



Extreme Marine Heatwaves Alter Kelp Forest Community Near Its Equatorward Distribution Limit

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Climate change is increasing the frequency and severity of marine heatwaves. A recent extreme warming event (2014–2016) of unprecedented magnitude and duration in the California Current System allowed us to evaluate the response of the kelp forest community near its southern (warm) distribution limit. We obtained sea surface temperatures for the northern Pacific of Baja California, Mexico, and collected kelp forest community data at three islands, before and after the warming event. The warming was the most intense and persistent event observed to date, with low-pass anomalies 1°C warmer than the previous extremes during the 1982–1984 and 1997–1998 El Niños. The period between 2014 and 2017 accounted for ~50% of marine heatwaves days in the past 37 years, with the highest maximum temperature intensities peaking at 5.9°C above average temperatures for the period. We found significant declines in the number of *Macrocystis pyrifera* individuals, except at the northernmost island, and corresponding declines in the number of fronds per kelp individual. We also found significant changes in the community structure associated with the kelp beds: half of the fish and invertebrate species disappeared after the marine heatwaves, species with warmer affinities appeared or increased their abundance, and introduced algae, previously absent, appeared at all islands. Changes in subcanopy and understory algal assemblages were also evident; however, the response varied among islands. These results suggest that the effect of global warming can be more apparent in sensitive species, such as sessile invertebrates, and that warming-related impacts have the potential to facilitate the establishment of tropical and invasive species.

Keywords: kelp forest, extreme warming event, marine heatwaves, community structure, tropicalization, trailing edge

INTRODUCTION

Climate change is predicted to increase the frequency and severity of extreme climatic events (Solomon et al., 2007; Perkins et al., 2012; Sydeman et al., 2013; Frölicher et al., 2018) such as marine heatwaves (MHWs) (Hobday et al., 2016), which are impacting coastal marine ecosystems worldwide (Garrabou et al., 2009; Marba and Duarte, 2010; Smale and Wernberg, 2013; Wernberg et al., 2013, 2016; Cavole et al., 2016; Hughes T. P. et al., 2017; Oliver et al., 2017; Smale et al., 2019), as well as the human populations that depend on them (McCarthy et al., 2001; Harley et al., 2006). In the past decades, MHWs have already increased in frequency and severity, with a global average of 50% more MHW days registered per year (Frölicher et al., 2018; Oliver et al., 2018). Temperate foundation (habitat-forming) species, are reported to be sensitive to MHWs (Wernberg et al., 2019), especially to warmer water temperatures and to decreases in nutrient availability due to thermal stratification or to a weakening of coastal upwelling (Carr and Reed, 2015; Schiel and Foster, 2015). They are particularly susceptible to MHWs when located close to their equatorward (warm) range edges (Smale et al., 2019). Changes in the abundance and distribution of these foundation species could have consequences for the structure and function of the entire ecosystem (Harley et al., 2012; Schiel and Foster, 2015; Smale et al., 2019).

The temperate ecosystems of the California Current System (CCS) were recently exposed to a sustained and intense warming event. It began in November 2013 in the Gulf of Alaska (Gentemann et al., 2017), with positive (warm) sea surface temperature anomalies (SSTAs) in the upper ocean layer (~100 m). By May 2014, it spread south to the coasts of Baja California, lasting until April 2015 (Di Lorenzo and Mantua, 2016). Nicknamed the “Blob,” temperature anomalies exceeded 3°C above previous climate records (Bond et al., 2015; Di Lorenzo and Mantua, 2016). Severe El Niño Southern Oscillation (Jacox et al., 2016) (nicknamed Godzilla) conditions (SSTAs of ~2.3°C, as measured by el Niño 3.4 index) followed this event, extending the warming in Baja California until the end of 2016 (Di Lorenzo and Mantua, 2016; Jacox et al., 2016). Reports of biological changes across the entire food web of the CCS (Cavole et al., 2016; Sanford et al., 2019) followed these extreme conditions. However, limited knowledge exists regarding the corresponding responses of temperate coastal ecosystems.

Kelp forest ecosystems in the northeastern Pacific Ocean are distributed along the coasts of the CCS, from Alaska, United States, to their southern distribution limit in Baja California, Mexico (Graham et al., 2007; Carr and Reed, 2015; Schiel and Foster, 2015). The giant kelp, *Macrocystis pyrifera*, one of the foundation species in kelp forests of this region, creates a three-dimensional biogenic marine habitat that sustains diverse biological assemblages, and provides valuable ecosystem services (Foster and Schiel, 1985; Costanza et al., 1997; Carr and Reed, 2015). The occurrence of periodic warm oceanographic events, such as El Niño, which tend to generate warm and nutrient-poor environmental conditions, as well as episodic strong storms that dislodge *M. pyrifera* individuals (Dayton, 1985; Foster and Schiel, 1985; Byrnes et al., 2011), can cause the decrease or

loss of *M. pyrifera* forests (Dayton and Tegner, 1984; Foster and Schiel, 1985; Zimmerman and Robertson, 1985; Edwards, 2004), and alter the structure of entire communities (Dayton and Tegner, 1984; Dayton et al., 1984, 1992; Tegner and Dayton, 1987; Schiel and Foster, 2015).

Kelp forest ecosystems located near temperate-subtropical transition zones, where conditions are more variable and extreme, are more vulnerable to warming events than those found at higher latitudes (Steneck et al., 2002; Edwards, 2004; Edwards and Estes, 2006; Johnson et al., 2011; Wernberg et al., 2013, 2016; Vergés et al., 2014). During El Niño 1997–1998, in the CCS, almost all of Baja California's *M. pyrifera* forests disappeared, and while heavy losses were reported for central California, only minor impacts were observed for northern California (Edwards, 2004; Edwards and Estes, 2006). *M. pyrifera* forests are resilient to disturbance and quickly recover after catastrophic events due to their rapid responses to changes in nutrient supply, short lifespans, rapid growth rates, constant spore production, and propensity to generate a bank of microscopic stages that endure stressful conditions (Dayton et al., 1992; Reed et al., 1996; Ladah et al., 1999; Filbee-Dexter and Scheibling, 2014). Also, during El Niño 1997–1998, recovery rates for *M. pyrifera* were slower in Baja California than in central and northern California (Edwards, 2004; Edwards and Hernandez-Carmona, 2005; Edwards and Estes, 2006). The secular trend toward increasing temperatures might be challenging the capacity of *M. pyrifera* forests to recover near their southern (warm) limit in the CCS. This notion is supported by observations that their historical southern distribution edge has already suffered considerable poleward range contraction (Hernandez-Carmona et al., 2000), and that they might continue to contract poleward due to climate change.

Long-term, large-scale monitoring programs have proven to be extremely valuable to understand the response of complex marine ecosystems to extreme environmental changes (Hughes B. B. et al., 2017). But the high cost of collecting ecological data is shifting research efforts toward studies of sentinel species for climate change (early indicators of climate change), such as *M. pyrifera* (Krumhansl et al., 2016; Reed et al., 2016). It is particularly valuable to monitor such species when located in sentinel areas for climate change, that is regions such as Baja California, where ocean surface temperatures have changed rapidly, and are projected to continue to do so (Hobday and Pecl, 2014). Despite the sensitivity of Baja California's kelp forest to warming events (Hernández Carmona, 1988; Ladah et al., 1999; Hernandez-Carmona et al., 2001; Edwards, 2004; Edwards and Hernandez-Carmona, 2005; Edwards and Estes, 2006; Torres-Moye et al., 2013; Beas-Luna and Ladah, 2014; Woodson et al., 2018), they have received far less attention than those further north (Ramírez-Valdez et al., 2017). Moreover, given the relevance of kelp forests near the southern end of their distributional range, understanding changes associated with an extreme environmental event might provide insights into how climate change will alter kelp forest ecosystems in the CCS.

Islands are vulnerable environments, where isolation can preclude recovery after an extreme event due to restricted adult migration, and larval input (Johnson and Black, 2006; Bell, 2008), making them good candidate sites in which to

study ecosystem responses to MHWs. In December 2016, the Mexican government declared all Islands in the Pacific Coast of Baja California as a biosphere reserve. This action made them priority areas for conservation in the region, raising the need to understand the consequences of extreme events, which can endanger ongoing protection efforts in these vulnerable marine ecosystems.

The goal of this study is to provide a comprehensive report on the ecological impacts of the 2014–2016 warming event in the southern kelp forest communities of the CCS. We selected three islands, separated from each other at roughly 125 km intervals, to represent a latitudinal gradient off the coast of Baja California, and documented changes in community attributes from before to after the MHWs. We hypothesized that *M. pyrifera* kelp forests would suffer greatest impacts from the MHWs at the southernmost locations, since these are closer to the warm edge of their distribution limit, and that these changes would be reflected in the assemblage structure of invertebrates, fish, and algae.

MATERIALS AND METHODS

Study Sites

Our study sites encompass three inhabited islands that are part of the Baja California Pacific Islands biosphere reserve in Mexico: Isla Todos Santos (ITS), Isla San Martin (ISM), and Isla San Jeronimo (ISJ) (Figure 1). Located in the CCS, these islands stretch along a 250 km latitudinal gradient (29.8°–31.8°N) near the southern biogeographic distribution limit of boreal populations of *M. pyrifera*. They are internationally recognized for their high diversity, the abundance of their flora and fauna, the relative natural integrity of their ecosystems, and their high levels of endemism (Samaniego-Herrera et al., 2007). The marine areas adjacent to these islands, support various fisheries, most of them targeting species dependent on *M. pyrifera* as a source of food and habitat (Montaño-Moctezuma et al., 2014).

Sea Surface Temperature

We obtained satellite-derived data of sea surface temperature by using the GHRSSST Level 4 AVHRR Optimally Interpolated Global Blended Sea Surface Temperature Analysis (GDS version 2), from the National Centers for Environmental Information (2016), available at the physical oceanography distributed active archive center (PODAAC) of the NASA Jet Propulsion Laboratory (Last access: 2019-01-19). Daily sea surface temperature data are available at a 0.25° spatial resolution for 37 years (from September 1981 to present) (Reynolds et al., 2007; Banzon et al., 2016). To have a historical perspective of the strength of the 2014–2016 warming event, we calculated sea surface temperature anomalies for each 0.25° grid cell by subtracting the 1982–2018 local mean. We used a Fourier low-pass filter to show the contribution of interannual (basin-scale) processes (e.g., El Niño and the Blob) by removing signals with periods shorter than 18 months (cut off frequency), retaining inter-annual variability.

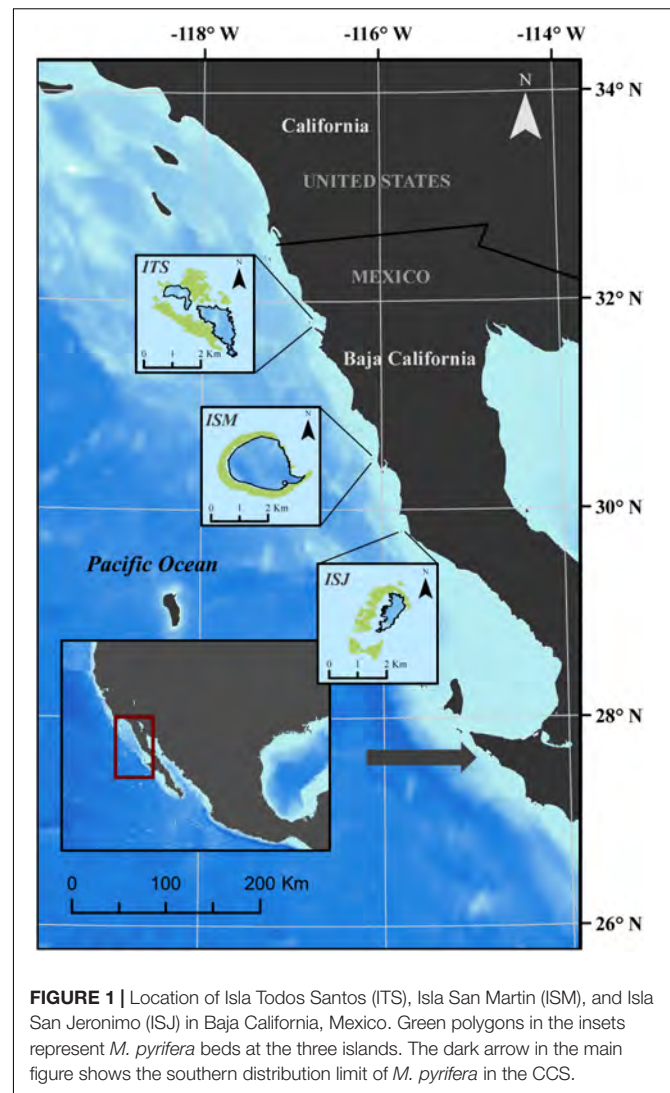


FIGURE 1 | Location of Isla Todos Santos (ITS), Isla San Martin (ISM), and Isla San Jeronimo (ISJ) in Baja California, Mexico. Green polygons in the insets represent *M. pyrifera* beds at the three islands. The dark arrow in the main figure shows the southern distribution limit of *M. pyrifera* in the CCS.

MHWs

We identified MHWs, defined by Hobday et al. (2016) as discrete prolonged anomalously warm-water events in a location, using the same daily sea surface temperature database for the 1982–2018 period. As with other studies of MHWs, we focused on upper percentiles of SSTAs, rather than on absolute SSTs. This approach accounts for the likelihood that marine populations are adapted to local temperature conditions, with anomalies indicating deviation from normal conditions that might elicit location-specific responses to thermal stress. We used the Matlab toolbox (Zhao and Marin, 2019) to identify periods of time where temperatures were above the 90th percentile threshold relative to the climatology (seasonally varying mean), and with a duration of at least 5 days. We identified the start and end dates and calculated the duration and intensity for each MHW event.

Biological Monitoring

We collected ecological data from the three islands. At each island, two sampling sites were selected (i.e., northern and

southern sites). Within each of these sites, we used underwater survey techniques (depth ranges of 10–15 m) to characterize the assemblages of invertebrates, fish, and algae at three transects. Data were collected by experienced, trained divers to ensure constancy in survey methods, and species lists compiled over the years. We estimated abundance of *M. pyrifera* and fish *in situ* by census transects and assessed abundance of invertebrates and algae by analyzing video transects. To corroborate the results of the *in situ* estimate of *M. pyrifera* abundance and better understand the effects of the MHWs, we estimated kelp biomass using remote-sensed Landsat imagery. We conducted the field surveys in late autumn 2013 and 2016, but due to bad weather in 2016, we had to extend the field work to early winter 2017 (henceforth “2016”).

Census Transects

For each island and year, we conducted three fish transects of 30 m × 2 m (60 m²) at each sampling site (six transects in total). Divers recorded identity and abundance of fish species along each transect. To assess the importance of the MHWs for fish species with different thermal affinities, we classified fish species from north to south, based on the centroid of their latitudinal distribution (FishBase). We evaluated the density of *M. pyrifera* by counting all the individuals (sporophytes), taller than 1 m, and the number of fronds (also known as stipes) per individual (measured above the holdfast), reporting the number of individuals per unit area. In 2013, we counted the number of *M. pyrifera* fronds along the transects in a sub-sample of randomly picked 9 individuals: three at the beginning of the transect (0–10 m), three at 10–20 m, and three at 20–30 m. In 2016, we counted the fronds for all *M. pyrifera* individuals found along the transect.

Video Transects

For each island and year, we conducted three video transects at each sampling site (six transects in total). In 2013, the transects were 10 m × 1.5 m (15 m²), while in 2016 they were 20 m × 2 m (40 m²). We analyzed each video transect to estimate the number of individuals of all invertebrate species. We grouped algae into subcanopy, introduced and understory species, and reported as numbers of individuals per square meter for the subcanopy and introduced species (to account for different sampled areas). We grouped understory algae into coralline crustose, coralline articulated, red crustose, red branch, and brown algae and estimated per cent cover of each group by using the ImageJ software (Schneider et al., 2012). For this group, we manually captured images from the video transects in VLC Media Player software and improved if necessary with Microsoft Office Picture Manager 2010. Then we estimated the total area of each picture based on an object of known size. Finally, we manually selected the area covered by each algal group, and the software calculated the total area for each group as a percentage cover.

Satellite Images

We used multispectral Landsat imagery to estimate *M. pyrifera* canopy biomass at 30-m resolution for a 10-year period (from January 1, 2009 to December 31, 2018) following

Cavanaugh et al. (2011). We analyzed each atmospherically corrected Landsat image using multiple endmember spectral unmixing (MESMA) (Roberts et al., 1998). This analysis enables estimates of kelp canopy area and biomass using observed relationships between MESMA-derived canopy fractions and diver-measured canopy biomass (Cavanaugh et al., 2011). These relationships were developed using data from the Santa Barbara Channel. There are 2 Landsat “scenes” that cover our study sites, and each scene has about 60 images between 1984–present, allowing us to determine seasonal canopy biomass for each 30 m × 30 m pixel.

Statistical Analysis

For all analyses comparing data collected before and after the MHWs, we used the parallel approach of modeling the response as a function of the crossed fixed factors Island (three levels: ITS, ISM, and ISJ) and Time (two levels: Before and After). In each instance, we assumed the six replicates taken at each time at each island (three replicates taken from two sites at each island) to comprise an independent, representative sample for that island. For univariate counts, we fit generalized linear models (GLMs) with Poisson errors, and simplified these based on standard log-likelihood ratio tests. For these models, we assessed approximate significance of pair-wise differences based on 95% confidence intervals. For multivariate responses, we used permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) in the R package *vegan* (Oksanen et al., 2013) on the basis of Bray-Curtis distance matrices derived from square-root transformed data, and used non-Metric Multidimensional Scaling (nMDS) to visualize multivariate patterns in community structure. Where *post hoc* tests were required, we employed pairwise PERMANOVAs, with false-discovery-rate adjustment for multiple tests (Benjamini and Hochberg, 1995), using functions in the R package *RVAideMemoire* (Hervé, 2018). We used Dufrene-Legendre Indicator Species Analysis (Dufrene and Legendre, 1997) to distinguish which species were contributing to significant clusters identified by these *post hoc* tests, using functions from the R Package *labdsv* (Roberts, 2018).

The time series of Landsat estimates of kelp biomass were the only long-term data available to explore whether observations from the period after the MHWs were beyond the bounds of natural variation for the period before the MHWs. We could not use standard linear modeling approaches in this instance, because observations would be expected to contain significant temporal autocorrelation, violating assumptions of independence. We therefore used automatic algorithms from the R package *tsoutliers* (López-de-Lacalle, 2019) to detect outliers from ARIMA (0,1,1) time series fitted to the log₁₀(x + 1)-transformed data from each island. This approach has the advantage over a random walk model of smoothing the fit using an exponentially weighted moving average of preceding values, rather than placing excessive emphasis on the most recent observation. Outliers detected in this way can be assumed to arise from a process not inherent to that which generated the other observations in the time series (i.e., they are outside the natural variation associated with the time series).

We programmed all analyses in R version 3.5.2 (R Core Team, 2013), setting $\alpha = 0.05$.

RESULTS

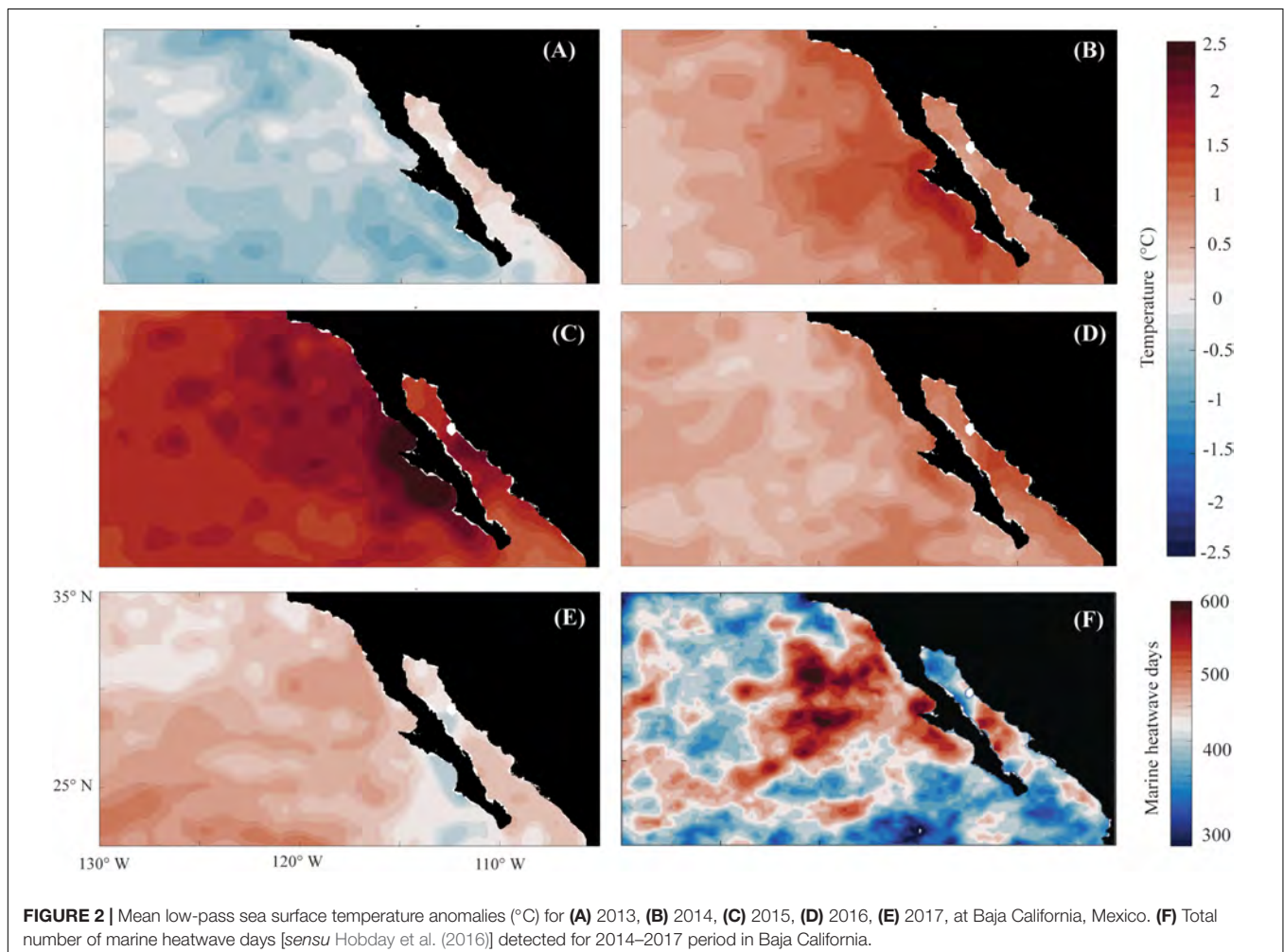
Sea Surface Temperature Changes

Along the Baja California coast, 2013 was in a slightly cold stage, with negative (cold) anomalies and no evidence of the “Blob” (Figure 2A), until 2014, when the warming event became evident (Figure 2B). By 2015, the additional El Niño effect boosted the warm anomalies and extended their distribution offshore and along the coastal waters of Baja California (Figure 2C). Toward the end of 2016, this effect had weakened (Figure 2D), but warm water anomalies remained throughout 2017 (Figure 2E and Supplementary Figure S1). After removing the annual cycle, the average low-pass anomalies were more than 1°C warmer than the extreme El Niño 1982–1984 and 1997–1998 events (Supplementary Figure S1). The 2014–2016 warm-event anomaly registered on the three islands was the largest in extent and most prolonged in duration observed to date, with SSTAs slightly lower at

the northernmost site (ITS) than the southernmost sites (ISM and ISJ), with anomalous temperatures peaking on summer 2015 at 2.15, 2.32, and 2.39°C above average, respectively (Supplementary Figure S1).

Marine Heatwaves

Around 50% of the identified MHW days between 1982–2017 registered at the three study sites occurred during 2014–2017 (Figure 2F and Supplementary Figure S3A). The period 2014–2015 accounted for 545 MHW days at ITS (58%), 466 at ISM (51%), and 476 at ISJ (53%) (Figures 3A,C). The year with the highest number of MHW days registered was in 2015 for ITS (261 days), ISM (242 days) and ISJ (256 days) (Figures 3A,C). For ITS, the longest continuous MHW comprised 152 days, lasting from November 2014 until late April 2015, while ISM and ISJ registered events lasting 123 and 124 consecutive MHW days, respectively, between late August and late December 2015 (Supplementary Tables S1–S3). In autumn 2015, the highest maximum temperature during a MHW were identified for the three islands, peaking at 5.6, 5.9, and 5.7°C, respectively (Figures 3A,B and Supplementary Tables S1–S3). These values are higher than the maximum registered during previous strong



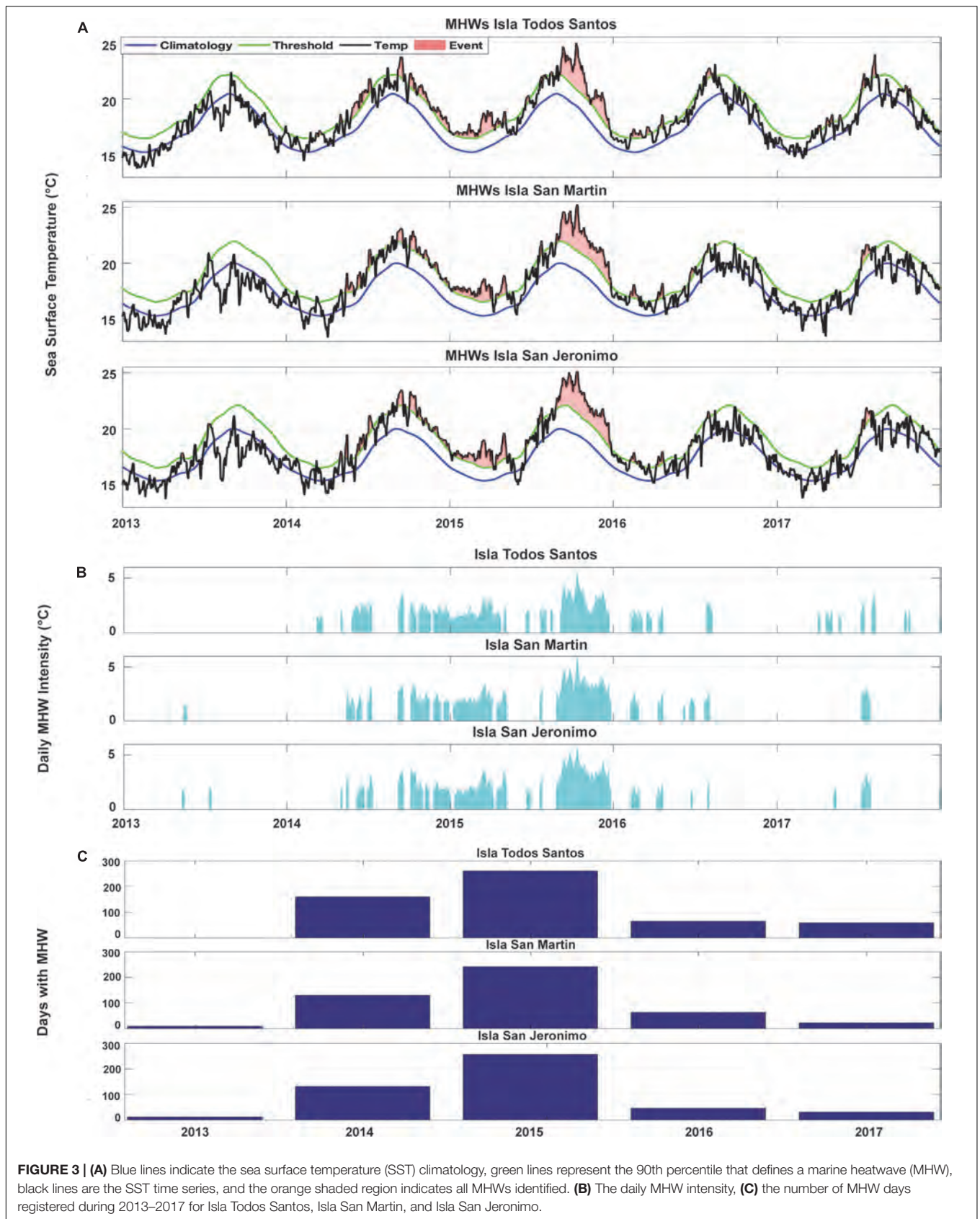


FIGURE 3 | (A) Blue lines indicate the sea surface temperature (SST) climatology, green lines represent the 90th percentile that defines a marine heatwave (MHW), black lines are the SST time series, and the orange shaded region indicates all MHWs identified. **(B)** The daily MHW intensity, **(C)** the number of MHW days registered during 2013–2017 for Isla Todos Santos, Isla San Martin, and Isla San Jeronimo.

1982–1984 (4.1, 3.3, and 3.3°C) and 1997–1998 El Niños (3, 3.4, and 3.7°C) (Supplementary Figures S2, S3B).

Changes in *Macrocystis pyrifera*

We detected significant interactions between Island and Time in our Poisson GLMs models of the numbers of *M. pyrifera* individuals per transect as well as the numbers of fronds per individual before and after the MHWs (Table 1). For the northernmost island, ITS, the number of individuals increased significantly after the MHWs. In contrast, we found significant decreases at the southern islands, ISM and ISJ, with only a few individuals per transect observed after the MHWs (Figure 4A). For all the islands we found a strong, consistent and significant decline in the numbers of fronds per *M. pyrifera* individual (Figure 4B).

Remote-sensed kelp biomass estimates were highly variable, but we clearly detected the MHWs signal at both ISM and ISJ (Figure 4C). As was the case for number of *M. pyrifera* individuals (Figure 4A), kelp biomass at ITS contrasted from the pattern at ISM and ISJ, although in this case, the time series analysis suggested no long-term trend (Figure 4C). Irrespective, it was clear that kelp biomass during and after the MHWs at the southernmost islands, ISM and ISJ, was well beyond the bounds of natural variability observed prior to the MHWs. Qualitatively, satellite-derived kelp biomass estimates allowed us to document the loss of the kelp forests during the MHWs at all islands. Immediately after summer 2015, the satellite images did not detect kelp at the surface of the three islands, and the biomass remained negligible until the end of 2016 (Figure 4C). By winter and spring 2017, kelp biomass at ITS had recovered to previous seasonal values, but at ISM and ISJ there was no recovery, and values stayed very low until the end of the time series (end of 2018). Note that very low values of biomass do not necessarily mean that the kelp forest completely disappeared, since satellite images do not detect sub-surface smaller individuals.

TABLE 1 | Results from the analysis of deviance variance for Poisson generalized linear models (A) for the number of *M. pyrifera* individuals per 60-m² transect, (B) for the number of fronds per *M. pyrifera* individuals, and (C) for species richness of the fish and invertebrate assemblage.

Factors	DF	Deviance Resid	Df	Resid. Dev	Pr(>Chi)
(A) <i>M. pyrifera</i> individuals					
Island	2	238.13	32	911.38	2.20E-16
Time	1	70.09	31	841.28	2.20E-16
Island × Time	2	488.86	29	352.43	2.20E-16
(B) Number of fronds					
Island	2	37.85	312	2834.2	6.03E-09
Time	1	1093.59	311	1740.5	<2.2E-16
Island × Time	2	19.51	309	1721.0	5.79E-05
(C) Species richness					
Island	2	11.13	32	67.168	3.83E-03
Time	1	40.737	31	26.432	1.74E-10
Island × Time	2	2.391	29	24.040	3.03E-01

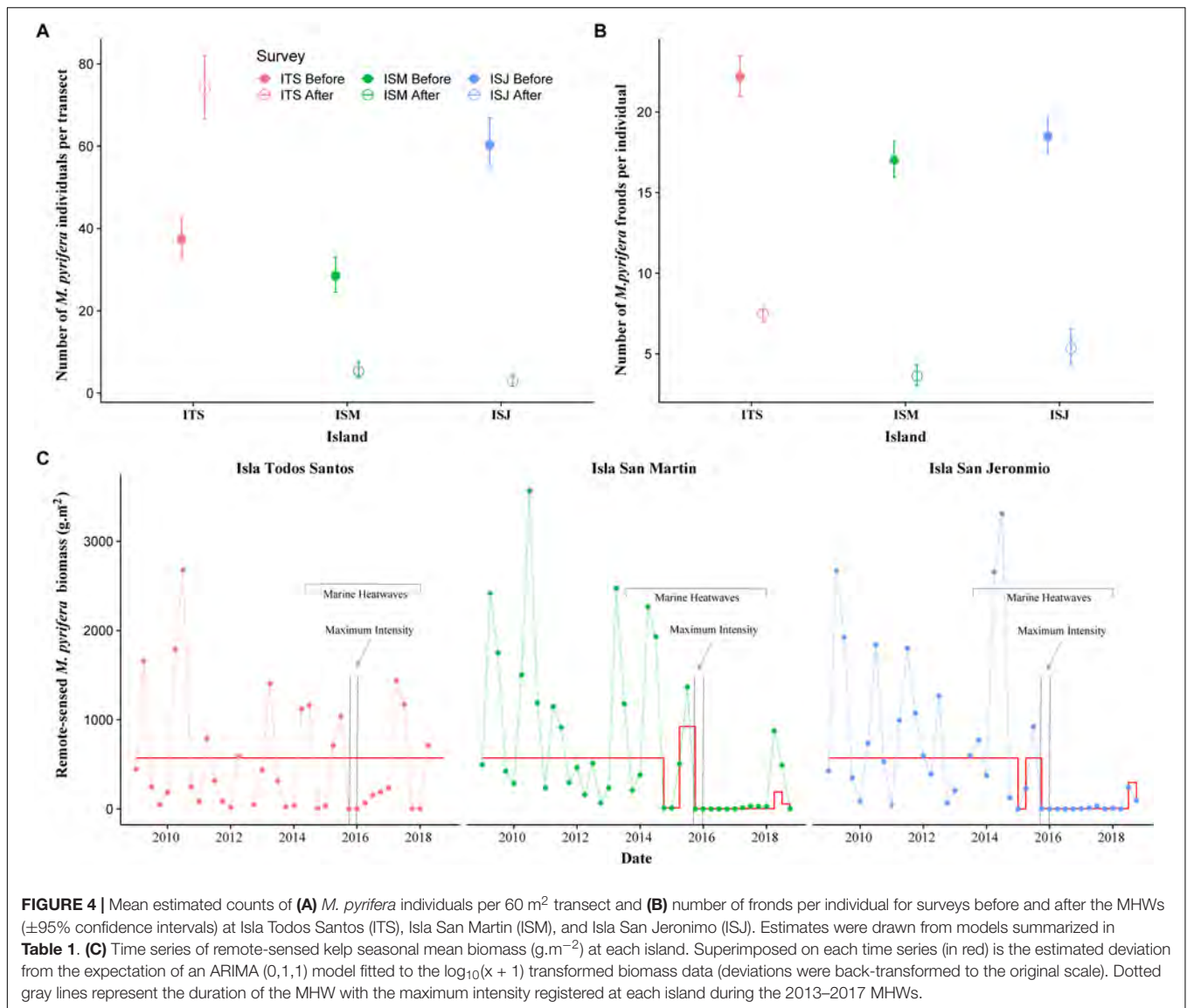
Community Changes

Fish and Invertebrates

For the combined fish and invertebrate assemblages, our Poisson GLM of species richness (Figure 5A and Table 1) found significant and consistent declines from before to after the MHWs at all islands (significant main effect for Time). Species richness was significantly higher at ITS than the more-southerly islands (significant main effect for Island), but the analysis revealed no evidence that this decline differed by Island (no significant Time × Island interaction). Proportionally, we observed similar reductions for fish and invertebrate species richness at ITS (57 and 54%, respectively), but the decline in invertebrate species richness was greater at ISM (39 and 53%) and it was dramatic at ISJ (41 and 81%) (Figures 6, 7).

Corresponding multivariate analysis of assemblage structure for fish and invertebrates (PERMANOVA) (Table 2) and associated *post hoc* tests (Supplementary Table S4A) revealed not only differences among islands and among times, but that the magnitude of the multivariate difference from before to after the MHWs differed by island (significant Time × Island interaction). The nMDS biplot shows clear differences in assemblage structure from before the MHWs to after (Figure 5B). *Post hoc* tests confirmed that significant changes in assemblage structure occurred from before the MHWs to afterward at each island ($p < 0.043$). Because we are most interested in species characterizing the periods before and after the MHWs (rather than differences among islands), we identified species with significant indicator-species values characteristic of these periods (Supplementary Table S6). Before the MHWs, assemblages were characterized by four fish species and fourteen invertebrate species (with the first five most important invertebrate species being more important indicator species than any of the fish). In accordance with the declining species richness in surveys after the MHWs, this period was characterized by four fish species and only one invertebrate species (Supplementary Table S6).

The loss or decrease of many species with cool-water affinities and the increase or appearance of some warm-affinity species (two species appeared after the MHWs) (Figure 6) drove the fish assemblage changes. The ten species exhibiting the northernmost distributions (based on their latitudinal centroid) (Supplementary Table S5) were absent at the three islands after the MHWs. All *Sebastes* species, except *S. atrovirens* and *S. serriceps* (which registered only one individual of each species at ITS in 2016), disappeared from the islands. *S. atrovirens* and *S. serriceps* are the most southerly of the *Sebastes* species recorded here, with distribution centroids in central California to central Baja California, compared to other *Sebastes* spp., which have centroids from northern California up to Alaska (FishBase). The three-characteristic fish species before the MHWs, *Oxylebius pictus*, *Rhinogobiops nicholsii* and *Rhacochilus toxotes* (Supplementary Table S6), have a centroid distribution from Oregon, north California and south California, respectively. Of the four-characteristic species after the MHWs, *Halichoeres semicinctus*, *Hypsypops rubicundus*, *Paralabrax clathratus* and *Semicossyphus*



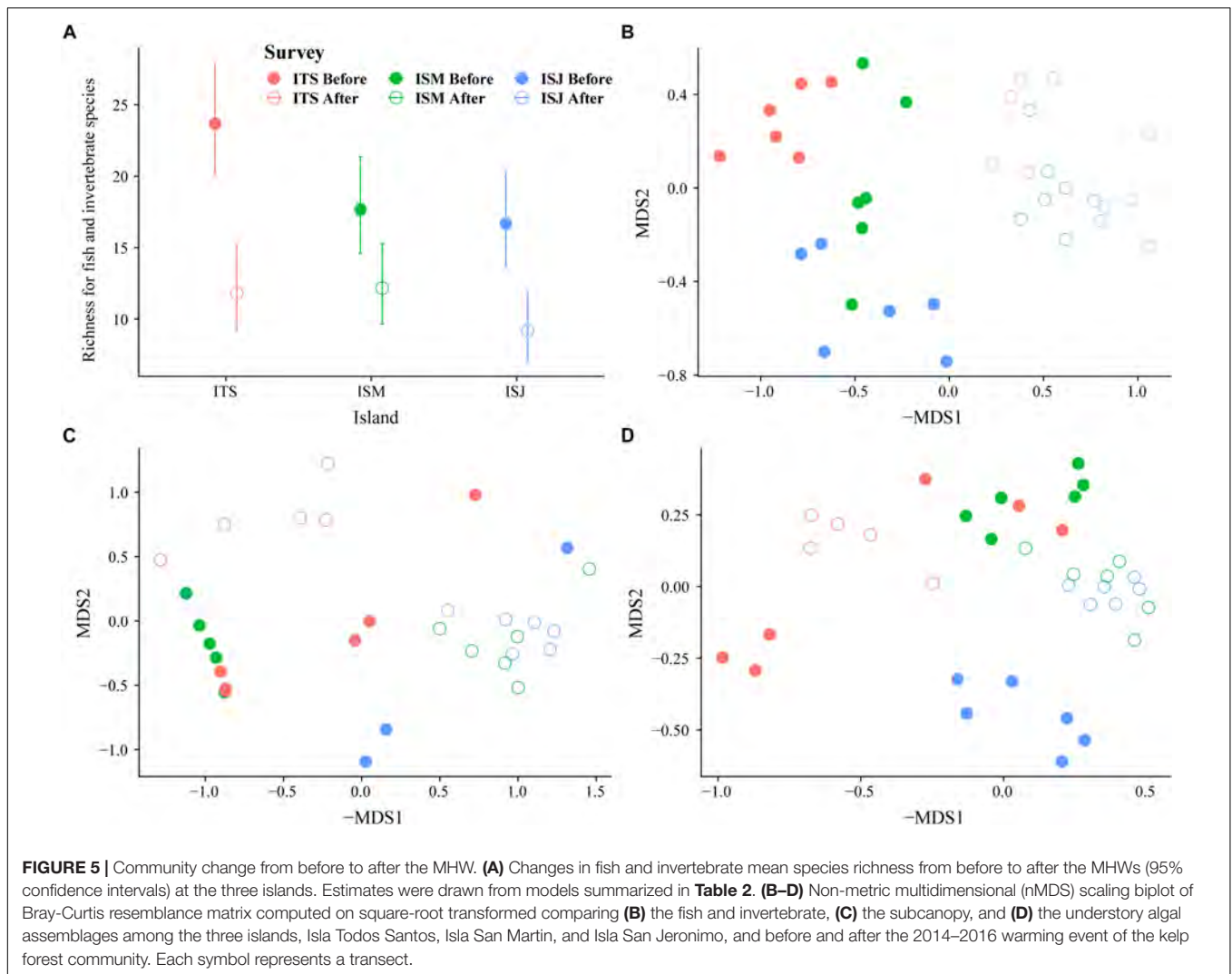
pulcher, all except *P. clathratus* have a southerly distribution, with centroids from northern to central Baja California (**Supplementary Tables S5, S6**).

A generalized decrease in species richness drove invertebrate assemblage changes (**Figure 7**). The number of species in all studied taxonomic groups declined from before to after the MHWs, with the loss of almost all sessile invertebrate species, especially cnidarians. Non-sessile species were also negatively affected. The number of echinoderm species decreased at ITS and ISM, with a notable decline at ISJ, where no echinoderms were present after the MHWs (**Figure 7**). Both red (*Mesocentrotus franciscanus*) and purple urchin (*Strongylocentrotus purpuratus*) densities decreased at ITS and ISM, while *Centrostephanus coronatus*, absent before the MHWs, appeared after at both islands (**Figure 7**). The starfish *Henricia leviuscula* and *Patiria miniata* were common before the MHWs, and almost disappeared afterward; furthermore, *Pisaster*

giganteus disappeared from all islands (**Figure 7**). The only invertebrate species that was characteristic after the MHWs is *C. coronatus* (**Supplementary Table S6**), which has a southern distribution from southern California, United States, to the Galapagos Islands, Ecuador.

Subcanopy and Understory Algae

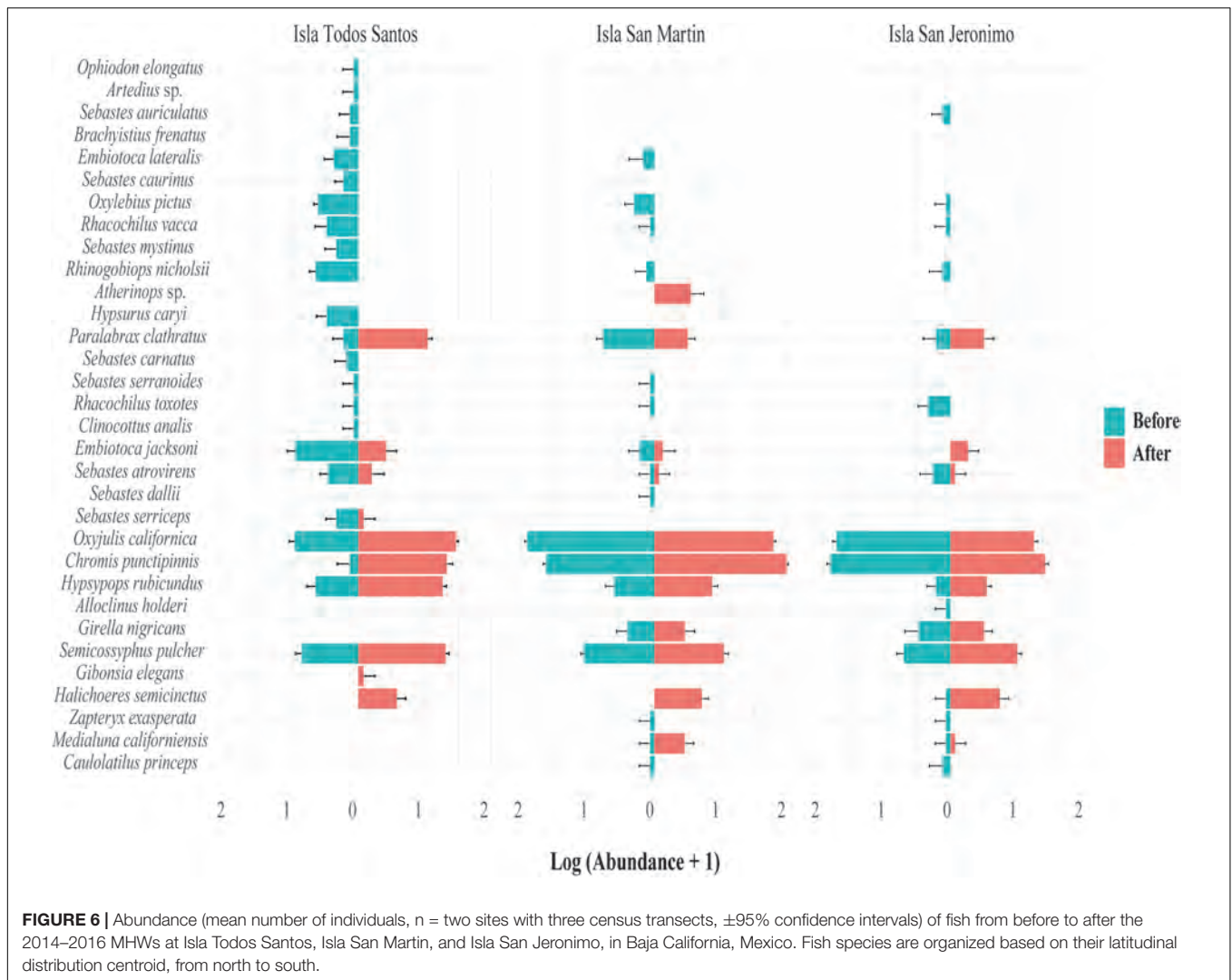
For both subcanopy and understory algae, PERMANOVA revealed not only that the assemblage structures differed significantly from before to after the MHWs ($p < 0.0135$ and 0.0063 for subcanopy and understory species, respectively), but also that the magnitude differed by island (**Table 2**). This pattern was reflected in corresponding nMDS biplots (**Figures 5C,D**) and associated *post hoc* tests (**Supplementary Tables S4B,C**). For subcanopy assemblage structure, only ISM and ITS differed significantly ($p = 0.0086$) before the MHWs (largely due to the substantial variability in assemblage structure within



islands – **Figure 5C**). After the MHWs, assemblage structure differed significantly among ITS and the southernmost islands ($p = 0.0086$), but not between ISM and ISJ. For understory species, assemblage structure differed significantly among islands before the MHWs ($p < 0.0298$) and afterward ($p < 0.0063$), except between the southernmost islands. The limited number of species in each of these analyses meant that there were few significant indicator species in each instance. Previously absent introduced algae species, *Undaria pinnatifida*, appeared after the warming event at ITS, and *Sargassum hornerii* at ISM and ISJ (**Figure 8A**). For subcanopy species, *Laminaria farlowii* was characteristic of assemblages before the MHWs, while *Ecklonia arborea*, *Cystocira* sp., and the introduced *S. hornerii* were characteristic afterward (**Figure 8A** and **Supplementary Table S6**). For the understory algal assemblages, red crustose algae were characteristic before the MHWs, with brown algae and articulated coralline species characteristic afterward (**Figure 8B** and **Supplementary Table S6**). In the three islands, the percent cover of non-coralline crustose algae increased after the warming event (**Figure 8B**).

DISCUSSION

Anthropogenic climate change is expected to remain one of the main threats to biological systems throughout the 21st century (Thomas et al., 2004; Pereira et al., 2010; Pecl et al., 2017), making it a central theme in ecology, and challenging science to understand and predict ecosystems' responses to these changing conditions. Among the manifestations of climate change is the intensification of MHWs (Oliver et al., 2018), with corresponding impacts reported globally in different taxonomic groups and geographic areas (Garrabou et al., 2009; Marba and Duarte, 2010; Smale and Wernberg, 2013; Voerman et al., 2013; Short et al., 2015; Cavole et al., 2016; Oliver et al., 2017; Tuckett et al., 2017; Ruthrof et al., 2018; Smale et al., 2019). In this context, it is relevant to identify and monitor those areas where sentinel species for climate change are more responsive to warming and to MHWs in particular, such as near warm edge distribution limit. We evaluated changes in the kelp forest community structure after the extreme 2014–2016 warming event, near the southern distribution limit of *M. pyrifera* in the CCS. The timing of this



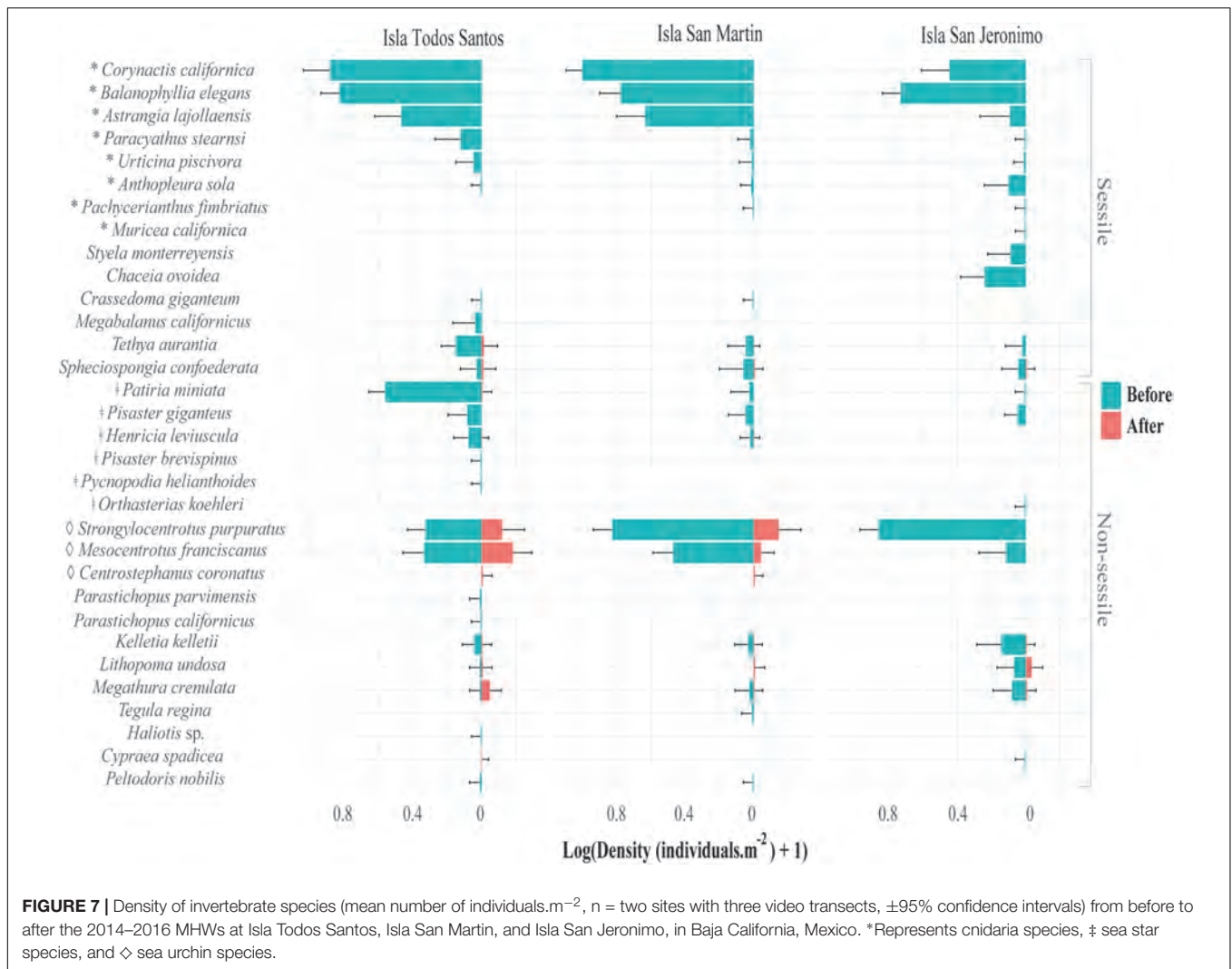
study revealed the sensitivity of our study sites to the MHWs, with loss of *M. pyrifera* forests and significant assemblage changes for fish, invertebrates and algae.

MHWs and the Loss of *M. pyrifera*

The 2014–2016 warming was the most intense and sustained event, with the highest percentage of MHW days registered, in the 37-year historical series for the CCS. Contrary to past El Niños, which appeared after negative temperature anomalies, the strong 2015–2016 El Niño began with an already warmer ocean (“Blob”) (Jacox et al., 2016). The unprecedented combination of these two events preceded the loss of *M. pyrifera* after summer of 2015, corresponding with the maximum temperature anomalies, which peaked at 5.9°C warmer than the climatology (this heatwave lasted for around 4 months). These anomalies were ~2°C warmer than any previous registered (El Niños), most likely with temperatures exceeding physiological thresholds for growth, survival, and reproduction of *M. pyrifera* (Zimmerman and Robertson, 1985; Hernández Carmona, 1988; Tegner et al., 1997; Hernandez-Carmona et al., 2001). The absence of significant

wave disturbance during this event (Reed et al., 2016) suggests a combination of thermal stress and nutrient-poor waters (Whitney, 2015) as the primary drivers behind kelp canopy disappearance in Baja California. Our results are consistent with previous work that reports the sensitivity of *M. pyrifera* in southern California and Baja California to warm, nutrient-poor waters (Zimmerman and Kremer, 1984; Hernandez-Carmona et al., 2001) during El Niño events (Dayton and Tegner, 1984; Dayton, 1985; Zimmerman and Robertson, 1985; Tegner and Dayton, 1987, 1991; Hernández Carmona, 1988; Tegner et al., 1996; Ladah et al., 1999; Hernandez-Carmona et al., 2001; Edwards, 2004; Edwards and Hernandez-Carmona, 2005; Edwards and Estes, 2006).

Reed et al. (2016) found no ecosystem effects in *M. pyrifera* kelp forests at Santa Barbara, California, to the same extreme warming event. They argued that the variability of giant kelp biomass was high during the 15 studied years and that the observed decline was within normal variability. However, fewer impacts to kelp forests located at Santa Barbara are expected since they are located ~1000 km north of the southern



distribution limit (i.e., the upper limit of thermal tolerance of *M. pyrifera*). There, average SSTs are ~3.3°C cooler than at our study sites, providing a greater population-level thermal safety margin (Pinsky et al., 2019). We found similar results in our northernmost site, ITS, located ~400 km south of Santa Barbara (nevertheless satellite derived biomass estimates remained very low during autumn 2015 and all 2016). However, in the southernmost sites, ISM and ISJ, located 550 and ~650 km south of Santa Barbara, respectively, we clearly detected the MHWs signal on *M. pyrifera* forests. Thus our results support previous studies in the CCS and other regions (Edwards, 2004; Edwards and Estes, 2006; Johnson et al., 2011; Wernberg et al., 2013, 2016; Horta e Costa et al., 2014), which reported kelp forest located near temperate-subtropical transition zones to be more vulnerable to historical warming events than those at higher latitudes. For example, following the MHWs of 2011 in Western Australia, Wernberg et al. (2016) reported a regime shift from a kelp to a seaweed turf dominated ecosystem in sites located near temperate-subtropical transition zones, but little or no change in communities at higher latitudes. Similarly, after 2017/2018

MHWs in New Zealand, Thomsen et al. (2019), found that *Durvillaea* spp. species located at warmer sites were more affected than those found in cooler ones. Although Reed et al. (2016), challenged the status of *M. pyrifera* as a sentinel species for climate change, our work suggests that sentinel status should be evaluated in a site-by-site or regional basis, and reinforces the status of Baja California as a sentinel area for climate change (Hobday and Pecl, 2014).

Macrocystis pyrifera forests in the CCS have proven to be dynamic and resilient ecosystems (Dayton et al., 1992; Filbee-Dexter and Scheibling, 2014), recovering quickly after previous El Niño events. La Niña conditions that usually follow El Niño events bring cold, nutrient-rich waters, representing favorable conditions for *M. pyrifera* (Dayton et al., 1992; Tegner et al., 1997; Edwards and Estes, 2006). The lack of La Niña conditions after the 2014–2016 warming event and the persistence of anomalously high SST during 2017 (around 50 days registered as MHWs) is probably challenging the capacity of *M. pyrifera* to recover.

Nevertheless, after the warming event *M. pyrifera* recovered at ITS, the northernmost site. We found higher densities of

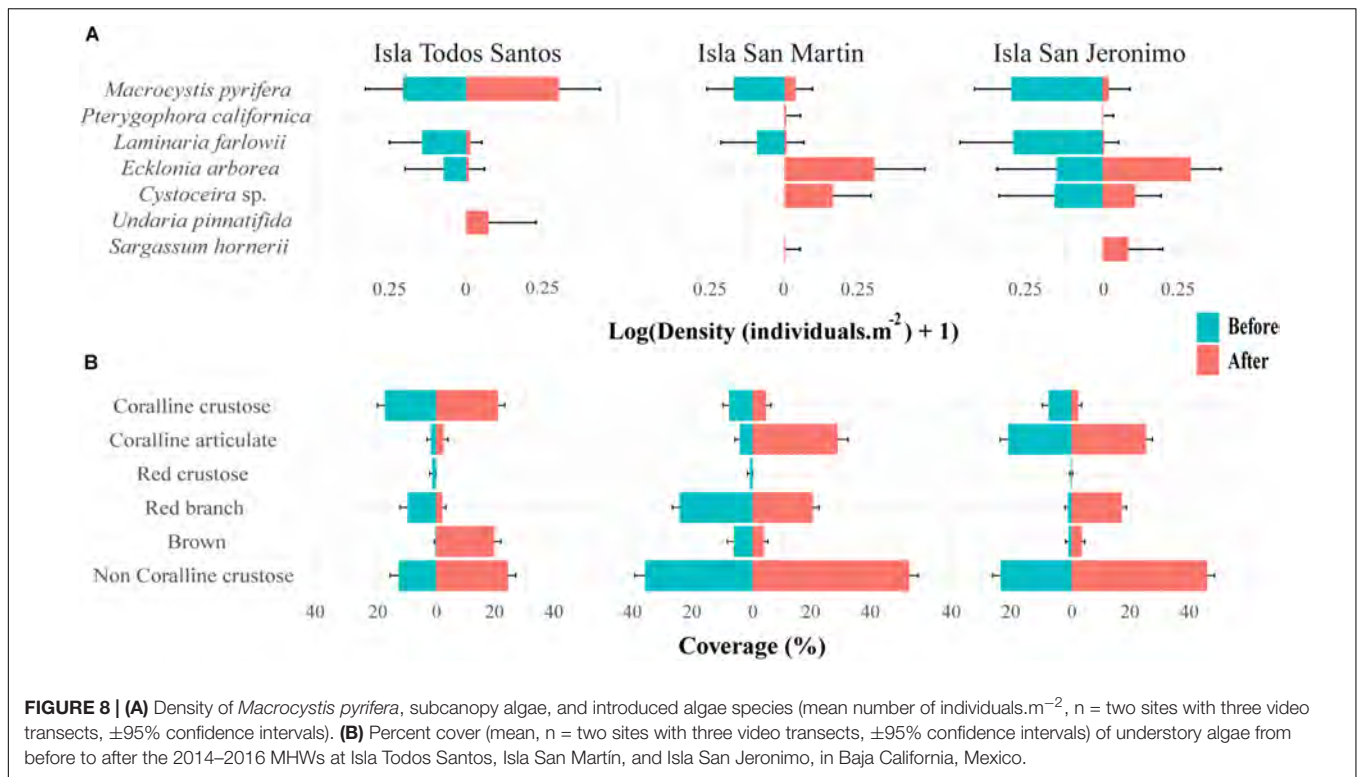


FIGURE 8 | (A) Density of *Macrocystis pyrifera*, subcanopy algae, and introduced algae species (mean number of individuals.m⁻², n = two sites with three video transects, ±95% confidence intervals). **(B)** Percent cover (mean, n = two sites with three video transects, ±95% confidence intervals) of understory algae from before to after the 2014–2016 MHWs at Isla Todos Santos, Isla San Martín, and Isla San Jerónimo, in Baja California, Mexico.

TABLE 2 | Results from the analysis of multivariate variance for PERMANOVAs of response variables as a function of the crossed factors Island and Time based on Bray-Curtis distance matrices derived from square-root transformed data, for (A) density of fish and invertebrate, (B) relative abundance of subcanopy algae, and (C) percent cover of understory algae species per survey.

Factors	Df	Sums of Sq	Mean Sq	F. Model	R ²	Pr(> F)
(A) Fish and invertebrates						
Island	2	1.2449	0.62243	7.300	0.17383	0.001
Time	1	2.8081	2.80806	32.934	0.39212	0.001
Island × Time	2	0.6357	0.31786	3.728	0.08877	0.005
Residuals	29	2.4726	0.08526		0.34528	
Total	34	7.1612			1	
(B) Subcanopy algae						
Island	2	1.1518	0.57591	5.0149	0.13323	0.002
Time	1	2.4372	2.43724	21.2231	0.28191	0.001
Island × Time	2	1.8408	0.92040	8.0147	0.21292	0.001
Residuals	28	3.2155	0.11484		0.37193	
Total	33	8.6454			1	
(C) Understory algae						
Island	2	1.22335	0.61168	20.6507	0.43458	0.001
Time	1	0.34778	0.34778	11.7413	0.12354	0.001
Island × Time	2	0.38492	0.19246	6.4975	0.13674	0.001
Residuals	29	0.85899	0.02962		0.30514	
Total	34	2.81504			1	

individuals than before the MHWs, but with significantly lower number of fronds per individual, indicating the dominance of young *M. pyrifera* individuals. The presence of some productive individuals (≥ 16 fronds/individual) implies that *M. pyrifera* did not lose its reproductive capacity, since sporophylls begin

to differentiate and have fertile sori when they have around 16 fronds/individual (Dayton et al., 1992). We found a strong effect of the MHWs on *M. pyrifera* densities and number of fronds per individual at the southernmost sites, ISM and ISJ, suggesting a very low density of fertile individuals. Biomass satellite time-series corroborate that kelp forest at ITS recovered after the MHWs, while at ISM and ISJ biomass values remained below average seasonal values throughout 2018. The three islands have similar mean SSTs, suggesting similar thermal safety margins, however, SSTAs and the maximum intensities registered during the MHWs were slightly higher at the southernmost sites than at ITS, which could explain the different latitudinal responses of the kelp forest to the extreme warming. However, it is also true that the differences in the anomalies were very small ($\sim 0.2^\circ\text{C}$) between islands and other factors such as local seascape complexity, which might create “microclimates” (Woodson et al., 2018; Pinsky et al., 2019), could also contribute to the observed differences. Previous studies found that deeper sites represented local refugia and individuals living there could find and survive strong warming events such as El Niño, possibly serving as a source of spores and recruits to colonized shallower rocky areas (Ladah et al., 1999). Further research could test whether the observed differences are a result of local seascape variability, latitudinal gradients in SSTAs, or perhaps a combination of both.

Community-Level Impacts

The extreme conditions resulted in dramatic changes in the invertebrate, fish, and algal assemblages, with the loss of over half of invertebrate species. The significant reduction or disappearance of *M. pyrifera* can have profound effects on other

members of the community (Graham, 2004) due to a release of resources (space and light) (Reed and Foster, 1984; Dayton, 1985) and a decrease in food availability (Ebeling et al., 1985; Harrold and Reed, 1985). Although we found evident changes, we cannot separate between the effects of high SSTs and loss of canopy on the community, since both are synergistically affecting all food web levels. Importantly, we found that *M. pyrifera* dynamics at the two southernmost islands in our study immediately after the MHWs were beyond the limits of natural variation in the previous 5 years, and remained that way until the end of our study in 2018. Although all other metrics we analyzed represented only two periods, a year before and a year after the MHW, this finding that kelp biomass was significantly and persistently impacted by the MHW gives us some confidence in attributing community-wide impacts to the effects of the MHWs.

Loss of Sessile Invertebrates and Sea Stars

After the warming event, almost all sessile invertebrates disappeared, and all cnidarians were absent. Sessile invertebrates are highly sensitive to extreme temperature conditions due to their inability to escape from unfavorable conditions (Przeslawski et al., 2008) and their dependence on phytoplankton and suspended organic matter as food sources that might decrease during warming events (e.g., during El Niño events, when upwelling is suppressed). Reports of mass mortality of sessile species and bleaching of corals in temperate and tropical ecosystems (Berkelmans and Willis, 1999; Hoegh-Guldberg, 1999; Cerrano et al., 2000; Marshall and Baird, 2000; Perez et al., 2000; Garrabou et al., 2001, 2009; Caputi et al., 2014; Couch et al., 2017; Hughes T. P. et al., 2017) suggest that SSTs at our sites probably peaked at values in excess of their physiological tolerances (Lejeune et al., 2010). Moreover, almost all sea star species disappeared or dramatically decreased their abundance. In 2014, an epidemic outbreak of wasting disease from Alaska to Mexico led to mass mortalities of many sea star species (Hewson et al., 2014). Anomalously warm water conditions in the CCS have been suggested to favor the spread of the densovirus linked to this disease and thus increase the mortality rate in sea stars (Eckert et al., 2000; Hewson et al., 2014).

Loss of Cold-Water Species and Increase in Some Warm Affinity Ones

For the entire community, we report the loss or decrease in abundance of many species with cold-water affinities and the appearance or increase in abundance of some species with warm-water affinities. The tropicalization of fish species near temperate transition zones has already been attributed as the primary driver of composition change in the fish assemblage (Wernberg et al., 2013, 2016; Caputi et al., 2014; Horta e Costa et al., 2014; Vergés et al., 2014; Smale et al., 2019). The loss of the ten fish species having the most northerly distribution centroids suggests SSTs peaked above their thermal tolerances and favored species with stronger affinity to warmer waters, such as *H. semicinctus* (Fishbase). We also reported the presence of the sea-urchin *C. coronatus* at ITS and ISM, which has the southernmost

distribution range of invertebrate species described in this study. Similar patterns favoring *C. coronatus* have been reported during El Niño 2009–2010, where populations in one site at Oaxaca (Pacific southern Mexico) increased (López-Pérez et al., 2016), and during El Niño 2015 in southern California, with reports of poleward range expansion (Freiwald et al., 2016). Another example is a species from the same genus, *Centrostephanus tenuispinus*, which was the main winner after an extreme MHW in 2011 on the west coast of Australia (Smale et al., 2017).

The effect of warm water temperatures was also evident in kelp forest subcanopy species *L. farlowii* and *E. arborea*. *L. farlowii* was the characteristic subcanopy species before the MHWs, probably due to the absence (or very low densities) of the competitively superior *Pterygophora californica* (Tegner et al., 1997). In 2016, abundance of *L. farlowii* dramatically decreased, despite favorable niche conditions (light and space) after the loss of *M. pyrifera* forest. The sensitivity of *Laminaria* species to warm water conditions (Schiel et al., 2004) might explain its decrease after the extreme warming. On the contrary, abundances of *E. arborea*, known to be favored during El Niño conditions due to its tolerance to warm, nutrient-poor conditions (Dayton et al., 1984; Hernandez-Carmona et al., 2000; Matson and Edwards, 2007), increased at the two southernmost islands.

The influence of the warming event on the understory algae was less evident and more variable than for the rest of the community. For the southernmost islands (ISM and ISJ), we found a decrease in cover of coralline crustose algae, which have been reported to be sensitive to MHWs (Martin and Gattuso, 2009; Smale and Wernberg, 2013; Voerman et al., 2013; Wernberg et al., 2013, 2016; Short et al., 2015; Thomsen and South, 2019). However, the role of heatwaves in regulating abundance of coralline algae is still not clearly understood, since other factors, such as the loss of canopy cover (Irving et al., 2004, 2005; Flukes et al., 2014) or ocean acidification (McCoy and Kamenos, 2015), might also be influential for this group. The presence of coralline crustose algae can be facilitated by canopy-forming kelp species as they exclude other macroalgal competitors (Thomsen and South, 2019). This could explain the decrease of this taxon at the southernmost islands after the MHWs, while at the northernmost site, their cover and the abundance of *M. pyrifera* remained high. Little attention has been paid to coralline crustose algae, despite representing important habitats, and food sources for diverse epifaunal invertebrates (Graham et al., 2007; Thomsen and South, 2019), as well as providing chemical cues for abalone settlement (Morse et al., 1979; Miner et al., 2006). A generalized increase in the coverage of non-crustose coralline understory algae at all sites suggests that the combined loss of canopy kelp, sessile invertebrates, and coralline crustose algae might have modified light conditions and liberated free space for recruits (Reed and Foster, 1984), which probably favored the rest of the understory assemblage (Reed and Foster, 1984; Dayton et al., 1992; Tegner et al., 1997; Clark et al., 2004).

The Appearance of Invasive Species

Finally, we report the appearance of two invasive macroalgal species, *U. pinnatifida* at ITS and *S. hornerii* at ISM and

ISJ. In Baja California, *U. pinnatifida* was first detected in 2003 (Aguilar-Rosas et al., 2004) and *S. hornerii* in 2005 (Aguilar-Rosas et al., 2007). In 2013, both species appeared during monitoring surveys at the protected side of the three islands, but were absent from the exposed sides (our study sites) (Montaño-Moctezuma et al., 2014). *U. pinnatifida* is an opportunistic cosmopolitan invasive species (Lowe et al., 2000) able to tolerate a wide range of temperatures (Morita et al., 2003), allowing this species to colonize empty spaces left by canopy-forming kelps. Nevertheless, without disturbance, *U. pinnatifida* rarely establishes under a dense canopy (Valentine and Johnson, 2003; Thomsen and South, 2019; Thomsen et al., 2019). Similar findings have been reported in other parts of the world as a result of both MHWs (Thomsen et al., 2019) and manipulated removal experiments (Thomsen and South, 2019). For example, in summer 2017–2018, strong MHWs in New Zealand caused the decline of the canopy-forming kelp species *Durvillaea* spp., and a successive subsequent invasion by *U. pinnatifida* (Thomsen and South, 2019; Thomsen et al., 2019). Our study supports previous research that opportunistic and invasive species are usually outcompeted by native species, but adverse conditions can leave empty niche space and trigger their expansion (Valentine and Johnson, 2003, 2004; Occhipinti-Ambrogi, 2007; Epstein and Smale, 2017; South et al., 2017). Although it is difficult to predict the long-term effect of invasive species, more frequent MHWs might increase the probability that invasive species colonize and perhaps displace native species.

General Implications

With one-time observation before and after, the ecological changes we describe cannot be confidently attributed to the MHWs. However, we chose our study sites on inhabited islands, since they are less impacted by cumulative human activities (Arafteh-Dalmau et al., 2017) than coastal areas, but are vulnerable ecosystems due to their isolation (Johnson and Black, 2006; Bell, 2008) making them ideal sites to understand kelp forests response to MHWs. Our study sites span a 250-km latitudinal gradient (almost half of the distribution of kelp in Baja California), allowing us to capture a good portion of the biogeographic variability of the region. There is also strong circumstantial evidence that the MHWs were, indeed, the driver of the observed changes: not only was there a corroborating signal in remote-sensed time series of kelp biomass, but we are unaware of any other plausible human-induced changes during the 2013–2018 period that could have altered the community structure in this way. Nevertheless, considering that the response of communities to the same disturbance might vary within the same region (Wernberg et al., 2013, 2016; Thomsen et al., 2019) and even within sites (Woodson et al., 2018), we acknowledge the need to understand the dynamics of these ecosystems at broader spatial and temporal scales and emphasize that our results should not be extrapolated without due care.

Kelp forest coverage has been reduced worldwide (Krumhansl et al., 2016; Wernberg et al., 2019), in part, due to climate change. Moreover, in some areas, their historical distribution limit has contracted poleward (Johnson et al., 2011; Wernberg et al., 2013, 2016), with clear signs of tropicalization of temperate ecosystems

(Vergés et al., 2014). If positive temperature anomalies persist (2018 was still an anomalously warm year), the chronic effects of these warming events might shift Baja California's ecosystems to a new alternative state, potentially precipitating range contractions for *M. pyrifera* and other species. Although future ecological states are difficult to predict in such dynamic ecosystems, our findings might be an early indication of a possible tropicalization of Baja California's kelp forest (Cheung et al., 2013) under climate change, emphasizing the need to monitor and manage these ecosystems.

Southern kelp forests of the CCS are a shared marine resource between the south of California and the north of Baja California (Ramírez-Valdez et al., 2017). Advancing the understanding of the ecological impacts of MHWs (Hobday and Pecl, 2014) in this transboundary region to promote adequate management strategies will require a binational effort (Aburto-Oropeza et al., 2018). Thus, the protection of these valuable ecosystems needs immediate actions and close collaboration between southern California and Baja California (Arafteh-Dalmau et al., 2017). If we fail to act, once-abundant, extensive *M. pyrifera* forests could experience important local declines, as they have in other regions (Johnson et al., 2011), leading to detrimental ecological and socio-political outcomes (Frölicher and Laufkötter, 2018).

DATA AVAILABILITY

All datasets generated for this study are included in the manuscript and/or the **Supplementary Files**.

AUTHOR CONTRIBUTIONS

GM-M, GT-M, and NA-D designed the initial project with the final review of RB-L, JM, and DS. NA-D, GT-M, RB-L, and JM collected the data. NA-D, GM-M, and DS conducted the data analysis and interpretation and were discussed by all other authors. NA-D and GM-M drafted the work and was revised by all other authors. All authors approved the version to be published and agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00499/full#supplementary-material>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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