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LETTER

Multi-Trophic Level Responses to Marine Heatwave Disturbances in the California Current Ecosystem

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ABSTRACT

Marine heatwaves (MHWs) caused by multiple phenomena with days to months duration are increasingly common disturbances in ocean ecosystems. We investigated the impacts of MHWs on pelagic communities using spatially resolved time-series of multiple trophic levels from the Southern California Current Ecosystem. Indices of phytoplankton biomass mostly declined during MHWs because of reduced nutrient supply (excepting *Prochlorococcus*) and were generally more sensitive to marine heatwave intensity than duration. By contrast, mesozooplankton (as estimated by zooplankton displacement volume) were somewhat more strongly correlated with MHW duration than intensity. Zooplankton anomalies were also positively correlated with fucoxanthin (diatom) anomalies, highlighting possible bottom-up influences during MHWs. Mobile consumers (forage fish) showed more complex responses, with fish egg abundance declining during MHWs but not correlating with any MHW characteristics. Our findings provide partial evidence of how MHW characteristics can shape variable ecological responses due to the differing life spans and behaviours of different trophic levels.

1 | Introduction

Marine heatwaves (MHWs), defined as anomalous warming events lasting days or more, are increasingly common disturbances in marine ecosystems (Hobday et al. 2016, 2018; Oliver et al. 2018). These events result in significant consequences for marine ecosystems, from coral bleaching and mass kelp mortality to altered phytoplankton production patterns and decreased fisheries yield (Cheung and Frölicher 2020). While much research has focused on extended, high-intensity marine heatwaves, the impact of shorter and less intensive MHWs is likely also substantial. MHW impacts extend across multiple trophic levels and impact important ecosystem services (Smale et al. 2019). Because of the possible irreversible effects of MHWs on marine organisms and ecosystems (Frölicher, Fischer, and Gruber 2018), they have emerged as a pressing global concern (Smith et al. 2022).

MHW effects on pelagic ecosystems are numerous and variable across regions, with intersecting impacts of disruptions in nutrient supply, stratification, and direct physiological effects of altered temperature. During MHWs, phytoplankton biomass, as evidenced by chlorophyll concentration, tends to decrease in the tropics and mid-latitude regions, while increasing in higher latitudes (Le Grix et al. 2021; Noh, Lim, and Kug 2022). Size distributions of phytoplankton tend to shift towards smaller size classes (Wyatt, Resplandy, and Marchetti 2022; Zhan et al. 2023). The aforementioned changes are likely linked to altered mixed layer depth and nitrate concentrations (Wyatt, Resplandy, and Marchetti 2022; Hayashida, Matear, and Strutton 2020). In

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addition to changes in size structure, MHWs may favour the proliferation of warm-water species (Peterson et al. 2017; Lilly and Ohman 2021). These changes often reverberate to higher trophic levels, driving altered zooplankton community structure, reduced overall abundance (Evans et al. 2020; Batten et al. 2022) and shifts in size structure (Robertson and Bjorkstedt 2020). Some zooplankton species also exhibit poleward shifts in their geographic distributions during MHWs (Evans et al. 2020; Peterson et al. 2017; Sanford et al. 2019; Lilly and Ohman 2021). Additionally, MHWs can enhance a top-down influence on trophic interactions by enhancing zooplankton metabolism and grazing pressure (Batten et al. 2022).

While a handful of studies have examined the impacts of specific marine heatwaves across trophic levels (Arafeh-Dalmau et al. 2019; Jiménez-Quiroz et al. 2019; Michaud, Reed, and Miller 2022; Jones et al. 2018; Rogers-Bennett and Catton 2019), generalising results across different regions and disturbance regimes remains challenging. Global-scale studies are typically based on a limited set of observed biological variables (mostly satellite-derived sea-surface colour) or model simulations (Le Grix et al. 2021; Noh, Lim, and Kug 2022; Hayashida, Matear, and Strutton 2020). Notably, such studies show that quantifiable characteristics of MHWs (e.g., maximum intensity and duration) influence biotic responses at the base of the food web (Noh, Lim, and Kug 2022). Whether and how such disturbance responses translate to higher trophic levels remains uncertain due to the inability to quantify higher trophic level dynamics from satellites and a paucity of time series suitable for addressing biotic responses to marine heatwaves with varying characteristics. Quantitative understanding of trophic responses is necessary, given research from other ecosystems showing that heatwave duration can increase the probability of crossing ecosystem tipping points (van der Bolt et al. 2018).

Long-term, spatially resolved time series are invaluable for quantitatively relating biotic responses to MHW disturbances. Here, we utilise results from the joint CalCOFI (California Cooperative Oceanic Fisheries Investigations) and CCE-LTER (California Current Ecosystem, Long-Term Ecological Research) time series (Bograd, Checkley, and Wooster 2003; Ohman and Venrick 2003) to investigate the importance of MHW intensity and duration across at least three trophic levels (phytoplankton to forage fish). The Southern California Current System (SCCS) is an excellent study region for such questions because it encompasses a gradient of trophic states from a rich, coastal upwelling domain to a low-productivity oligotrophic region; it includes a biogeographic boundary region, and it is the site of one of the longest running plankton time series (CalCOFI). The SCCS also experiences MHWs with distinctly different types of physical forcing (e.g., Lilly et al. 2019), including El Niño-driven events (Lilly and Ohman 2021; Lynn and Bograd 2002), extended extratropical MHWs driven by North Pacific atmospheric patterns (Di Lorenzo and Mantua 2016; Amaya et al. 2020), and shorter events driven by ephemeral atmospheric phenomena. For instance, the recent extratropical MHWs in 2014–2015 led to decreased chlorophyll and net primary production (Kahru, Jacox, and Ohman 2018; Kelly et al. 2018; Morrow et al. 2018), a shift towards smaller phytoplankton (Landry et al. 2024b) and compression of the upwelling-influenced coastal domain (McClatchie et al. 2016; Santora et al. 2020). The extreme prolonged event also induced substantial shifts in mesozooplankton and ichthyoplankton communities that were qualitatively similar to the shift towards subtropical species experienced during El Niño events, although the mechanistic drivers were likely different (Lilly and Ohman 2018, 2021; Thompson et al. 2022). At higher trophic levels, the 2014–2015 MHW led to northward shifts and reduced abundances of sardine, jack mackerel and anchovy eggs (Leising et al. 2015; McClatchie et al. 2016; Auth et al. 2018) and unprecedented numbers of whale entanglements nearshore (Santora et al. 2020). Despite these demonstrated impacts, a mechanistic framework for predicting biotic responses to varying types of MHW disturbances does not exist.

MHW intensity and duration are suggested to be essential factors in determining the magnitude of chlorophyll responses to MHWs (Noh, Lim, and Kug 2022). Therefore, we investigate their effects across multiple trophic levels of plankton communities. We hypothesise that the relative importance of disturbance intensity and duration varies with the organism life span. Specifically, we predict that short-lived microbes (phytoplankton and bacteria) are more sensitive to disturbance intensity (defined as the magnitude of the temperature anomaly relative to the long-term mean) while longer-lived metazoans (e.g., zooplankton and fish) are more sensitive to MHW duration (defined as the length of time that the surface temperature anomaly exceeds the 90th percentile, Hobday et al. 2016).

2 | Materials and Methods

2.1 | Sea Surface Temperature (SST)

Daily SST with 0.25° spatial resolution from 1982 to 2021 was obtained from the AVHRR optimally interpolated dataset (Reynolds et al. 2007, https://podaac.jpl.nasa.gov/dataset/AVHRR_OI-NCEI-L4-GLOB-v2.0). We focus on the region of 29–35.5° N, 117–125° W.

2.2 | Satellite Chlorophyll *a* Concentration

A multi-satellite merged 4-km surface chlorophyll *a* concentration (Satellite Chla) dataset encompassing estimates from 1996 to 2020 (https://spg-satdata.ucsd.edu/CC4km/) was used for surface Chla in the SCCS (Kahru et al. 2012, 2015; Kahru, Jacox, and Ohman 2018). It covers a grid from 30–35.5° N to 117–125 °W (Table S1).

2.3 | CalCOFI In Situ Sampling Data

In situ data are available from ca. quarterly CalCOFI cruises in the California Current System, and we focus on the region south of line 76.7 (29–36° N, 117–125° W) because this region has consistent measurements across trophic levels (Figure 1a). Data collected from 1982 onward were utilised, including nitrate, picoplankton and bacteria abundance, size-fractionated Chla concentration, vertically-integrated Chla, vertically integrated primary production, phytoplankton taxon-specific pigments from high-performance liquid-chromatography (HPLC) analysis, zooplankton displacement volume, zooplankton

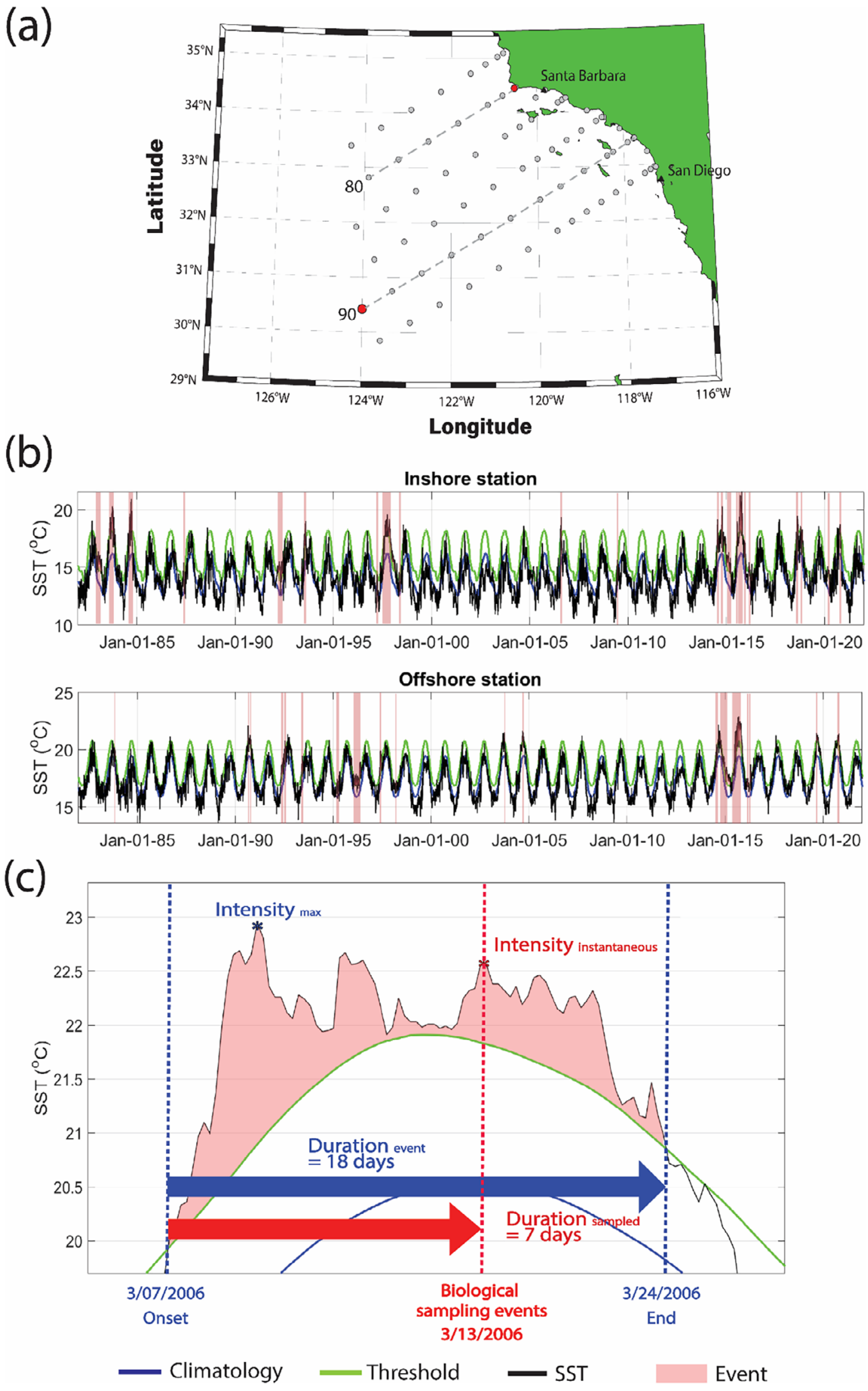


FIGURE 1 | (a) CalCOFI sampling region (b) the detection of MHW occurrence at the inshore and offshore station from 1982 to 2021 and (c) our definition of MHW characteristics. In (a), both grey and red points indicate the sampling stations for biological data, while red points are two stations (inshore/offshore) on the transect line 80 and 90 that are chosen to illustrate the detection of MHW occurrence; in (b), *y*-axis is the temperature (°C), *x*-axis is time. Black, blue and green lines indicate the observed SST, climatology means and the threshold of 90th percentile of the climatology mean, respectively. The marked red areas indicate MHW events. In (c), *y*-axis is temperature (°C), and the *x*-axis is time. Blue, green and black lines and red area are same as in (b). Blue dashed lines indicate the onset and end date of an MHW event, while red dash line indicates the date when a biological sampling event occurred. The blue asterisk indicates the maximum temperature anomaly during the event (intensity$_{\text{event}}$ = the SST anomaly at the time of intensity $_{\text{max}}$ divided by standard deviation of temperature at that location across the entire ca. 40-year timeseries). The red asterisk indicates the instantaneous temperature anomaly at the time that the biological sample was collected (intensity$_{\text{sampled}}$ = the SST anomaly at the time of intensity $_{\text{instantaneous}}$ divided by standard deviation of temperature). The blue arrow indicates the whole duration of each MHW event (duration$_{\text{event}}$), while the red arrow indicates the duration of the the MHW event at the time that the biological sample was collected (duration$_{\text{sampled}}$).

taxon-specific abundance and fish egg and larvae abundance. Sampling frequency and dataset duration are variable, but all datasets extend for more than a decade and are publicly available from the CalCOFI or CCE-LTER data repositories (Table S1).

2.3.1 | Nutrient

The phytoplankton macronutrients nitrate, nitrite, silicic acid, phosphate and ammonium are analysed in seawater using a colorimetric assay in which light absorbance is measured versus known standards. Nitracline depth, calculated as the shallowest depth at which nitrate equals or exceeds 1 μmol L^{-1}, was used as an index of nutrient availability.

2.3.2 | Size-Fractionated Chlorophyll *a* Concentration

Surface seawater samples were collected at depths <10 m using Niskin bottles and filtered through five different pore-size filters (Whatman GF/F; 1, 3 and 8-μm Nuclepore filters; and 20-μm Nitex filters), each in triplicate. Filters were extracted in 90% acetone in darkness at −18°C for 24 h, and then measured using the acidification method on a Turner Designs 10-AU fluorometer.

2.3.3 | Vertically Integrated Chlorophyll *a* Concentration and Primary Production

Vertically integrated chlorophyll *a* concentration (VerIntChla) was determined from depth-resolved Chla samples collected at three to eight depths spanning the euphotic zone, filtered onto GF/F filters, and processed as described above for surface size-fractionated Chla. Vertically integrated net primary production (VerIntPP) was determined using $H^{14}CO_3$- assimilation experiments. Water samples were taken each day shortly before local apparent noon at six incubation depths, ranging from 56% to 0.3% surface irradiance. Subsequently, triplicate samples (two light, one dark control) from each productivity sample depth were inoculated with ^{14}C-labelled $NaHCO_3$ and incubated at the same relative light levels from noon to dusk in a surface-seawater-cooled incubator. Samples were filtered onto Millipore HA filters, 0.5 mL of 10% HCl was added to remove HCO_3^- and ^{14}C was measured with a liquid scintillation counter.

2.3.4 | High Performance Liquid Chromatography (HPLC) Pigment Analysis

HPLC was used to quantify phytoplankton diagnostic pigments. Samples were filtered onto GF/F filters and frozen until shore-based analyses in either the Goericke Lab at UCSD (pre-2014) or the Horn Point Analytical Lab (post-2014). Data were quality controlled following Peloquin et al. (2013). Only divinyl Chla (unique to *Prochlorococcus*), hexanoyloxyfucoxanthin (diagnostic for prymnesiophytes) and fucoxanthin (diagnostic for diatoms) were used here. Based on comparative analyses of paired samples and inspection of the resulting time series, no differences were found between the concentrations of these pigments in the two analytical labs. Pigment concentrations were averaged from all samples collected in the upper 16 m.

2.3.5 | Picoplankton and Bacteria Abundances

Seawater subsamples (2 mL) were preserved with 100 μL of prefiltered 10% paraformaldehyde and flash-frozen in liquid nitrogen. A shore-based flow cytometer was used to quantify the abundance of heterotrophic bacteria, *Prochlorococcus*, *Synechococcus* and picoeukaryotes (Taylor and Landry 2018). Samples from the upper 10 m depth were considered in our analysis.

2.3.6 | Zooplankton Displacement Volume and Taxon-Specific Abundance

Zooplankton displacement volumes were measured from double oblique bongo net tows (0.71-m diameter, 0.505-mm mesh, 0.333 mm codend, towed to 210-m depth or within 10 m of the bottom at shallower stations; Kramer et al. 1972; Smith 1974; Smith and Richardson 1977; Thompson et al. 2017). Zooplankton abundances, on the other hand, are from vertical tows with a Planktonic Rate Processes in Oligotrophic Ocean Systems (PRPOOS) net (0.5-m diameter, 0.2-mm mesh, 210 m to surface along CalCOFI lines 80 and 90 (Figure 1a). Preserved samples were analysed by ZooScan (Gorsky et al. 2010; Ohman et al. 2012). Images were pre-classified using Deep Learning methods (*cf.* Ellen, Graff, and Ohman 2019), then 100% of the images were manually validated. The taxa analysed here include the copepod categories Calanoida, Eucalanidae, Harpacticoida, Poecilostomatoida and *Oithona*, as well as nauplii, euphausiids and thaliaceans (doliolids, salps and pyrosomes).

2.3.7 | Fish Egg and Larval Abundances

The Continuous Underway Fish-Egg Sampler (CUFES) collected pelagic fish eggs from ca. 3-m depth on a moving ship with 30-min resolution. Seawater was pumped to the concentrator, where the particles were concentrated and filtered into a cod end. Fish eggs were identified and counted at sea. In this study, we focus on the two dominant forage species, *Engraulis mordax* (northern anchovy; henceforth 'anchovy') and *Sardinops sagax* (Pacific sardine; henceforth 'sardine'). Data were integrated into daily resolution at each 0.25° grid cell.

Fish larvae were collected using the same oblique net tows that quantified zooplankton displacement volume and preserved in 1.8% formaldehyde buffered with sodium tetraborate. Samples were sorted and identified onshore (Moser 1996). As with fish eggs, we focused on sardine and anchovy larvae. To account for differences in tow depths and volume of water filtered, raw abundances for all taxa were multiplied by a standard haul factor (Smith and Richardson 1977). In cases where zooplankton displacement volume was very high, a fraction of the sample was sorted, and abundances were divided by this fraction.

2.4 | MHW Occurrence and Characteristics

MHW sampling events and their characteristics (duration and intensity) were defined following the methods in Hobday et al. (2016). A MHW is an anomalous warming event with sea temperatures exceeding the 90th percentile threshold of the daily local climatological mean (1982–2021) for ≥ 5 days. The package *m_mhw1.0* in MATLAB (Zhao and Marin 2019) was used for calculating daily SST anomalies and identifying MHW events for each satellite pixel.

Two key MHW characteristics (intensity and duration) were defined for each biological sampling event based on the modification of the definition in Hobday et al. (2016) (Figure 1c): $\text{duration}_{\text{sampled}}$ was defined as the length of time that the temperature anomaly had exceeded the 90th percentile threshold at the date of sampling; $\text{intensity}_{\text{sampled}}$, defined as the temperature anomaly (°C) at the sampling date divided by the standard deviation of SST at that location. Division by the standard deviation was done to avoid biases introduced by cross-shelf gradients in temperature variability. In the case of daily satellite-observed surface Chla for each MHW event, $\text{intensity}_{\text{event}}$ was defined as the maximum normalised SST anomaly during the events and $\text{duration}_{\text{event}}$ was the total duration of the MHW. $\text{Intensity}_{\text{event}}$ and $\text{duration}_{\text{event}}$ were then compared to the most negative surface Chla anomaly during the event.

2.5 | Plankton Abundance Anomaly

Continuous biological data (all datasets except abundances of zooplankton taxa, fish eggs and fish larvae) were $\log_{10}$-transformed and tested for normality following de Castro (2024). Because of the prevalence of zeroes, abundance data and nitracline data were normalised using a Yeo-Johnson transformation. For in situ observations, anomalies were calculated from seasonal means at each sampling location. For satellite-observed surface Chla anomalies were calculated relative to the daily climatological mean for each pixel, and the most negative Chla anomaly during a MHW event was used for comparison to MHW characteristics.

2.6 | Statistical Analyses

Significances of biological anomalies during MHW were assessed by *t*-test. Correlations between parameters were assessed using nonparametric Spearman's rank correlation analysis. Because no variables were measured without error, all regressions were calculated using type II (geometric mean) linear regression. All analyses were done in MATLAB except for Yeo-Johnson transformations, which were conducted in R.

3 | Results

3.1 | Oceanographic Conditions

We illustrate patterns in MHW occurrence by focusing on two stations—one at (34.45° N, 120.52° W; station 80–51) near a center of recurrent coastal upwelling and the other offshore (30.42° N, 124° W; station 90–120) in stratified, oligotrophic waters (Figure 1a). SST at the offshore station averaged 3.2°C higher, and temperatures were generally more stable than those at the coastal upwelling station (standard deviation of temperature anomalies were 0.45°C offshore and 0.66°C at the upwelling site). Before 2015, the inshore station experienced more MHW days and more intense MHW events compared to the offshore station, and MHWs were generally asynchronous between the two stations (Figure 1b). However, a significant MHW (the extratropical Northeast Pacific 'Blob') was observed at both inshore and offshore stations for much of 2014–2016.

Across the study region, MHWs were detected in 164,378 grid-cell points. SST anomalies varied from 1.31 to 6.17°C, with a mode of 1.8°C (Figure 2). A large proportion of the events (48.2%) exhibited anomalies <2°C, 50.7% from 2 to 4°C, and 1.1% above 4°C. $\text{Duration}_{\text{event}}$ varied from 5 to 370 days. Most events (58.7%) lasted less than 10 days, 38.9% lasted 10–100 days and 2.5% persisted over 100 days. We found a positive correlation between MHW $\text{intensity}_{\text{event}}$ and $\text{duration}_{\text{event}}$ ($\rho = 0.6$, $p \ll 0.01$), indicating that stronger MHWs tend to last longer.

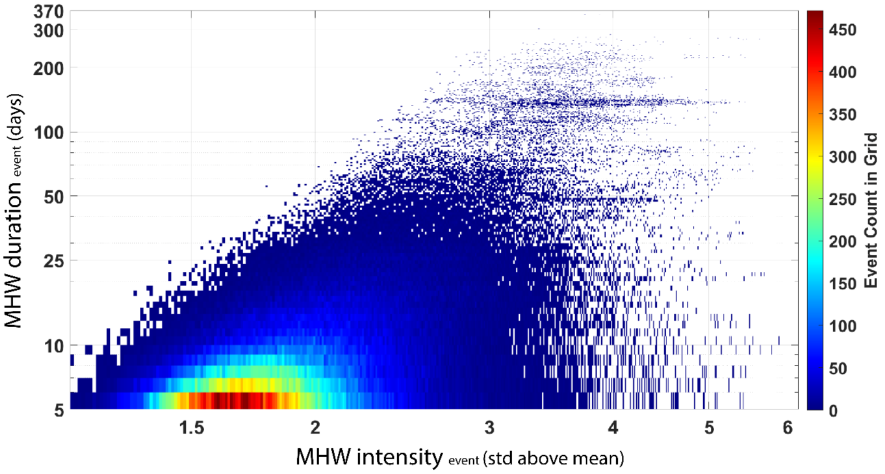
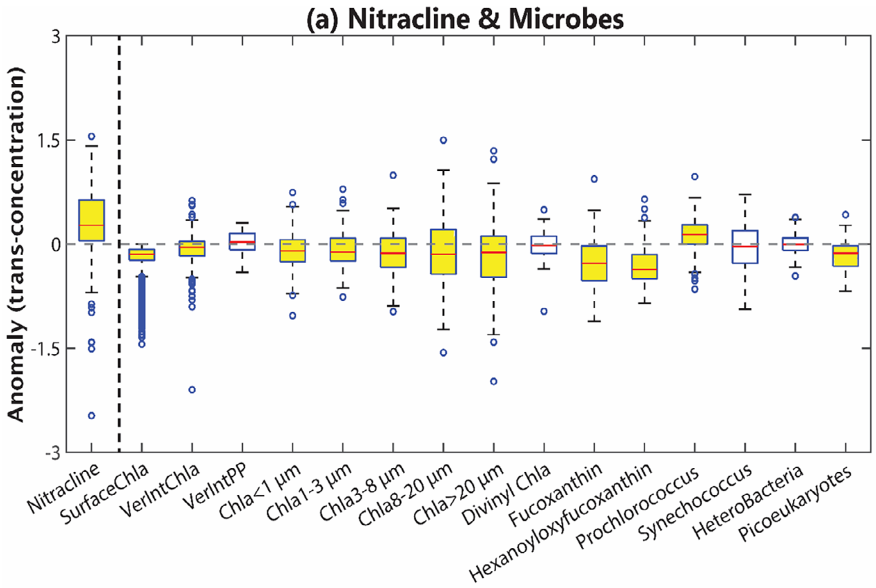


FIGURE 2 | MHW intensity and duration across the southern CCE region from 1982 to 2021. The *x*-axis is the MHW maximum normalised intensity ($\text{intensity}_{\text{event}} =$ maximum anomaly normalised by standard deviation)) in each event, and the *y*-axis is the MHW duration. The colour indicates the number of grid cell (0.25°) days with specific MHW intensity-duration characteristics.

3.2 | Biological Impacts

3.2.1 | Biological Anomalies During MHW Events

MHW events had a greater impact on the nitracline depth and the biomasses (or abundances) of short-lived microbes (phytoplankton and bacteria, Figure 3a) than longer-lived metazoans (Figure 3b). Nitracline depth anomalies increased substantially during MHWs (mean ± SD of Yeo-Johnson transformed depths, $m = 0.3 \pm 0.52$), indicating lower nutrient availability. Phytoplankton biomass decreased during MHWs, as evidenced by satellite-observed surface Chla anomalies (mean ± SD of $\log_{10}$ Chla mg $m^{-3} = -0.18 \pm 0.15$) and vertically integrated Chla from CalCOFI bottle sample anomalies ($\log_{10}$ Chla, mg*$m^{-2} = -0.08 \pm 0.24$, respectively) during MHWs. However, integrated primary production (PP) was not substantially different during MHWs ($\log_{10}$ PP, mgC*m^{-2}*half-light $day^{-1} = 0.02 \pm 0.15$). All Chla size fractions showed negative anomalies during MHWs with larger size fractions showing more negative responses ($\log_{10}$ Chla, $\mu g\,L^{-1} = -0.17 \pm 0.6$ for >20-µm cells). We used HPLC-derived pigment concentrations to investigate changes in major phytoplankton taxa. Fucoxanthin (diagnostic for diatoms) and hexanoyloxyfucoxanthin (diagnostic for prymnesiophytes, including coccolithophores) showed substantial negative anomalies ($\log_{10}$ pigments, $\mu g\,L^{-1} = -0.27 \pm 0.41$ and -0.29 ± 0.33, respectively). Divinyl Chla (diagnostic for *Prochlorococcus*) showed insignificant change during MHWs ($\log_{10}$ pigments, µg $L^{-1} = -0.03 \pm 0.25$). *Prochlorococcus* abundance exhibited positive anomalies (log-10 transformed anomalies, cells $mL^{-1} = 0.13 \pm 0.27$), while picoeukaryotes exhibited negative anomalies (-0.16 ± 0.21) during MHWs. *Synechococcus* and heterotrophic bacteria



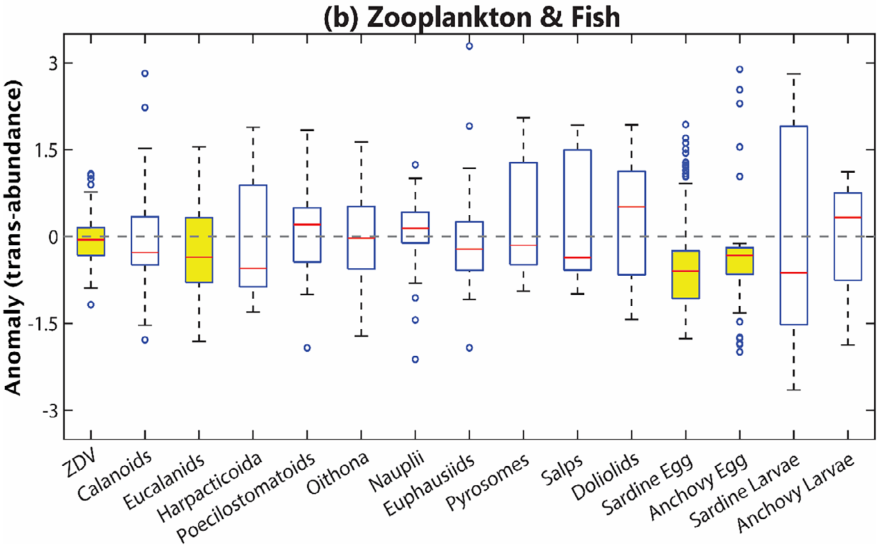


FIGURE 3 | Nutrient and biological anomalies during MHW events: (a) nitracline depth and microbes (bacteria and phytoplankton), and (b) metazoan zooplankton and forage fish. The *x*-axis delineates measurement types, and the *y*-axis indicates box plots of power-transformed anomalies: Log-transformation for microbes and zooplankton displacement volume (ZDV) and Yeo-Johnson transformation for nitracline depth, zooplankton taxon-specific abundance, and fish eggs, and larvae. The horizontal dashed lines indicate zero anomaly. The red lines in the box indicate the median. Yellow box plots indicate that the variable has a mean that is statistically different from zero (*t*-test $p < 0.05$). Blue circles indicate outliers.

were essentially unchanged (-0.04 ± 0.35 and -0.01 ± 0.15, respectively).

Zooplankton displacement volume, an imperfect proxy for metazoan zooplankton biomass (Lavaniegos and Ohman 2007), displayed negative anomalies ($\log_{10}$ displacement volume, m^3 per $1000\,m^3$ strained $= -0.06 \pm 0.37$) during MHWs. However, taxon-specific abundances of copepods (except for eucalanids), euphausiids and thaliaceans did not show major responses during MHWs (anomaly of Yeo-Johnson transformed abundance, individuals $m^{-2} = -0.25 \pm 0.82$). This response disparity may be due to the limited number of ZooScanned PRPOOS net samples ($n = 46$) coinciding with MHWs, compared to samples for displacement volumes ($n = 157$).

For forage fish, sardine eggs (anomaly of Yeo-Johnson transformed count number $= -0.49 \pm 0.81$) were substantially less abundant during MHWs. Abundance of anchovy eggs also substantially decreased (-0.33 ± 0.93), although the distribution was distinctly not Gaussian due to a large number of zeros. In contrast to eggs, neither sardine nor anchovy larvae showed distinct responses to MHWs (anomalies of Yeo-Johnson transformed abundances $= 0.05 \pm 1.82$ for sardines and 0.05 ± 0.87 for anchovy).

3.2.2 | Impacts of MHW Characteristics on Biological Anomalies

MHW intensity had a marked effect on short-lived plankton. Phytoplankton biomass was negatively correlated with MHW intensity (correlation between satellite-observed surface Chla and $\text{intensity}_{\text{event}}$ was $\rho = -0.22$, $p \ll 0.001$, Figure 4a). Every Chla size fraction demonstrated negative correlations with MHW $\text{intensity}_{\text{sampled}}$ and these correlations were mostly significant for the larger size fractions ($\rho = -0.24$ for 1- to 3-μm cells, $p = 0.03$; $\rho = -0.32$ for 8- to 20-μm cells, $p < 0.01$; $\rho = -0.3$ for >20-μm cells, $p < 0.01$), suggesting that large phytoplankton were more impacted during intense MHWs compared to smaller forms. Surprisingly, no phytoplankton group (from HPLC or flow cytometry samples) showed a statistically significant relationship to MHW $\text{intensity}_{\text{sampled}}$. For zooplankton, no significant correlations were found between any zooplankton variable and MHW $\text{intensity}_{\text{sampled}}$ (Figure 4b), except for *Oithona*-like copepods exhibiting a significant positive relationship ($\rho = 0.36$, $p = 0.01$). For sardine and anchovy, both egg and larvae abundance anomalies were positively correlated with MHW $\text{intensity}_{\text{sampled}}$, although these correlations were not statistically significant.

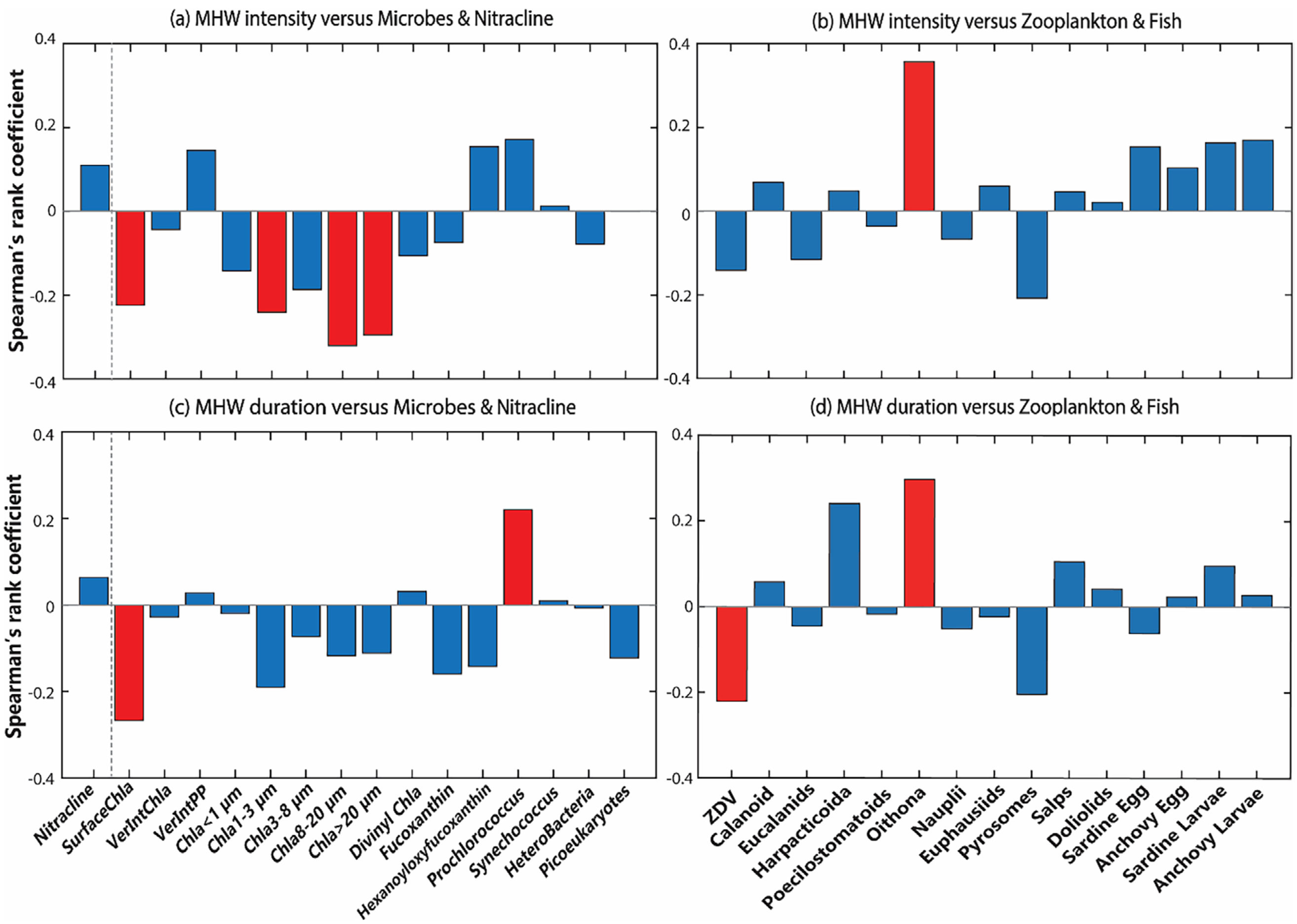


FIGURE 4 | Correlation coefficients for MHW characteristics (intensity in (a) and (b); duration in (c) and (d)) versus the anomalies of the transformed abundance for each plankton variable and transformed nitracline depth: (a, c) nitracline & microbes and (b, d) metazoan zooplankton and forage fish. The x-axis indicates the plankton variable, and the y-axis indicates Spearman's correlation coefficient (ρ). Statistically significant correlation coefficients ($p < 0.05$) are shown as red bars.

Phytoplankton responses to MHW duration were generally weaker than their responses to MHW intensity (Figure 4c,d). Satellite-observed surface Chla displayed a significant negative correlation with duration$_{\text{event}}$ ($\rho = -0.27$, $p \ll 0.01$), which is similar in magnitude to its correlation with intensity$_{\text{event}}$. No statistically significant relationships were found between duration$_{\text{sampled}}$ and any phytoplankton size classes, although a statistically significant positive correlation was found with *Prochlorococcus* abundance ($\rho = 0.22$, $p = 0.03$), indicating higher cell densities during longer MHW events. For zooplankton, displacement volumes exhibited a significant negative correlation with MHW duration$_{\text{sampled}}$ ($\rho = -0.22$, $p < 0.01$), suggesting reduced zooplankton biomass during longer MHW events. Among zooplankton groups, only *Oithona* exhibited a significant (positive) correlation with MHW duration$_{\text{sampled}}$ ($\rho = 0.3$, $p < 0.05$). Neither fish egg nor fish larvae had significant correlations with MHW duration$_{\text{sampled}}$. Across all taxa that showed significant correlations with either intensity or duration, *Prochlorococcus* was the only phytoplankton taxon substantially more positively sensitive to duration than intensity, and the zooplankton displacement volume was more strongly correlated with duration than intensity (Figure 5).

3.2.3 | Impacts of MHW on Plankton Trophic Interactions

To investigate potential trophic coupling during MHWs, we tested correlations between zooplankton displacement volume anomaly and four phytoplankton parameters considered potential drivers of zooplankton biomass: surface Chla, vertically integrated Chla, large-cell (>20 µm) Chla and fucoxanthin. While all variables were positively correlated with zooplankton displacement volume during MHWs, the correlations with surface and vertically integrated Chla were very weak and not statistically significant. The correlation between displacement volume and >20-µm Chla was stronger, but still not statistically significant ($\rho = 0.12$, $p > 0.1$). The correlation with fucoxanthin was statistically significant and the strongest overall ($\rho = 0.43$, $p = 0.016$, Figure 6). This suggests that, although fucoxanthin was not statistically correlated with either MHW intensity or duration, the abundance of diatoms during a MHW is likely important in determining zooplankton responses to the disturbance.

3.2.4 | Biological Impacts of Nutrient Availability During MHW Events

Nitracline depth did not display any significant relationships with MHW intensity$_{\text{sampled}}$ or duration$_{\text{sampled}}$. However, both the anomalies of satellite-observed surface Chla and vertically integrated Chla displayed significant negative correlations with the nitracline anomaly ($\rho = -0.48$, $p \ll 0.01$ and $\rho = -0.31$, $p \ll 0.01$, respectively) during MHWs, suggesting that bottom-up nutrient supplied was important to phytoplankton biomass responses to these disturbances. Surprisingly, heterotrophic bacteria and picoeukaryotes showed significant positive correlations ($\rho = 0.28$, $p = 0.01$ and $\rho = 0.31$, $p < 0.01$, respectively) with the nitracline anomaly. Notably, however, when we looked at all sampling data (not just during MHWs), there were no correlations between nitracline depth and heterotrophic bacteria and picoeukaryotes ($\rho = -0.02$, $p = 0.33$ and $\rho = -0.02$, $p = 0.37$, respectively).

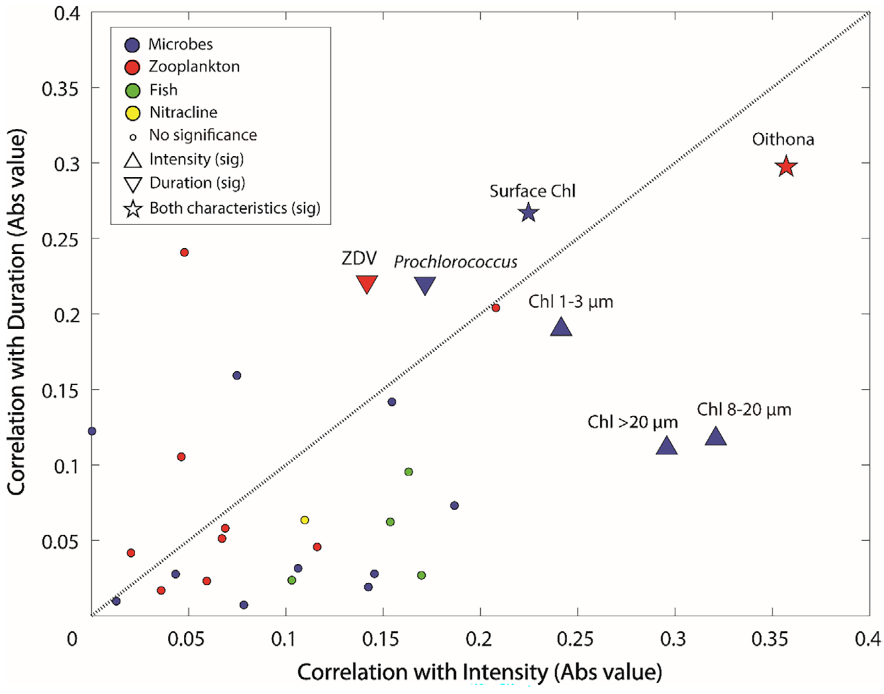


FIGURE 5 | Correlations of biological variables versus MHW characteristics. The x-axis indicates the absolute correlation coefficient with MHW intensity, and the y-axis indicates the absolute correlation coefficient with MHW duration. The blue, red, green and yellow points indicate the variables of microbes, zooplankton, forage fish and nitracline depth, respectively. The upward-pointing triangle, downward-pointing triangle and pentagram indicate that correlation coefficients are statistically significant for intensity, duration, or both, respectively, while small circles indicate non-statistically significant correlation coefficients. The dotted line indicates the 1:1 line.

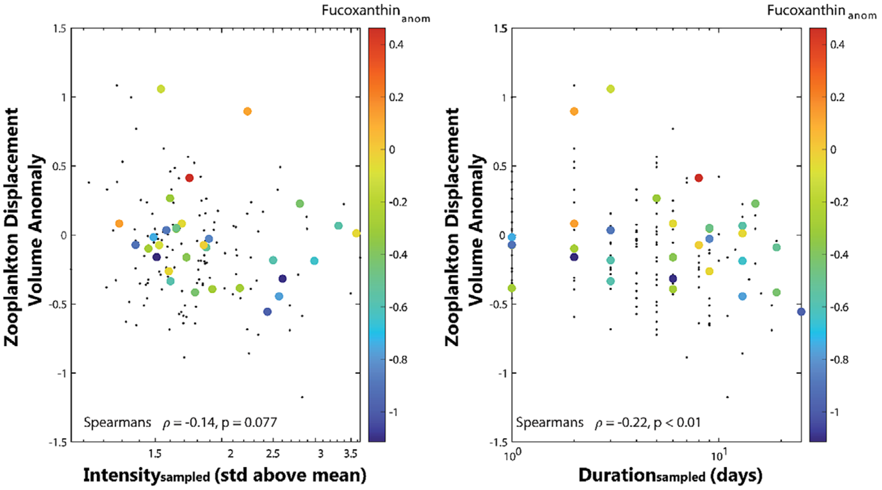


FIGURE 6 | Zooplankton displacement volume anomaly responses to MHW intensity (left), duration (right) and fucoxanthin anomaly (colour in both plots): The *x*-axis indicates MHW characteristics (intensity$_{sampled}$ or duration$_{sampled}$) and the *y*-axis indicates zooplankton displacement volume anomaly. Coloured circles indicate fucoxanthin anomaly (diagnostic pigment for diatoms). Small black circles indicate locations and times when zooplankton displacement volume was sampled and fucoxanthin was not.

4 | Discussion

The expected increased impacts of MHWs due to climate change necessitate a detailed understanding of ecological responses. In the CCE two distinct types of intense, prolonged MHW disturbances have been extensively studied: El Niño events that have been dominant sources of interannual variability for many decades (Chavez et al. 2002; Kahru and Mitchell 2000; Jacox et al. 2016) and extratropical MHWs including the record-breaking 'Blob' event in 2013–2015 and a subsequent strong MHW in 2019 (Bond et al. 2015; Di Lorenzo and Mantua 2016; Thompson 2019; Weber et al. 2021). Ecological responses to these events are similar in some ways, including a shift towards warm-water euphausiid taxa (Lilly and Ohman 2021) and reduced surface chlorophyll and primary production (Kahru, Jacox, and Ohman 2018; Morrow et al. 2018). However, they also differ in distinct ways: El Niños form in the tropical Pacific leading to anomalous poleward advection in the CCE and transport of subtropical taxa into the ecosystem, especially within the subsurface California Undercurrent (Lilly and Ohman 2021; Lynn and Bograd 2002). Recent extratropical MHWs originated in the North Pacific and were driven not by advection but by surface heating, with a reduced subsurface expression and commensurately greater stratification (Amaya et al. 2020; Bond et al. 2015). Thus, even seemingly similar responses (e.g., positive abundance anomalies for *Euphausia eximia*) can be driven by different processes during El Niños (poleward advection) and extratropical MHWs (sustained reproduction within the CCE domain, Lilly and Ohman 2021). Understanding these distinct differences, not to mention the response of the system to far more frequent short MHWs, necessitates investigation of how distinct characteristics of an MHW shape community structure.

Our results yield potentially important insights into mechanistic linkages between MHW disturbances and pelagic ecosystems. Phytoplankton biomass responses to MHWs were sensitive to the magnitude of the nitracline-depth anomaly during the heatwave, which indicates that bottom-up nutrient supply is an important mechanism driving microbial community response. Results also offered some support for our hypothesis that MHW intensity was more important than duration for microbial taxa. Anomalies of most Chla size fractions (1–3, 8–20 and >20-µm) were more strongly related to intensity than duration. The latter two larger size classes are particularly important because larger primary producers contribute disproportionately to trophic transfer to fisheries and carbon sequestration (Ryther 1969; Michaels and Silver 1988) and comprise a greater proportion of total phytoplankton biomass in productive locations and times (Goericke 2011; Taylor and Landry 2018). In contrast, satellite-observed surface Chla anomalies were similarly correlated with MHW intensity and duration ($\rho = -0.22$ for intensity; $\rho = -0.27$ for duration). This was initially surprising because microbial populations should respond rapidly to MHW events, suggesting that longer durations may not be necessary to see maximal effects. This may result, however, from multiple other reasons: (i) there was a strong correlation between MHW intensity and duration (Figure 2), (ii) Chla anomalies can reflect a combination of biomass changes and physiological responses (altered C:Chla ratios), (iii) while phytoplankton growth rates are rapid (typical growth rates in CCE are ca. 0.4 day^{-1}; Li et al. 2010), their *net* growth rates can be substantially lower because growth is often closely balanced by protistan grazing (Landry et al. 2009, 2023) leading to much longer population doubling times and (iv) most MHW events in the dataset were <2-week duration. This highlights the importance of understanding the impact of frequent, short-duration MHW disturbances which may lead to distinctly different ecosystem responses than El Niño or 'Blob'-like events. Characterisation of heatwave events within the 'press and pulse' ecological framework (Harris et al. 2018; Clark-Wolf et al. 2023) thus needs to consider both the characteristics of the event and the response times of the study organisms (Ratajczak et al. 2017).

Prochlorococcus was the only microbial taxon with a mean significant positive anomaly during MHWs and the only taxon for which MHW duration was a substantially stronger correlate than intensity. *Prochlorococcus* decreases in absolute abundance when ecosystem productivity is high and is often absent from coastal upwelling locations, despite dominating offshore (Taylor and Landry 2018). Originally, this was attributed to the 'enhanced microbial loop' hypothesis, suggesting that when heterotrophic bacteria growth rates and abundances are high, shared predation on similarly sized *Prochlorococcus* cells will cause strongly negative net growth rates of *Prochlorococcus*. Recent evidence, however, shows substantially lower cyanobacteria mortality (relative to heterotrophic bacteria) due to grazing in productive coastal waters, suggesting that bottom-up processes and temperature-dependence of growth rates may be important in restricting *Prochlorococcus* habitat (Landry et al. 2023). Importantly, no sampling locations in our *Prochlorococcus* dataset had experienced a MHW lasting longer than 25 days at the time of sampling. For MHW events lasting 1 week or shorter, there was essentially no response to the MHW (transformed anomaly = 0.09 ± 0.28, mean ± SEM). For MHW events lasting longer than a week, *Prochlorococcus* was significantly enhanced in abundance (transformed anomaly = 0.2 ± 0.25). This suggests a ca. one-week lag time between the onset of disturbance and substantial changes in *Prochlorococcus* abundance, likely mediated by relatively small changes in net growth rate (Landry et al. 2024b). Regardless, *Prochlorococcus* experiences range expansion into the coastal domain during strong and long-lasting MHWs (Landry et al. 2024a). The proliferation of *Prochlorococcus* during MHWs can shape the microbial community structure, which may result in cascading effects across the food web (Brown et al. 2024).

At higher trophic levels, our results do not support our hypothesis that all longer-lived taxa will respond more to duration than intensity. However, they offer support for a modified hypothesis that mesozooplankton taxa will be more affected by MHW duration than intensity. While most zooplankton groups showed insignificant relationships with MHW intensity, correlations for *Oithona*-like copepods (positive) and zooplankton displacement volume (negative) were statistically significant. Displacement volume is the longest and most spatially resolved zooplankton time series for this region and is often used as a proxy for biomass changes, although it departs systematically from measures of zooplankton C biomass when the contribution of large, gelatinous zooplankton varies (Lavaniegos and Ohman 2007). Our results also suggest that MHW impacts on zooplankton are mediated, in part, by trophic interactions with phytoplankton. MHWs that induced greater declines in diatoms (fucoxanthin) elicited a greater decrease in zooplankton displacement volume. While it might seem strange that long-lived taxa that are often associated with cold coastal waters (e.g., some euphausiid species) were not more strongly impacted by MHWs, the lack of a strong correlation may result in part from the shorter duration of the PRPOOS net time series used for ZOOSCAN analyses and is also influenced by the multiple different taxa with differing responses to temperature shifts in this ecological transition zone (Brinton and Townsend 2003; Lilly and Ohman 2021).

The responses of mobile forage fish to MHWs were more complex. Egg abundances of forage fish are indices of spawning stock biomass (SSB; Lo et al. 1996). Environmental change can impact SSB by changing the overall breeding adult population size or inducing the movement of adults into or out of a study region. MHWs likely impact larval survival, year-class strength and future recruitment into the adult population. Entering the 2013–2016 MHW, the overall population sizes of both anchovy and sardine were historically low (MacCall et al. 2016; McClatchie et al. 2016; Thayer et al. 2017; Thompson 2019). During and after this MHW, however, anchovy recruitment was very high and by 2022 adult anchovy was close to the highest on record (Thompson et al. 2024) while sardine remained low (Thompson et al. 2022). Recent empirical (Swalethorp et al. 2023) and modelling (Fiechter et al. 2015) studies suggest that coastal pelagic fish recruitment is largely driven by the survival of young larvae. The results support this conclusion as there was a high larval to egg ratio for anchovy but not sardine during MHWs. Additionally, Thayer et al. (2017) found extremely low anchovy larval to egg ratios during low recruitment years (2006–2008) but an abrupt rise in 2014–2015. The mechanisms driving high anchovy recruitment during recent MHWs are not fully understood, but the availability of prey that efficiently transfer energy to young larvae (Swalethorp et al. 2023) and larval size at hatch (Garrido et al. 2015; Robidas 2023) correlate with high larval survival. Our recent realisation that anchovy populations can boom during MHWs is somewhat surprising as it was previously believed that sardine thrived under warm and anchovy under cold conditions (Chavez et al. 2003). These results shed further light on the nuanced and unexpected response of forage fishes to MHWs (Muhling et al. 2020; Thompson 2019; Weber et al. 2021; Free et al. 2023).

Although our results are specific to the biota of an eastern boundary current upwelling system, similarities to results from other regions suggest possible wider applicability. Globally, phytoplankton biomass decreases during MHWs at middle and low latitudes (Le Grix et al. 2021; Noh, Lim, and Kug 2022), while the lower nutrient levels induced by MHWs (Hayashida, Matear, and Strutton 2020; Sen Gupta et al. 2020) would favour the dominance of small phytoplankton (Iriarte and González 2004; Kudela et al. 2006; Zhan et al. 2023). Indeed, the increases in *Prochlorococcus* in the CCE during MHWs (Figure 3a and Landry et al. 2024b) are related to a predicted global range expansion due to climate change (Flombaum et al. 2013). Nevertheless, there are likely many region-specific effects. For instance, in the Gulf of Alaska, the 2014–2015 MHW led to increased zooplankton biomass concurrently with substantially reduced diatom abundance, suggesting modified top-down grazing pressure (Batten et al. 2022). Impacts of MHWs on trophic linkages are thus likely variable across regions and determined by both the physicochemical regime and the relative life spans, mobilities and behaviours of different trophic levels. Indeed, even within the CCE, some MHW conditions (i.e., El Niños) have been shown to alter the balance of bottom-up and top-down processes (Lindegren et al. 2018). Specific characteristics of individual species, such as harmful algae taxa, may further alter ecological responses to MHWs (Roberts et al. 2019; McCabe et al. 2016).

Predictions of the impact of future MHWs on biota are further complicated because these disturbances may subject organisms to temperatures not experienced in their historical ranges

(Muhling et al. 2020). Phenological mismatches between predators and prey may also ensue, making the timing of disturbances a key determinant (Asch, Stock, and Sarmiento 2019; Shanks et al. 2020), while trophic restructuring may be important for critical early life stages (Swalethorp et al. 2023). The rate of temperature increase, the spatial extent of the disturbance and the subsurface extent of warming are likely also important, with differing responses that depend on the life span and mobility of specific taxa, while thermal displacement has been suggested as a metric of particular importance for mobile taxa (Jacox et al. 2020). Elucidating the complex effects of lagged responses across multiple trophic levels will require further work and potentially necessitate multiple sampling events under a Lagrangian framework within a single MHW event.

In conclusion, our findings showed limited support for one of our hypotheses. Microbial communities tend to be more sensitive to MHW intensity than duration. However, neither intensity nor duration were consistently important to metazoans, due to their complicated taxon-specific responses to MHW characteristics. Nevertheless, our results are a step towards understanding how two key characteristics of MHWs differentially impact short-lived and longer-lived taxa during these disturbances.

Author Contributions

T.-C.C. and M.S. designed the study, and T.-C.C. performed all analyses. M.R.L., M.D.O., M.K. and A.T. were responsible for flow cytometry, ZooScan, satellite chlorophyll, and fish larvae data, respectively. T.-C.C. and M.S. wrote the first draft of the manuscript and all authors contributed substantially to editing and revisions.

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Data Availability Statement

Time-series raw data are publicly available from the following websites: Satellite sea surface temperature (https://podaac.jpl.nasa.gov/dataset/AVHRR_OI-NCEI-L4-GLOB-v2.0), satellite chlorophyll concentration (https://spg-satdata.ucsd.edu/CC4km/), net primary production, vertically integrated chlorophyll and nutrient (https://calcofi.org/data/oceanographic-data/bottle-database/), size-fractionated chlorophyll (https://doi.org/10.6073/pasta/8ebed2a2ac22a27b23e7ba98f10dcbb4), HPLC (https://doi.org/10.6073/pasta/831e099fb086954d3d73638d33d3dd05), flow cytometry (https://doi.org/10.6073/pasta/994126a7ba3d90250cf371d92b134538), zooplankton displacement volume (https://calcofi.org/data/marine-ecosystem-data/zooplankton/), zooplankton taxon-specific abundance by ZooScan (https://oceaninformatics.ucsd.edu/zooscandb/), fish eggs (https://coastwatch.pfeg.noaa.gov/erddap/files/erdCalCOFIcufes/) and fish larvae (https://coastwatch.pfeg.noaa.gov/erddap/search/index.html?page=1&itemsPerPage=1000&searchFor=calcofi). Compiled data are available on the Environmental Data Initiative (EDI) repository (https://doi.org/10.6073/pasta/be6d2547424b1f9a6da933392b3c3979 and https://doi.org/10.6073/pasta/537aae78a89c161ffdf3d84c50e88156). All codes used in the analysis are posted on Github (https://github.com/tchen0515/MHW-CCE.git).

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Supporting Information

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