MPAs from 2010 to 2020 to calculate MPA daily temperature anomalies.

Finally, to assess how sensitive each MPA’s relative exposure to low pH and hypoxia was to our specific designated sublethal pH and DO thresholds (7.75 and 140 $\mu\text{mol/kg}$, respectively), we also analysed the frequency of exposure across MPAs using a more conservative and more liberal threshold for stress (7.6 and 7.9 for pH, respectively, and 100 and 180 $\mu\text{mol/kg}$ for DO; Supplementary Figure S2).

Assessing MPA exposure to temperature and DO stress before, during, and after the 2014–2016 MHWs

To understand how the 2014–2016 MHWs impacted combined temperature and hypoxia stress, we identified MPAs that had paired temperature and DO measurements (1) across the pre-heatwaves period (2010–2013), the MHWs period (2014–2016), and the post-heatwaves period (2017–2020), (2) where sampling depth, method, and sampling seasonality were consistent across these periods, and (3) with at least 25 samples in each period (Gentemann *et al.*, 2017). We found five MPAs that met this condition, all in southern California. We visualized the distribution of DO and temperature data across these MPAs using property–property plots and by calculating the 5th percentile of DO in each period. Due to the

paucity of regular pH sampling, no assessment of pH changes across the 2014–2016 MHWs was available.

Assessing the temporal stability of regional patterns in exposure to low pH and low DO across 2018–2020

To track how regional differences in exposure to low pH and hypoxia varied across time, we focused on the 2018–2020 time period because of the availability of consistent, continuous pH and DO time series spread across California. We limited our analysis to MPAs with daily or near-daily records of these variables to maximize the chance that short-term exposure to low pH or DO was captured and prioritized sites that measured both pH and DO. From these candidate MPAs, we chose six MPAs that represented different biogeographic regions to assess inter-regional variability. To examine how exposure to stressful conditions varied over 2018–2020, we calculated the 5th percentile of pH and DO for each month as a metric of potential exposure to stressful conditions.

Results

What data are available to assess multiple stressor impacts across this MPA network?

Out of 161176 daily mean oceanographic observations, 37.5% were inside an MPA or within 10 km of one. Over two-thirds of individual MPAs (69.35%) had some oceanographic observations within 10 km of their borders, and each of these MPAs had at least one season with monitoring of DO and pH in addition to temperature (Figure 1). The number of observations in each MPA in any season varied greatly, from just a single observation taken from an oceanographic cruise to thousands of data points taken in MPA-focused monitoring. Of the MPAs with oceanographic observations, observations of DO and/or pH in addition to temperature data were available in 44.0% of the seasons from 2010 to 2020, with most records occurring in the summer. Although observations of multiple stressors were available for the majority of MPAs, our ability to use the data to assess relative exposure across the network was limited, most often because there were too few observations to confidently characterize an MPA's exposure or because temporal, methodological, or depth differences limited our confidence in comparing across MPAs. Thus in the following analyses, we were able to directly evaluate and compare 5–19 MPAs depending on the specific analysis.

How does exposure to the dual stressors of hypoxia and anomalously high temperatures vary across California's MPAs?

We identified 19 MPAs with 50 or more paired observations of temperature and DO taken during multiple seasons (Supplementary Figure S1), including 9 MPAs with 350 observations or more (Figure 2). The presence of sublethal hypoxic conditions (≤ 140 $\mu\text{mol/kg}$) in these MPAs varied. DO never dropped below this threshold for two of the nine MPAs with 350+ observations [South Humboldt Bay State Marine Resource Management Area (SMRMA) and Long Point State Marine Reserve (SMR)], whereas in Point Arena SMCA, 21.37% of observations fell below this sublethal hypoxic threshold. Of these nine MPAs, only Morro Bay SMRMA ever dropped below the threshold for lethal hypoxia (61 $\mu\text{mol/kg}$), and it did so for $<1\%$ of all measurements. Because these dual stressor profiles

differed in exact timing and duration, some of the variability may reflect interannual variability. However, all of the MPAs included data from multiple seasons, many year-round, and thus represent seasonal variability.

At most MPAs, hypoxia was accompanied by colder water that was detected most often in spring and summer, suggesting an upwelled source [although see Bograd *et al.* (2009) for details on upwelling phenology]. Only Morro Bay SMRMA, an estuarine MPA, was exposed to sublethal hypoxia at temperatures in the middle of its temperature range, rather than the cold end of its temperature range. At another estuarine MPA, South Humboldt Bay SMRMA, the lowest DO concentrations were also associated with relatively warm temperatures, although those DO concentrations never met the threshold for hypoxia. Thus, while oceanic MPAs appear to most often experience low DO in combination with cold waters, estuarine MPAs appear at a higher risk of exposure to the combination of warm temperatures and hypoxia.

How does exposure to hypoxia, low pH, and MHWs vary across California's MPAs?

Only nine MPAs had high frequency (daily–weekly), continuous (minimum 6-month period), simultaneous monitoring of temperature, DO, and pH (Figure 3). The majority of these MPAs were monitored continuously for 1–2 years in the 2018–2020 period (Kroeker *et al.*, 2023), although Kashtayit SMCA was monitored from 2015 to 2016 (Supplementary Table S2). The percentage of time that oceanographic conditions in each MPA surpassed thresholds for single stressors and multiple stressors varied widely, from 0 to 75.0% of the time for single stressors and 0–25.3% of the time for multiple stressors (Table 1). MPAs in upwelling-dominated areas such as the northern half of the state from 37° to 42° latitude (Bograd *et al.*, 2009) exhibited the highest occurrence of multiple stressor conditions, usually in the form of low pH and hypoxia occurring with cooler waters. For instance, at Point Arena SMR, simultaneous low pH (<7.75) + hypoxic conditions (<140 $\mu\text{mol/kg}$) occurred 25.2% of the time, while in MPAs south of Monterey Bay, combined low pH and hypoxic conditions occurred $<4\%$ of the time.

Conversely, the four MPAs assessed in southern California encountered higher frequencies of warm temperature anomalies than the rest of the network, encompassing 15.2–74.3% of temperature observations across these MPAs. These elevated levels of temperature stress were not a feature of the 2014–2016 MHWs but rather characterized temperatures after the conclusion of this period, as monitoring for three of the four southern California MPAs began in 2018. However, most of the southern California MPAs experienced less stressful DO and pH conditions than those in other regions. Indeed, two of these MPAs (Long Point SMR and Kashtayit SMCA) were never exposed to either hypoxia or pH stress, although Abalone Cove SMCA was exposed to sublethal hypoxia in nearly 20% of observations. Given the absence of a universally applicable pH or DO lethal and sublethal thresholds, we also conducted a sensitivity analysis to assess how relative exposure to single and multiple stressors changed across MPAs if these thresholds were adjusted. We found that patterns of relative exposure to single and multiple stressors were largely insensitive to changes in pH and DO thresholds (Supplementary Figure S2). MPAs exposed to the highest and lowest levels of pH stress, hypoxia, and combinations of these

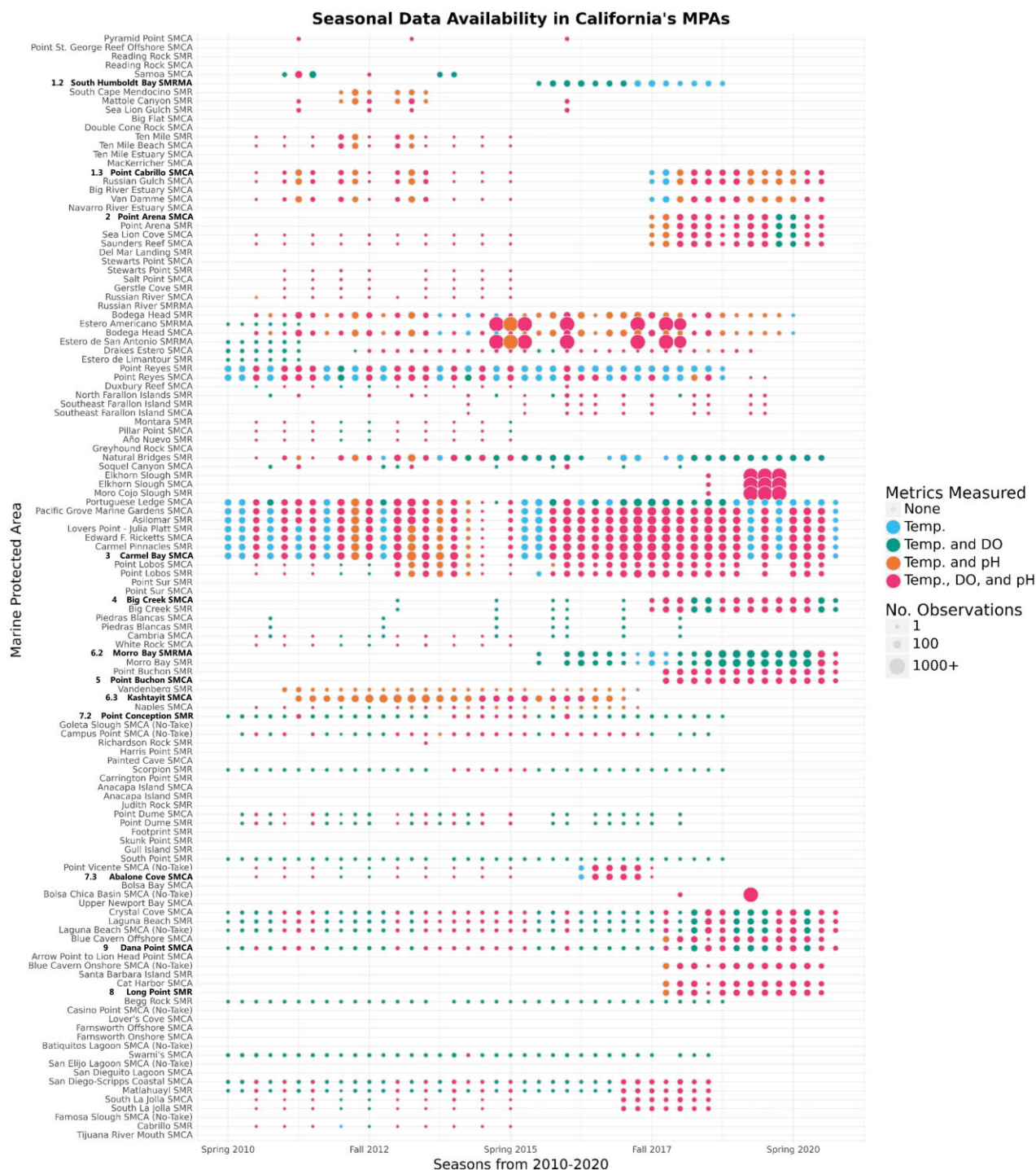


Figure 1. Oceanographic data availability for California's 124 MPAs. Each point represents the number of oceanographic observations available within 10 km of each MPA and the parameters measured, binned into spring (March–May), summer (June–Aug), fall (Sept–Nov), and winter (Dec–Feb) seasons starting in spring 2010 and going through fall 2020. MPAs are listed from northernmost to southernmost and either take the form of SMCA, SMR, or SMRMAs. Bolded MPAs correspond to the MPAs shown in Figures 2 and 3.

stressors remained the highest and lowest even when thresholds were adjusted higher or lower.

Did MPA exposure to low DO change during the 2014–2016 marine heatwave?

We identified five MPAs in southern California with at least 40 paired DO and temperature measurements prior to

the 2014–2016 MHWs period, during it, and after it that were all derived from similar methods, months, and depths. Most of the data that were comparable across time periods for these MPAs came from CalCOFI (<https://calcofi.com/>) oceanographic cruises that have occurred regularly for several decades. Because CalCOFI cruises sample multiple times a year, these measurements also represent seasonal variability. While the mean temperature increased reliably during the

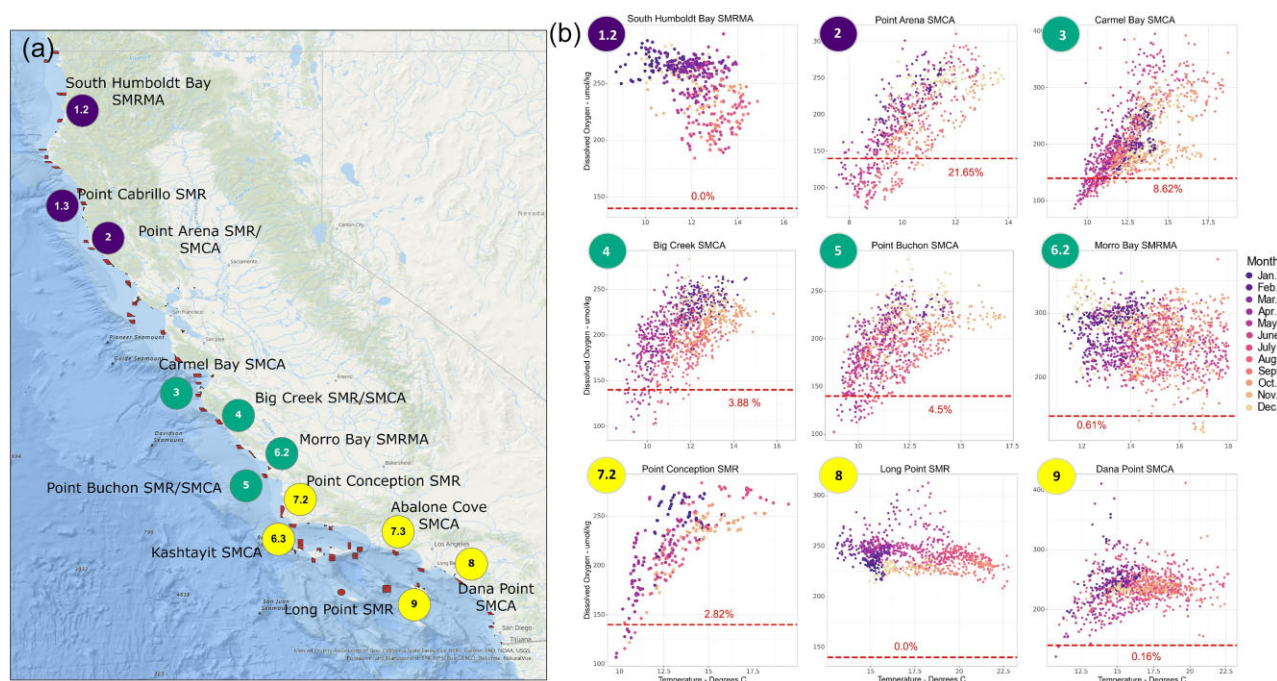


Figure 2. (a) Map of MPAs that had 350+ paired temperature and DO measurements during 2010–2020. MPAs labelled with a “2” or “3” indicate MPAs that were used either in the analysis for Figure 2 or in the analysis for Figure 3, respectively, whereas round numbers indicate MPAs used in both analyses. Dark red polygons indicate locations of all MPAs in the California network. (b) Temperature and DO property–property plots for nine MPAs in California. Point colour represents month of the year in which the measurement was taken. The red dashed line represents a sublethal hypoxia threshold of 140 $\mu\text{mol/kg}$ and red text indicates the percentage of all observations that fell below this threshold.

2014–2016 MHWs compared to pre-2014 for all five MPAs, we did not see consistent differences in mean DO during the MHWs (Supplementary Figure S3). Mean DO concentrations remained similar across the three time periods for all five southern California MPAs.

Although mean DO did not vary substantially, the exposure to low DO did. In all five MPAs, the 5th percentile of DO was higher during the 2014–2016 MHWs period than the 2010–2013 period and at four of the MPAs, the 5th percentile DO then dropped again after 2014–2016 MHW concluded (Figure 4). On average, the 5th percentile of DO was about 22.16 $\mu\text{mol/kg}$ higher from 2014 to 2016 than before 2014 for these MPAs. Thus, while these MPAs were exposed to increased temperature stress during the 2014–2016 MHW period, at depths of 8–23 m they may have simultaneously experienced less severe hypoxia stress than pre-2014 and post-2016.

Did spatial patterns of relative exposure to low DO and low pH values remain persistent across MPAs during 2018–2020?

A key question in understanding differential exposure to multiple stressors in MPAs is whether spatial patterns of exposure persist from year to year (Chan *et al.*, 2017). We were limited in our ability to fully investigate this question due to spatio-temporal patchiness in data availability. However, we identified six datasets from 2018 to 2020 and spanning multiple biogeographic regions of California’s coastline that had daily or near-daily measurements of DO and pH that were sufficiently continuous to allow for interannual comparison of the potential exposure to hypoxic and low pH conditions at these MPAs across years. In particular, we focused on the

monthly 5th percentile of DO and pH across MPAs and time (Figure 5).

We found that, in general, the relative exposure among these MPAs to stressful DO and pH conditions had seasonality and was fairly stable across years. Exposure to low DO and pH conditions was similar across all MPAs and regions during the fall and winter months. In contrast, exposure separated by region during the spring and summer upwelling months, with a general pattern of northern California MPAs having the lowest 5th percentile of DO and pH. MPAs in central California had less exposure (higher 5th percentile values) but still often crossed sublethal thresholds, while those in southern California remained well above these sublethal thresholds. There were, however, exceptions to these general patterns. For instance, in Spring 2018, the 5th percentile of pH observations in MPAs in central California were lower than those in northern California MPAs, possibly due to differences in the timing of the upwelling season. Additionally, in spring 2019, one MPA in southern California had lower DO concentrations than MPAs in northern and central California. These regional patterns seemed more distinct and consistent for DO than pH, but even for DO, for several months in spring 2020, the 5th percentile of monthly DO was quite similar between central and northern California MPAs.

Discussion

In this study, we leveraged a novel oceanographic synthesis dataset to understand differential exposure to combinations of potential stressors across California’s MPA network. We focus on assessing the prevalence of anomalous or particularly stressful environmental conditions, although it is worth noting that more subtle, long-term shift in the mean values

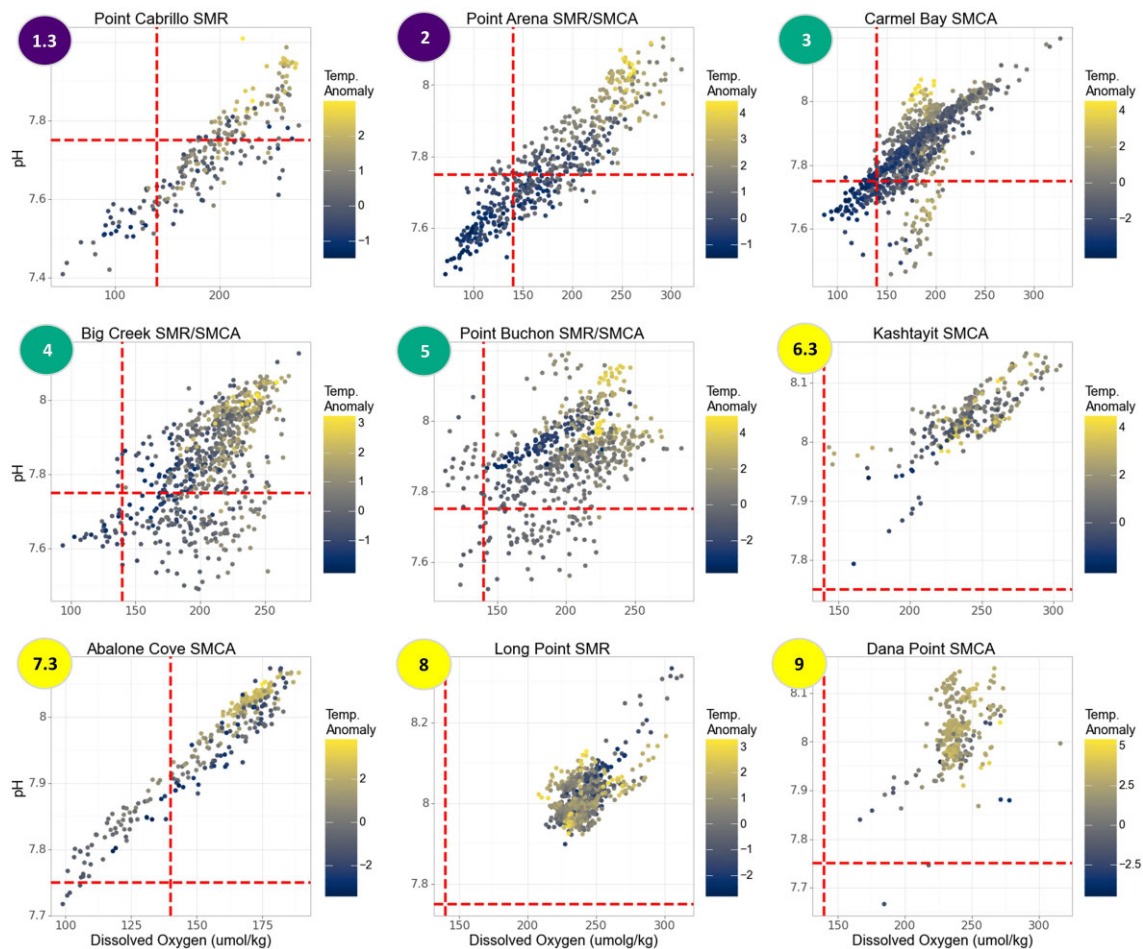


Figure 3. Daily observations of temperature, DO, and pH stress in nine MPAs spanning California's MPA network. The x-axis indicates DO concentrations (with a vertical dashed line representing a DO stress threshold of 140 $\mu\text{mol/kg}$), the y-axis pH levels (with a horizontal dashed line representing a pH stress threshold of 7.75), and the colour of the points the temperature anomaly compared to the average temperature on that day over the last 22–25 years (depending on site). The location of each MPA is indicated by the circled number at the upper left of each graph and correspond to the map in Figure 2a.

of temperature, DO, and pH will also shape species responses to climate change. We found that even in a system as heavily studied as coastal California, publicly available data have high spatial and temporal patchiness that limits how it can be used to systematically assess exposure to stressful ocean conditions. When the data did allow for a comparison of exposure across MPAs, we found high variability in the exposure to both single and multiple potential stressors. The most common combination of stressors came in the form of combined hypoxic and low pH conditions paired with cool temperatures, especially in the central and northern parts of the network. Conversely, while many MPAs in southern California had high exposure to potential temperature stress, those MPAs were less likely to be exposed to sublethal levels of hypoxia and low pH. Furthermore, temperature stress could be temporally decoupled from other potential stressors, as evidenced by the reduced potential exposure to hypoxia in southern California during the historic 2014–2016 MHWs. Finally, we found that the relative intensity of exposure to low DO and low pH was fairly stable across different parts of California and across years when measured in the same season. These findings have important implications for ecological communities living within California's MPAs as well as the human commu-

nities that rely on marine resources associated with MPAs and the managers and policymakers regulating these MPAs. Coupled with much needed studies on the links between changing ocean conditions, MPA effectiveness, and coastal communities, the findings from this study contribute to the ongoing discourse regarding the utility of MPAs as conservation tools under climate change.

These results both challenge and confirm existing hypotheses surrounding climate-smart MPAs. For instance, the high spatial variability in the exposure to both single and multiple stressors across California's MPA network provides evidence that networks spread the risk of exposure to climate stress in both single and multiple stressor dimensions. This insight supports the idea that, from a biophysical perspective, climate-smart MPAs may benefit from a network structure that provides an oceanographic portfolio effect, reducing negative impacts of extreme climate events (McLeod *et al.*, 2009; Jones *et al.*, 2016; Fredston-Hermann *et al.*, 2018). Thus, while including a diversity of habitats is considered a guiding principle when creating MPA networks (Young and Carr, 2015), an additional guiding principle may be to include sites that experience different modes of present and future climate stress across the region (McLeod *et al.*, 2009; Jones *et al.*, 2016).

Table 1. Frequency of exposure to single stressor and multiple stressor conditions within nine California MPAs over 1–4 years of continuous monitoring of temperature, DO, and pH (Supplementary Table S2).

MPA cluster	Region	Seasons	% Single stressor	% Multiple stressor
Point Cabrillo SMCA/SMR	North	Summer, Fall	Temp = 11.1% pH = 41.2% DO = 0%	DO + pH = 14.1% Temp + pH = 1.9%
Point Arena SMCA/SMR	North-Central	Summer	Temp = 22.2% pH = 20.7% DO = 1.5%	DO + pH = 25.2% Temp + pH = 0.7%
Carmel Bay SMCA	Central	Year round	Temp = 6.0% pH = 9.9% DO = 2.2%	DO + pH = 9.1% Temp + pH = 2.2%
Big Creek SMCA/SMR	Central	Year Round	Temp = 8.7% pH = 23.1% DO = 0.6%	DO + pH = 3.9%
Point Buchon SMCA/SMR	Central	Year round	Temp = 13.2% pH = 9.9% DO = 3.2%	DO + pH = 0.9% Temp + pH = 0.2%
Kashtayit SMCA	Southern	Year round	Temp = 44.5% pH = 0% DO = 0%	0%
Abalone Cove SMCA	Southern	Year round	Temp = 32.4% pH = 0% DO = 19.0%	DO + pH = 1.3%
Long Point SMR	Southern Channel Islands	Year round	Temp = 15.2% pH = 0% DO = 0%	0%
Dana Point SMCA	Southern	Winter, Spring, Fall	Temp = 74.2% pH = 0.5% DO = 0%	Temp + pH = 0.5%

For temperature, stressful conditions were defined exceeding the 90th percentile of a roughly 25-year temperature climatology, for dissolved oxygen daily mean $\text{DO} \leq 140 \mu\text{mol/kg}$, and for pH daily mean $\text{pH} \leq 7.75$.

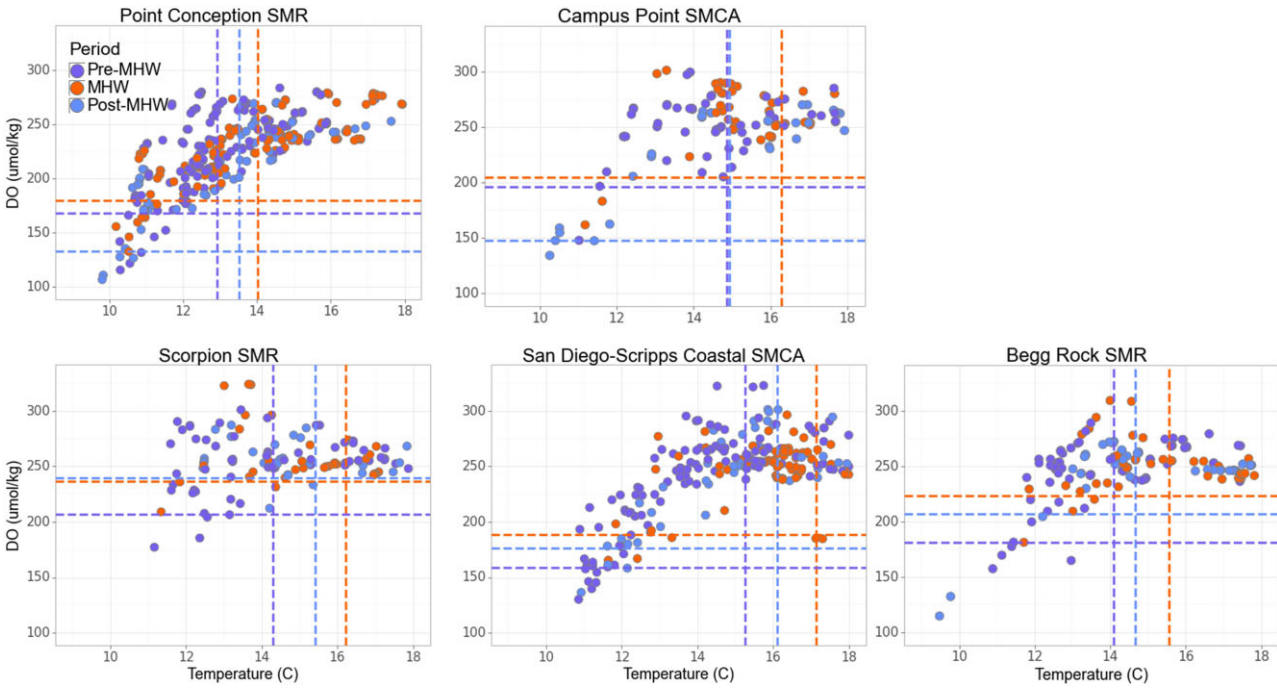


Figure 4. Temperature vs. DO property–property plots for five southern California MPAs that had comparable paired temperature and DO measurements across the pre-MHW period (2010–2013, purple), the MHW period (2014–2016, yellow), and post-MHW period (2017–2020, teal). Dashed vertical lines show mean temperature for each period and dashed horizontal lines show the 5th percentile of DO for each period.

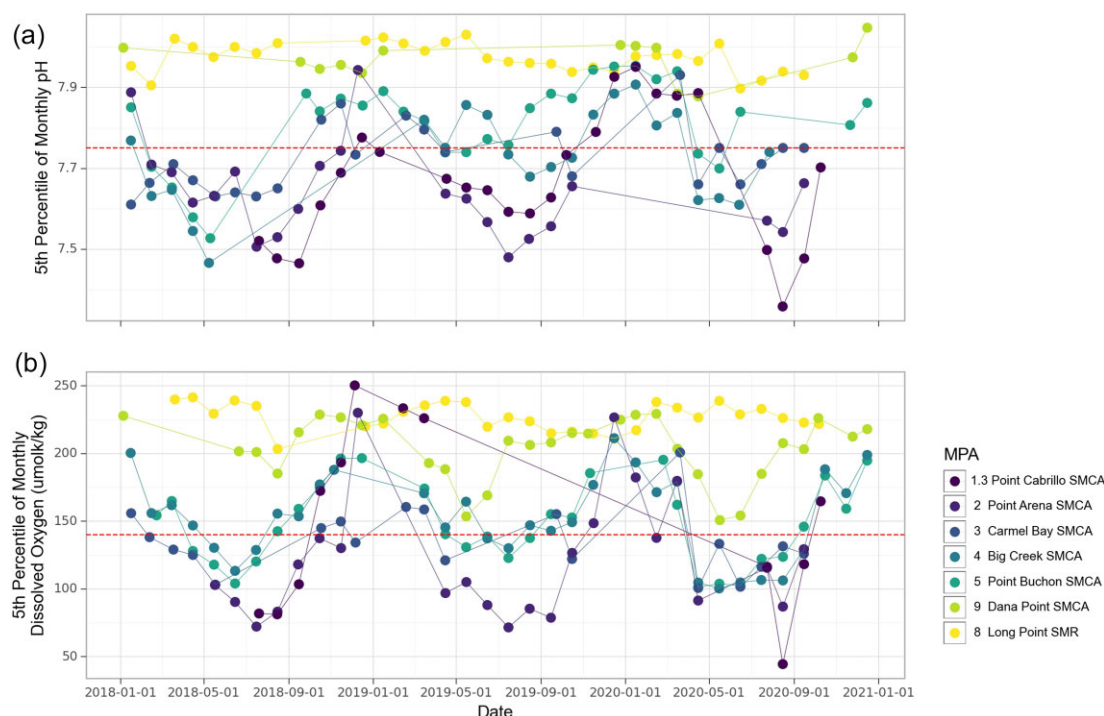


Figure 5. The monthly 5th percentile of pH (a) and DO (b) over the course of 3 years for 6–7 sites along the California coast based on daily monitoring at each site. Each colour represents a different MPA along the coast of California and legend numbers correspond with MPAs in Figure 2a. Gaps in time series for each site are related to sensor maintenance and weather conditions. Red dotted lines on each graph represent the sublethal threshold (pH 7.75, DO 140 umol/kg).

Conversely, an increasingly popular idea in the literature regarding siting new MPAs is that the efficacy of new MPAs may be maximized if they are sited in areas with low rates of warming (Arafteh-Dalmau *et al.*, 2021; Brito-Morales *et al.*, 2022). For instance, Brito-Morales *et al.*, (2022) identified areas of minimal temperature change to prioritize areas for new spatial protections on the high seas. However, this analysis supports Bruno *et al.* (2018) that siting MPAs to minimize the impacts of a single stressor may increase exposure to a different stressor. For instance, in California, placing MPAs in areas of reduced temperature stress would mean preferentially targeting MPAs for northern and central California over southern California, which would increase the likelihood of exposure to hypoxia and low pH in those MPAs. Further, while Brito-Morales (2022) points out temperature can be reliably related to other potential stressors such as pH and DO in the open ocean, in coastal areas where MPAs are often sited, these relationships can be the opposite of the open ocean and vary on small spatial scales. For instance, in areas of coastal upwelling, it is well established that cold temperatures are often coupled with low concentrations of DO, whereas in the open ocean warm water is more likely to be paired with low DO (Barth *et al.*, 2007; Chavez and Messié, 2009; Checkley and Barth, 2009; Bruno *et al.*, 2018).

This multiple stressor lens applied to California's MPAs also raises interesting ideas about ecosystem-level responses to stress. For instance, as we show, in southern California MPAs, DO concentrations did not get as low during the 3 years associated with the 2014–2016 MHWs as they did in the 4 years prior and the 4 years after. Thus, different stressors can be temporally decoupled from one another. This situation creates the potential for differential impacts to different parts of

the ecosystems protected by MPAs during extreme climatic events. For instance, temperature sensitive taxa such as kelps are particularly vulnerable to heatwaves (Cavanaugh *et al.*, 2019; Rogers-Bennett and Catton, 2019; Filbee-Dexter *et al.*, 2020), while animals such as Dungeness crab often show positive responses to increased temperatures but negative responses to hypoxia (Sunday *et al.*, 2022). Theoretically then, in southern California MPAs where the 2014–2016 MHWs were accompanied by reduced hypoxia (Figure 4), kelps may have experienced negative physiological conditions but Dungeness crabs positive conditions. This study suggests that monitoring multiple stressors gives insights into the particular flavour of climatic change in different areas, which can then be paired with information about the physiological vulnerability of key species and, when available, information about human community responses to climate. This information could help managers, policy-makers, and the impacted public contextualize differential outcomes of the species and ecosystems protected by MPAs during MPA evaluation processes and may trigger critical adaptation responses (Carr *et al.*, 2011).

A final implication of this work regards the effective monitoring of MPA networks. Given the extensive monitoring done alongside California's MPA network and the millions of oceanographic observations we compiled, we were surprised at how limited we were by data availability to systematically assess exposure to multiple stressors across the network through time (Murray and Hee, 2019). Two major factors contributing to this are: (1) incomplete public data access and (2) spatio-temporal and methodological patchiness in monitoring. The oceanographic dataset leveraged for these analyses is limited to publicly available datasets and therefore cannot make use of important datasets that are held privately or dif-

difficult to access (Trice *et al.*, 2021; Gabelica *et al.*, 2022). This analysis emphasizes the value and necessity of changing scientific funding and practices to value standardized, efficient public data access (Hampton *et al.*, 2013; Ruegg *et al.*, 2014). Regarding the second factor, because many of the datasets were collected with their own goals in mind, data were taken in different habitats (subtidal vs. intertidal), depths, seasons, frequencies, and periods of time. This suite of confounding variables limited our ability to directly compare exposure to climate stress across the network and to answer critical questions such as the seasonal variability in regional modes of climate stress. A valuable role for state and federal funding agencies can be to coordinate oceanographic monitoring efforts across MPA networks to minimize these confounding variables and to fund systematic monitoring that fills in gaps in data collection (e.g. Carr *et al.*, 2011; Weisberg *et al.*, 2020).

Given recently agreed upon global, federal, and state biodiversity frameworks that call for the protection of 30% of the world's oceans by 2030, how to best site, monitor, and evaluate MPAs and MPA networks in the context of climate change will continue to be important questions for the marine conservation community (Newsom, 2020; Biden, 2021; UN Environment Program, 2021). Here, we assessed differential exposure to multiple potential stressors across California's MPA network and discussed how a multiple stressors approach to climate impacts on coastal oceans can be used to improve MPA siting, monitoring, and evaluation. We also pointed out the need to both improve data availability, as well as the types of data taken, to include more studies related to the impacts of climate stressors on human communities, and their associated impacts on MPAs. Many aspects of the marine socio-environmental world are and will continue to change, and we can capture more of the complexity and nuance of these changes when we explicitly monitor and consider multiple axes of climate stress.

Acknowledgements

We thank all the people involved in the making, maintaining, and publishing of the publicly available data used in this paper for their crucial contributions to this study and many others. Finally, we appreciate the efforts of the many undergraduate students, research assistants, and others that helped create the synthesis dataset that underpins this work.

Supplementary material

Supplementary material is available at the *ICESJMS Journal* online version of the manuscript.

Author contributions

SLH—Conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft; EGK—data curation, formal analysis, investigation, methodology, writing—review and editing; MZ—data curation, formal analysis, investigation, methodology, writing—review and editing; TMH—conceptualization, formal analysis, funding acquisition, investigation, methodology, supervision, writing—review and editing; BG—formal analysis, funding acquisition, writing—review and editing; ES—formal analysis, funding acquisition, writing—review and editing; AMR—data curation, formal analysis, writing—review and

editing; MW—data curation, formal analysis, writing—review and editing; AKS—funding acquisition, writing—review and editing; KK—conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, supervision, writing—review and editing.

Funding

We are grateful for financial support from the David and Lucile Packard Foundation, Lenfest Ocean Program, and NOAA Ocean Acidification Program that made this work possible.

Conflict of interest

The authors of this paper have no conflicts of interest to declare.

Data availability

The full dataset used here is available on the National Centers for Environmental Information website under the title Multistressor Observations of Coastal Hypoxia and Acidification (<https://doi.org/10.25921/2vve-fh39>). The code and data subset used in this paper are available in the Corresponding Author's Github account at: <https://github.com/sarahamilton-593/MPAClimateStress>.

References

- Arafeh-Dalmau, N., Brito-Morales, I., Schoeman, D. S., Possingham, H. P., Klein, C. J., and Richardson, A. J. 2021. Incorporating climate velocity into the design of climate-smart networks of marine protected areas. *Methods in Ecology and Evolution*, 12: 1969–1983.
- Ban, N. C., Adams, V. M., Almany, G. R., Ban, S., Cinner, J. E., McCook, L. J., Mills, M. *et al.* 2011. Designing, implementing and managing marine protected areas: emerging trends and opportunities for coral reef nations. *Journal of Experimental Marine Biology and Ecology*, 408: 21–31.
- Barth, J. A., Menge, B. A., Lubchenco, J., Chan, F., Bane, J. M., Kirincich, A. R., McManus, M. A. *et al.* 2007. Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. *Proceedings of the National Academy of Sciences*, 104: 3719–3724.
- Bates, A. E., Cooke, R. S. C., Duncan, M. I., Edgar, G. J., Bruno, J. F., Benedetti-Cecchi, L., Côté, I. M. *et al.* 2019. Climate resilience in marine protected areas and the “Protection Paradox”. *Biological Conservation*, 236: 305–314.
- Bednaršek, N., Ambrose, R., Calosi, P., Childers, R. K., Feely, R. A., Litvin, S. Y., Long, W. C. *et al.* 2021a. Synthesis of thresholds of ocean acidification impacts on decapods. *Frontiers in Marine Science*, 8. <https://www.frontiersin.org/article/10.3389/fmars.2021.651102> (last accessed 18 January 2022).
- Bednaršek, N., Calosi, P., Feely, R. A., Ambrose, R., Byrne, M., Chan, K. Y. K., Dupont, S. *et al.* 2021b. Synthesis of thresholds of ocean acidification impacts on echinoderms. *Frontiers in Marine Science*, 8. <https://www.frontiersin.org/articles/10.3389/fmars.2021.602601> (last accessed 29 September 2022).
- Biden, J. 2021. Executive Order 14008: Tackling the Climate Crisis at Home and Abroad. <https://www.govinfo.gov/content/pkg/FR-2021-02-01/pdf/2021-02177.pdf>. (last accessed 15 March 2023).
- Bograd, S. J., Schroeder, I., Sarkar, N., Qiu, X., Sydeman, W. J., and Schwing, F. B. 2009. Phenology of coastal upwelling in the California Current. *Geophysical Research Letters*, 36: L01602.
- Bond, N. A., Cronin, M. F., Freeland, H., and Mantua, N. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophysical Research Letters*, 42: 3414–3420.

- Brito-Morales, I.**, Schoeman, D. S., Everett, J. D., Klein, C. J., Dunn, D. C., García Molinos, J., Burrows, M. T. *et al.* 2022. Towards climate-smart, three-dimensional protected areas for biodiversity conservation in the high seas. *Nature Climate Change*, 12: 402–407.
- Bruno, J. F.**, Bates, A. E., Cacciapaglia, C., Pike, E. P., Amstrup, S. C., van Hooidonk, R., Henson, S. A. *et al.* 2018. Climate change threatens the world's marine protected areas. *Nature Climate Change*, 8: 499–503.
- Byrne, M.**, and Przeslawski, R. 2013. Multistressor impacts of warming and acidification of the ocean on marine invertebrates' life histories. *Integrative and Comparative Biology*, 53: 582–596.
- Carr, M. H.**, Robinson, S. P., Wahle, C., Davis, G., Kroll, S., Murray, S., Schumacker, E. J. *et al.* 2017. The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27: 6–29.
- Carr, M. H.**, Woodson, C. B., Cheriton, O. M., Malone, D., McManus, M. A., and Raimondi, P. T. 2011. Knowledge through partnerships: integrating marine protected area monitoring and ocean observing systems. *Frontiers in Ecology and the Environment*, 9: 342–350.
- Cavanaugh, K. C.**, Reed, D. C., Bell, T. W., Castorani, M. C. N., and Beas-Luna, R. 2019. Spatial variability in the resistance and resilience of giant kelp in southern and Baja California to a multiyear heatwave. *Frontiers in Marine Science*, 6: 413.
- Cavole, L. M.**, Demko, A. M., Diner, R. E., Giddings, A., Koester, I., Pagniello, C. M. L. S., Paulsen, M-L. *et al.* 2016. Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: winners, losers, and the future. *Oceanography*, 29: 273–285.
- CDFW.** 2022. MPA Decadal Management Review. <https://wildlife.ca.gov/Conservation/Marine/MPAs/Management/Decadal-Review> (last accessed 28 September 2022).
- Chan, F.**, Barth, J. A., Blanchette, C. A., Byrne, R. H., Chavez, F., Cheriton, O., Feely, R. A. *et al.* 2017. Persistent spatial structuring of coastal ocean acidification in the California Current System. *Scientific Reports*, 7: 2526.
- Chavez, F. P.**, and Messié, M. 2009. A comparison of eastern boundary upwelling ecosystems. *Progress in Oceanography*, 83: 80–96.
- Checkley, D. M.**, and Barth, J. A. 2009. Patterns and processes in the California Current System. *Progress in Oceanography*, 83: 49–64.
- Cheresh, J.**, and Fiechter, J. 2020. Physical and biogeochemical drivers of alongshore pH and oxygen variability in the California Current System. *Geophysical Research Letters*, 47: e2020GL089553.
- Cinner, J. E.**, McClanahan, T. R., Graham, N. A. J., Daw, T. M., Maina, J., Stead, S. M., Wamukota, A. *et al.* 2012. Vulnerability of coastal communities to key impacts of climate change on coral reef fisheries. *Global Environmental Change*, 22: 12–20.
- Crain, C. M.**, Kroeker, K., and Halpern, B. S. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, 11: 1304–1315.
- Curtis, D. L.**, and McGaw, I. J. 2008. A year in the life of a Dungeness crab: methodology for determining microhabitat conditions experienced by large decapod crustaceans in estuaries. *Journal of Zoology*, 274: 375–385.
- Curtis, D. L.**, and McGaw, I. J. 2012. Salinity and thermal preference of Dungeness crabs in the lab and in the field: effects of food availability and starvation. *Journal of Experimental Marine Biology and Ecology*, 413: 113–120.
- Di Lorenzo, E.**, and Mantua, N. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nature Climate Change*, 6: 1042–1047.
- Dickson, A. G.**, Sabine, C. L., and Christian, J. R. 2007. Guide to best practices for ocean CO₂ measurements. *PICES Special Publication*, 3: 1–191.
- Donham, E. M.**, Strobe, L. T., Hamilton, S. L., and Kroeker, K. J. 2022. Coupled changes in pH, temperature, and dissolved oxygen impact the physiology and ecology of herbivorous kelp forest grazers. *Global Change Biology*, 28: 3023–3039.
- Eisaguirre, J. H.**, Eisaguirre, J. M., Davis, K., Carlson, P. M., Gaines, S. D., and Caselle, J. E. 2020. Trophic redundancy and predator size class structure drive differences in kelp forest ecosystem dynamics. *Ecology*, 101: e02993.
- Feely, R. A.**, Sabine, C. L., Hernandez-Ayon, J. M., Ianson, D., and Hales, B. 2008. Evidence for upwelling of corrosive “acidified” water onto the continental shelf. *Science*, 320: 1490–1492.
- Filbee-Dexter, K.**, Wernberg, T., Grace, S. P., Thormar, J., Fredriksen, S., Narvaez, C. N., Feehan, C. J. *et al.* 2020. Marine heatwaves and the collapse of marginal North Atlantic kelp forests. *Scientific Reports*, 10: 13388.
- Fredston, A.**, Pinsky, M., Selden, R. L., Szuwalski, C., Thorson, J. T., Gaines, S. D., and Halpern, B. S. 2021. Range edges of North American marine species are tracking temperature over decades. *Global Change Biology*, 27: 3145–3156.
- Fredston-Hermann, A.**, Gaines, S. D., and Halpern, B. S. 2018. Biogeographic constraints to marine conservation in a changing climate. *Annals of the New York Academy of Sciences*, 1429: 5–17.
- Freedman, R. M.**, Brown, J. A., Caldow, C., and Caselle, J. E. 2020. Marine protected areas do not prevent marine heatwave-induced fish community structure changes in a temperate transition zone. *Scientific Reports*, 10: 21081.
- Gabelica, M.**, Bojčić, R., and Puljak, L. 2022. Many researchers were not compliant with their published data sharing statement: a mixed-methods study. *Journal of Clinical Epidemiology*, 150: 33–41.
- Gattuso, J-P.**, Epitalon, J-M., Lavigne, H., Orr, J., Gentili, B., Hagens, M., Hofmann, A. *et al.* 2022, July 4. seacarb: Seawater Carbonate Chemistry. <https://CRAN.R-project.org/package=seacarb> (last accessed 29 September 2022).
- Gentemann, C. L.**, Fewings, M. R., and García-Reyes, M. 2017. Satellite sea surface temperatures along the West Coast of the United States during the 2014–2016 northeast Pacific marine heat wave. *Geophysical Research Letters*, 44: 312–319.
- Gleason, M.**, Fox, E., Ashcraft, S., Vasques, J., Whiteman, E., Serpa, P., Saarman, E. *et al.* 2013. Designing a network of marine protected areas in California: achievements, costs, lessons learned, and challenges ahead. *Ocean & Coastal Management*, 74: 90–101.
- Grorud-Colvert, K.**, Sullivan-Stack, J., Roberts, C., Constant, V., Horta e Costa, B., Pike, E. P., Kingston, N. *et al.* 2021. The MPA guide: a framework to achieve global goals for the ocean. *Science*, 373: eabf0861.
- Gunderson, A. R.**, Armstrong, E. J., and Stillman, J. H. 2016. Multiple stressors in a changing world: the need for an improved perspective on physiological responses to the dynamic marine environment. *Annual Review of Marine Science*, 8: 357–378.
- Gurney, G. G.**, Cinner, J., Ban, N. C., Pressey, R. L., Pollnac, R., Campbell, S. J., Tasidjawa, S. *et al.* 2014. Poverty and protected areas: an evaluation of a marine integrated conservation and development project in Indonesia. *Global Environmental Change*, 26: 98–107.
- Hamilton, S. L.**, Saccomanno, V. R., Heady, W. N., Gehman, A. L., Lonhart, S. I., Beas-Luna, R., Francis, F. T. *et al.* 2021. Disease-driven mass mortality event leads to widespread extirpation and variable recovery potential of a marine predator across the eastern Pacific. *Proceedings of the Royal Society B: Biological Sciences*, 288: 20211195.
- Hampton, S. E.**, Strasser, C. A., Tewksbury, J. J., Gram, W. K., Budden, A. E., Batcheller, A. L., Duke, C. S. *et al.* 2013. Big data and the future of ecology. *Frontiers in Ecology and the Environment*, 11: 156–162.
- Hobday, A. J.**, Alexander, L. V., Perkins, S. E., Smale, D. A., Straub, S. C., Oliver, E. C. J., Benthuyzen, J. A. *et al.* 2016. A hierarchical approach to defining marine heatwaves. *Progress in Oceanography*, 141: 227–238.
- Hofmann, G. E.**, Evans, T. G., Kelly, M. W., Padilla-Gamiño, J. L., Blanchette, C. A., Washburn, L., Chan, F. *et al.* 2014. Exploring local adaptation and the ocean acidification seascape—studies in the Cal-

- ifornia Current large marine ecosystem. *Biogeosciences*, 11: 1053–1064.
- Howard, E. M., Penn, J. L., Frenzel, H., Seibel, B. A., Bianchi, D., Renault, L., Kessouri, F. *et al.* 2020. Climate-driven aerobic habitat loss in the California Current System. *Science Advances*, 6: eaay3188.
- Jones, K. R., Watson, J. E. M., Possingham, H. P., and Klein, C. J. 2016. Incorporating climate change into spatial conservation prioritisation: a review. *Biological Conservation*, 194: 121–130.
- Keller, A. A., Ciannelli, L., Wakefield, W. W., Simon, V., Barth, J. A., and Pierce, S. D. 2017. Species-specific responses of demersal fishes to near-bottom oxygen levels within the California Current large marine ecosystem. *Marine Ecology Progress Series*, 568: 151–173.
- Kennedy, E. G., Zulian, M., Hamilton, S. L., Hill, T. M., Delgado, M., Fish, C. R., Gaylord, B. *et al.* 2023a. Multistressor Observations of Coastal Hypoxia and Acidification (MOCHA) Synthesis. NOAA National Centers for Environmental Information. Dataset. <https://www.ncei.noaa.gov/archive/accession/0277984>. (last accessed 15 May 2023).
- Kennedy, E. G., Zulian, M., Hamilton, S. L., Hill, T. M., Delgado, M., Fish, C. R., Gaylord, B. *et al.* 2023b. A high-resolution synthesis dataset for multistressor analyses along the U.S. West Coast. *Earth System Science Data*, doi.org/10.5194/essd-2023-205, preprint: not peer reviewed.
- Kroeker, K. J., Donham, E. M., Vylet, K., Warren, J. K., Cheresh, J., Fiechter, J., Freiwald, J. *et al.* 2023. Exposure to extremes in multiple global change drivers: characterizing pH, dissolved oxygen and temperature variability in a dynamic, upwelling dominated ecosystem. *Limnology and Oceanography*, doi.org/10.1002/lno.12371, preprint: not peer reviewed. (last accessed 20 July 2023).
- Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S., Duarte, C. M. *et al.* 2013. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global Change Biology*, 19: 1884–1896.
- Kroeker, K. J., Sanford, E., Rose, J. M., Blanchette, C. A., Chan, F., Chavez, F. P., Gaylord, B. *et al.* 2016. Interacting environmental mosaics drive geographic variation in mussel performance and predation vulnerability. *Ecology Letters*, 19: 771–779.
- Low, N. H. N., Micheli, F., Aguilar, J. D., Arce, D. R., Boch, C. A., Bonilla, J. C., Bracamontes, M. A. *et al.* 2021. Variable coastal hypoxia exposure and drivers across the southern California Current. *Scientific Reports*, 11: 10929.
- Marine Region GIS. 2019, January 1. California Marine Protected Areas [ds582]: SDE Feature Class. California Department of Fish and Wildlife, Monterey, California. <https://map.dfg.ca.gov/metadata/ds0582.html>. (last accessed 18 September 2022).
- McCabe, R. M., Hickey, B. M., Kudela, R. M., Lefebvre, K. A., Adams, N. G., Bill, B. D., Gulland, F. M. D. *et al.* 2016. An unprecedented coastwide toxic algal bloom linked to anomalous ocean conditions. *Geophysical Research Letters*, 43: 10366–10376.
- McClatchie, S., Goericke, R., Cosgrove, R., Auad, G., and Vetter, R. 2010. Oxygen in the Southern California Bight: multidecadal trends and implications for demersal fisheries. *Geophysical Research Letters*, 37: 1–5.
- McGaw, I. J., and McMahon, B. R. 1996. Cardiovascular responses resulting from variation in external salinity in the Dungeness crab, cancer magister. *Physiological Zoology*, 69: 1384–1401.
- McHenry, J., Welch, H., Lester, S. E., and Saba, V. 2019. Projecting marine species range shifts from only temperature can mask climate vulnerability. *Global Change Biology*, 25: 4208–4221.
- McLeod, E., Salm, R., Green, A., and Almany, J. 2009. Designing marine protected area networks to address the impacts of climate change. *Frontiers in Ecology and the Environment*, 7: 362–370.
- McPherson, M. L., Finger, D. J. I., Houskeeper, H. F., Bell, T. W., Carr, M. H., Rogers-Bennett, L., and Kudela, R. M. 2021. Large-scale shift in the structure of a kelp forest ecosystem co-occurs with an epizootic and marine heatwave. *Communications Biology*, 4: 1–9.
- Meyer-Gutbrod, E., Kui, L., Miller, R., Nishimoto, M., Snook, L., and Love, M. 2021. Moving on up: vertical distribution shifts in rocky reef fish species during climate-driven decline in dissolved oxygen from 1995 to 2009. *Global Change Biology*, 27: 6280–6293.
- Micheli, F., Saenz-Arroyo, A., Greenley, A., Vazquez, L., Montes, J. A. E., Rossetto, M., and Leo, G. A. D. 2012. Evidence that marine reserves enhance resilience to climatic impacts. *PLoS One*, 7: e40832.
- Murray, S., and Hee, T. T. 2019. A rising tide: california's ongoing commitment to monitoring, managing and enforcing its marine protected areas. *Ocean & Coastal Management*, 182: 104920.
- Newsom, G. 2020. Cal. Executive Order No. N-82-20. Cal. Code Regs. tit. 14, § 757. <https://www.library.ca.gov/wp-content/uploads/GovernmentPublications/executive-order-proclamation/40-N-82-20.pdf>. (last accessed 5 April 2023).
- Osovitz, C. J., and Hofmann, G. E. 2005. Thermal history-dependent expression of the hsp70 gene in purple sea urchins: biogeographic patterns and the effect of temperature acclimation. *Journal of Experimental Marine Biology and Ecology*, 327: 134–143.
- Piatt, J. F., Parrish, J. K., Renner, H. M., Schoen, S. K., Jones, T. T., Arimitsu, M. L., Kuletz, K. J. *et al.* 2020. Extreme mortality and reproductive failure of common murrelets resulting from the northeast Pacific marine heatwave of 2014–2016. *PLoS One*, 15: e0226087.
- Przeslawski, R., Byrne, M., and Mellin, C. 2015. A review and meta-analysis of the effects of multiple abiotic stressors on marine embryos and larvae. *Global Change Biology*, 21: 2122–2140.
- Queirós, A. M., Talbot, E., Beaumont, N. J., Somerfield, P. J., Kay, S., Pascoe, C., Dedman, S. *et al.* 2021. Bright spots as climate-smart marine spatial planning tools for conservation and blue growth. *Global Change Biology*, 27: 5514–5531.
- Roberts, C. M., O'Leary, B. C., McCauley, D. J., Cury, P. M., Duarte, C. M., Lubchenco, J., Pauly, D. *et al.* 2017. Marine reserves can mitigate and promote adaptation to climate change. *Proceedings of the National Academy of Sciences*, 114: 6167–6175.
- Rogers-Bennett, L., and Catton, C. A. 2019. Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. *Scientific Reports*, 9: 15050.
- Rüegg, J., Gries, C., Bond-Lamberty, B., Bowen, G. J., Felzer, B. S., McIntyre, N. E., Soranno, P. A. *et al.* 2014. Completing the data life cycle: using information management in macrosystems ecology research. *Frontiers in Ecology and the Environment*, 12: 24–30.
- Sampaio, E., Santos, C., Rosa, I. C., Ferreira, V., Pörtner, H.-O., Duarte, C. M., Levin, L. A. *et al.* 2021. Impacts of hypoxic events surpass those of future ocean warming and acidification. *Nature Ecology & Evolution*, 5: 311–321.
- Sanford, E., Sones, J. L., García-Reyes, M., Goddard, J. H. R., and Largier, J. L. 2019. Widespread shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves. *Scientific Reports*, 9: 4216.
- Schmidt, D. N., Pieraccini, M., and Evans, L. 2022. Marine protected areas in the context of climate change: key challenges for coastal social-ecological systems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 377: 20210131.
- Somero, G. N. 2005. Linking biogeography to physiology: evolutionary and acclimatory adjustments of thermal limits. *Frontiers in Zoology*, 2: 1.
- Somero, G. N., Beers, J. M., Chan, F., Hill, T. M., Klinger, T., and Litvin, S. Y. 2016. What changes in the carbonate system, oxygen, and temperature portend for the northeastern Pacific Ocean: a physiological perspective. *Bioscience*, 66: 14–26.
- Sunday, J. M., Howard, E., Siedlecki, S., Pilcher, D. J., Deutsch, C., MacCready, P., Newton, J. *et al.* 2022. Biological sensitivities to high-resolution climate change projections in the California current marine ecosystem. *Global Change Biology*, <https://onlinelibrary.wiley.com/doi/full/10.1111/gcb.16317>. (last accessed 29 July 2022).
- Sunday, J. M., Pecl, G. T., Frusher, S., Hobday, A. J., Hill, N., Holbrook, N. J., Edgar, G. J. *et al.* 2015. Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, 18: 944–953.

- Trice, A., Robbins, C., Philip, N., and Rumsey, M. 2021. Challenges and Opportunities for Ocean Data to Advance Conservation and Management. Ocean Conservancy, Washington, D.C.
- UN Environment Program. 2021. First draft of the post-2020 global biodiversity framework. <https://www.cbd.int/doc/c/abb5/591f/2e46096d3f0330b08ce87a45/wg2020-03-03-en.pdf>. (last accessed 4 April 2023).
- Vaquer-Sunyer, R., and Duarte, C. M. 2008. Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences*, 105: 15452–15457.
- Weisberg, S., Chan, F., Barry, J., Boehm, A., NOAA, S. B., Cooley, S., Feely, R. *et al.* 2020. Enhancing California's Ocean Acidification and Hypoxia Monitoring Network: Recommendations to the Ocean Protection Council from the California Ocean Acidification and Hypoxia Science Task Force. California Ocean Science Trust, Sacramento, CA.
- Whitney, C. K., and Ban, N. C. 2019. Barriers and opportunities for social-ecological adaptation to climate change in coastal British Columbia. *Ocean & Coastal Management*, 179: 104808.
- Woodson, C. B., Micheli, F., Boch, C., Al-Najjar, M., Espinoza, A., Hernandez, A., Vázquez-Vera, L. *et al.* 2019. Harnessing marine microclimates for climate change adaptation and marine conservation. *Conservation Letters*, 12: e12609.
- Young, M., and Carr, M. 2015. Assessment of habitat representation across a network of marine protected areas with implications for the spatial design of monitoring. *PLoS One*, 10: e0116200.

Handling editor: Marta Coll