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Heatwave restructures marine intertidal communities across a stress gradient

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Abstract

Significant questions remain about how ecosystems that are structured by abiotic stress will be affected by climate change. Warmer temperatures are hypothesized to shift species along abiotic gradients such that distributions track changing environments where physical conditions allow. However, community-scale impacts of extreme warming in heterogeneous landscapes are likely to be more complex. We investigated the impacts of a multiyear marine heatwave on intertidal community dynamics and zonation on a wave-swept rocky coastline along the Central Coast of British Columbia, Canada. Leveraging an 8-year time series with high seaweed taxonomic resolution (116 taxa) that was established 3 years prior to the heatwave, we document major shifts in zonation and abundance of populations that led to substantial reorganization at the community level. The heatwave was associated with shifts in primary production away from upper elevations through declines in seaweed cover and partial replacement by invertebrates. At low elevations, seaweed cover remained stable or recovered rapidly following decline, being balanced by increases in some species and decreases in others. These results illustrate that, rather than shifting community zonation uniformly along abiotic stress gradients, intense and lasting warming events may restructure patterns of ecological dominance and reduce total habitability of ecosystems, especially at extreme ends of pre-existing abiotic gradients.

KEYWORDS
biodiversity, foundation species, intertidal zonation, marine heatwave, marine rocky shore, seaweed, thermal stress

INTRODUCTION

Understanding ecological responses to climate challenges science and society (Peters & Darling, 1985; Vasseur et al., 2014). Temperature is a fundamental driver of biological processes across ecological and evolutionary scales, yet we lack a complete understanding of how warming will interact with existing environmental

variation to restructure communities. Because ecosystems are shaped by multiple environmental factors, warming is unlikely to elicit the same responses across environments (McManus et al., 2020; Usinowicz & Levine, 2018). This complicates our ability to predict and attribute ecological changes without first understanding underlying environmental variation (Bruno & Selig, 2007). A comprehensive understanding of how climate change will impact ecological systems—from species distributions to ecosystem functioning—therefore requires understanding how ecological impacts of warming map to local, heterogenous environments.

A few generalizable patterns have been established for how species distributions shift with directional climate change; for example, changes in elevation and latitude have been explored and documented for decades (Parmesan & Yohe, 2003). Species track changing environments through demography and migration (Mclaughlin & Zavaleta, 2012; Pinsky et al., 2013), often expanding parts of ranges unless physical habitat boundaries (Kelly & Goulden, 2008; Wernberg et al., 2011), physiological constraints (Pörtner & Farrell, 2008), dispersal limitation (Pringle et al., 2017), or species interactions (Clark et al., 2011; Usinowicz & Levine, 2021) prevent such tracking. What remains unclear is how shifts in population abundance and distribution along changing abiotic gradients will alter the structure and functioning of ecological communities.

While gradual increases in temperature are already impacting populations and communities near physiological limits and habitat boundaries (Freeman et al., 2018; Verges et al., 2014), some of the most profound ecological effects of climate change have been observed in response to extreme climate events such as heatwaves (Cavole et al., 2016; Guest, 2021; Peterson et al., 2021). As the frequency, severity, and duration of heatwaves increase over time with climate change (e.g., Mazdiyasni & AghaKouchak, 2015; Oliver et al., 2019), the need to understand ecosystem responses becomes more essential and immediate. Heatwave events that involve temperatures exceeding physiological thresholds or that occur across critical life cycle transitions may lead to complex shifts in demography, biodiversity, and ecosystem stability (e.g., Ives & Carpenter, 2007). Observational field studies conducted in changing environments provide opportunities to investigate real-time fluctuations in diverse and complex living systems, informing ecological theory in a changing world (Sagarin & Pauchard, 2010).

Between 2014 and 2016, the Northeast Pacific experienced a marine heatwave of unprecedented duration and intensity linked to persistent high pressure in the North Pacific that prevented cooling and a major El Niño (Di Lorenzo & Mantua, 2016; Laufkötter et al., 2020; Tseng et al., 2017). This event elicited varied responses across a wide range of taxa and habitats, with some taxa benefiting from the warmer conditions and others experiencing severe detrimental impacts (Cavole et al., 2016). Like most marine heatwaves and climate oscillations (e.g., El Niño), the 2014–2016 NE Pacific heatwave was oceanographic and atmospheric in its manifestation, and a growing number of studies have documented how coastal ecosystems above and below water responded to accumulative stress associated with this heatwave (Cavanaugh et al., 2019; Sanford et al., 2019; Shi et al., 2021; Starko et al., 2022; Suryan et al., 2021).

Here, we examine the community-level impacts of this sustained warming event in a rocky intertidal ecosystem dominated by seaweeds. Work on rocky shores has informed our understanding of many ecosystems, in part because compact physical settings make observations and experiments in multispecies communities feasible across strong gradients in physiological stress (Connell, 1971; Harley, 2011; Lubchenco, 1978). At higher tidal heights, organisms spend more time exposed to air during low tide, reaching higher body temperatures (Helmuth et al., 2002), and experiencing greater thermal and desiccation stress (Blouin et al., 2011; Drake et al., 2017). Consequently, abiotic stress is a central driver of species' upper elevation limits in intertidal ecosystems. Because intertidal organisms often live at or near their physiological limits (Somero, 2002), warming is expected to alter vertical distributions by compounding existing stressors (e.g., desiccation, acute heat stress, photooxidation) that, together with species interactions, determine a stereotypical intertidal pattern of horizontal bands of dominant species and their associates ("zonation"). Patterns of zonation may shift with changes in individual populations or community interactions (Harley, 2011; Harley & Paine, 2009), but there are few researched examples of intertidal community responses to heatwaves that include more than a few dominant taxa (Spiecker & Menge, 2022; Suryan et al., 2021, but see Miner et al., 2021).

Using an 8-year time series of intertidal seaweed biodiversity spanning the historic marine heatwaves that began in 2014 (Chen et al., 2021; Di Lorenzo & Mantua, 2016), we characterized shifts in seaweed populations and communities across an elevation gradient that coincided with changing environmental conditions. We asked whether changes in communities were consistent with similar observations made during this prolonged heatwave (e.g., Miner et al., 2021; Suryan et al., 2021; Weitzman et al., 2021) and with ecological predictions of climate change. We hypothesized that (1) species would decline in elevation when abiotic stress increases and (2) species living at higher elevations would experience the greatest declines in abundance because those species adapted to the largest fluctuations in environmental

conditions may have less ability to acclimate during extreme climate events (Harley, 2003; Stillman, 2003). Further, while we expected abundance responses to vary across taxa (Cavole et al., 2016; Straub et al., 2019), we hypothesized that (3) seaweed functional groups would reveal group-level responses within communities. While such coarse groupings ultimately sacrifice information (Mauffrey et al., 2020), they remain common when species identities are difficult to assess in the field and continue to be used to understand ecological responses to anthropogenic stressors (e.g., Filbee-Dexter & Wernberg, 2018; Smith et al., 2016). Last, the historically prolonged nature of the heatwaves led us to hypothesize that (4) heatwave duration (i.e., stretches of anomalously warm days) would predict changes in total community abundance (e.g., total percentage cover of seaweeds) and local species richness.

METHODS

Sites and surveys

We monitored intertidal biodiversity and abundance on Calvert Island, Central Coast British Columbia, Canada, within the Hakai-Lúxvbálís Conservancy (Figure 1). Calvert Island is home to a diverse and widely distributed marine flora (e.g., Lindstrom et al., 2021), making results from these communities potentially applicable across a broad latitudinal range. In 2011, we selected three sites to represent the variety of moderately exposed coastlines (Cook et al., 2017) where diverse intertidal seaweed assemblages are accessible. Foggy Cove (51.6514° N, 128.1433° W) is a boulder field, while North Beach (51.6655° N, 128.1353° W) and Fifth Beach (51.6409° N, 128.1568° W) are bedrock benches that differ in slope and exposure to sun, winds, and waves (Appendix S1: Figure S1). At each site, we established three permanent transects (marked by stainless steel bolts) running parallel to shore at different elevations representing low, middle, and high intertidal zones (Table 1). Although absolute elevations and distances between transects differed among sites (Appendix S1: Figure S1), we laid transects based on commonalities in seaweed and invertebrate assemblages to maximize community similarity within zones: low zones were characterized by kelps and *Neorhodomela larix*, middle zones commonly featured primary cover by coralline red algae, and high zones were dominated by *Fucus distichus*, *Endocladia muricata*, barnacles, and mussels (Appendix S1: Figure S2). Transects were surveyed annually from 2012 to 2019 during a spring tide series (3–4 days) between May and July (Appendix S1: Table S1, Figure S3).

Each year, we randomly selected 10 positions at meter intervals along each transect and visually estimated the percent cover of sessile organisms in a 0.5×0.5 m quadrat at each position (Appendix S1: Figure S4). We also photographed surveyed quadrats. In order to estimate continuous tidal heights along topographically variable transects, we measured elevation relative to the Canadian chart datum at every possible quadrat position using a stadia rod and laser level (Table 1). Because of the layered growth of species, the total percent cover in a quadrat could exceed 100%. Seaweed taxa were identified using Gabrielson et al. (2012), and the identities of many were confirmed with DNA sequencing following Lindstrom et al. (2011) or Hind et al. (2019). Invertebrates were identified to genus or order (Appendix S1: Table S1) and included in the analysis, but we focus our interpretation on seaweeds and acknowledge that we cannot attribute higher-level responses of invertebrates to individual species known to differ in ecology and life history.

Environmental data

To assess the environmental context for trends in survey data, we drew upon publicly available temperature records from three nearby lighthouses (Figure 1; Appendix S2: Figure S1). Specifically, we collated daily sea surface temperature records from Pine Island (50.975° N, 127.728° W; 1937–2019) and McInnes Island (52.262° N, 128.723° W; 1954–2019), as well as daily air temperatures from Addenbroke Island (51.608° N, 127.844° W; 1978–2019), all available through the Government of Canada at https://open.canada.ca/data/en/dataset/719955f2-bf8e-44f7-bc26-6bd623e82884/resource/2a1463cc-53c8-4268-9986-654e0e729506. We used principal components analysis (PCA) to reduce the dimensionality of the three time series, starting in 1978, and to create a single metric capturing oceanographic and atmospheric features of the heatwave. We first imputed missing values using the R function "imputePCA" before running the PCA (Josse & Husson, 2016). The first PCA axis explained 87.8% of all data across the three time series and was associated with increasing temperature at all three lighthouses (loadings >0.90; Appendix S2: Figure S2). We used this first PCA axis to categorize anomalous regional temperature conditions based on Hobday et al. (2016), characterizing warm and cold periods lasting 5 days or more relative to the 90th and 10th percentiles of climatology as heatwaves and cold snaps, respectively. Specifically, we calculated the intensity (i.e., maximum anomaly) and duration (i.e., number of heatwave days) of each heatwave using 41 years of aggregated daily measures of temperature.
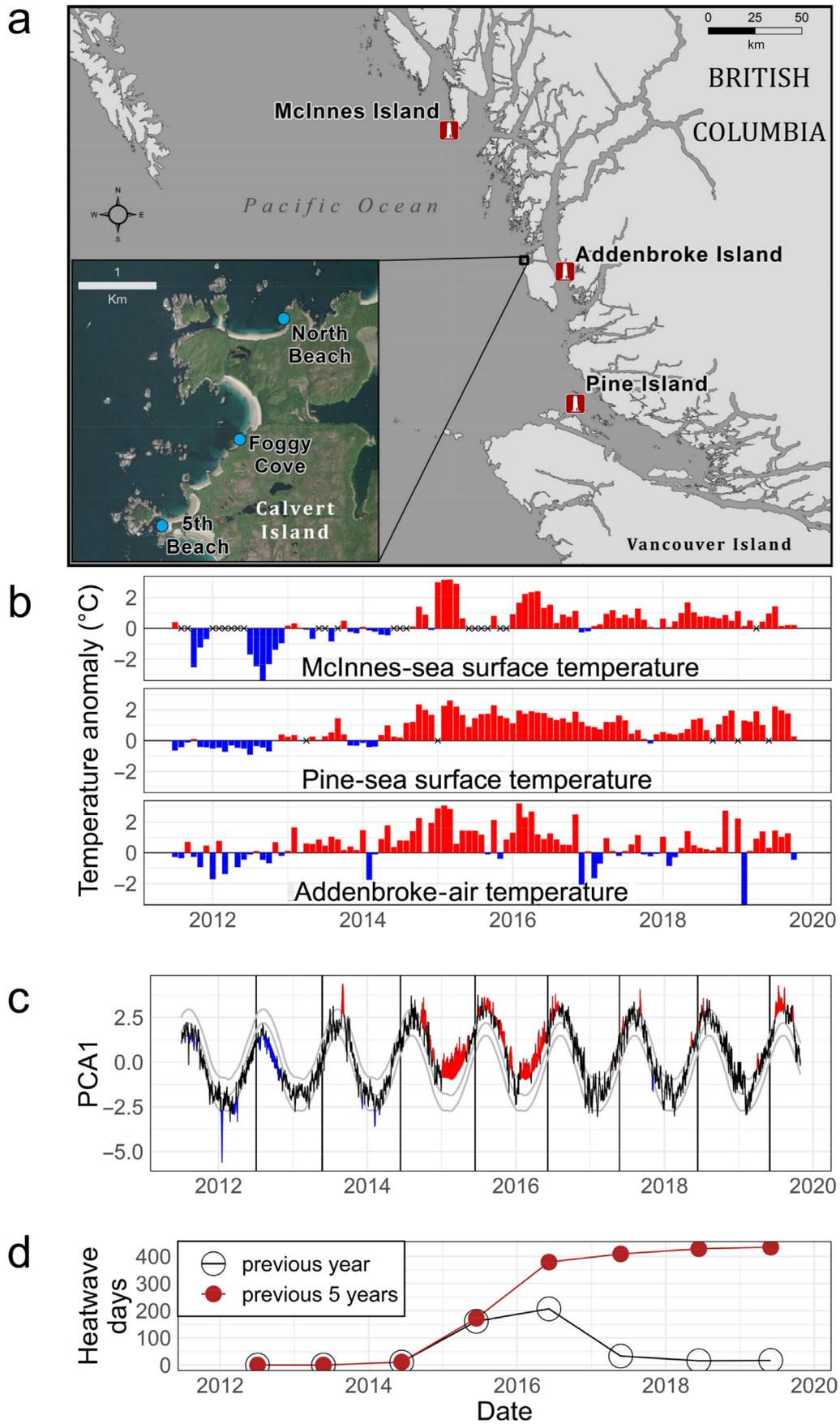
FIGURE 1 Legend on next page.

TABLE 1 Tidal elevation and length of each transect.

Site	Area (m²)	Slope mean (°)	Transect location	Elevation mean (m)[a]	Elevation range (m)[a]	Transect length (m)
Foggy Cove	2274	15.1	High zone	2.62	1.84–3.52	44
			Mid zone	1.88	1.55–2.59	49
			Low zone	1.02	0.61–1.38	36
North Beach	274	22.9	High zone	2.98	2.02–3.82	24
			Mid zone	2.51	1.84–2.85	24
			Low zone	1.25	0.90–1.72	23
Fifth Beach	281	28.2	High zone	3.25	2.43–3.81	29
			Mid zone	2.23	1.70–2.59	26
			Low zone	1.64	1.15–2.29	24

[a]Elevation measurements are meters above lower low water large tide (https://tides.gc.ca/en/vertical-datum-chart-references).

Lighthouse data were highly correlated with a shorter time series of water temperature from Calvert Island (Appendix S2: Section S1, Figure S3), suggesting that environmental anomalies captured by the lighthouses reflect the relative thermal conditions experienced at the study sites. We also collected in situ rock temperatures from the high-shore transect at Foggy Cove (Appendix S2: Section S2, Figures S4 and S5), but we use only lighthouse data in our statistical analysis because these time series span the entire survey period and include a sufficiently long historical baseline to define heatwaves.

Functional group assignments

In order to determine how morpho-functional traits influenced community responses, we classified macroalgal and seagrass species into functional groups, largely following Steneck and Dethier (1994) but with fewer categories. Their "leathery macrophytes" (kelps and fucoids) we called canopy-formers to include the nonleathery canopy-forming species, *Phyllospadix* spp., and their "crustose algae" we called crusts. Other categories were modified to reflect algal function beyond strict anatomical delineations. Thus, their "filamentous algae" and some smaller "corticated macrophytes" became our thin turfs; larger "corticated macrophytes," some "corticated foliose

algae," and "articulated corallines" became our turfs; and their "foliose algae" and some of their "corticated foliose algae" became our blades. We adopted the broad definition of turf from Filbee-Dexter and Wernberg (2018) but further assigned thick (e.g., *Mastocarpus* spp.) and thin (e.g., *Cladophora columbiana*) turfs based on the thickest branch diameter (more or less than ~2 mm, respectively). The following five seaweed functional groups were included in the final analyses: canopy-former, blade, crust, thin turf, and thick turf (Appendix S3: Table S1).

Species-level changes in abundance and elevation

We used hierarchical modeling of species communities (HMSC; Ovaskainen et al., 2017) to explore how the distribution and abundance of individual taxa changed over time and elevation, using quadrats ($n = 717$) as the unit of replication (Appendix S1: Figure S3). We used a hurdle approach, consisting of (1) a probit model of presence-absence data (occurrences) and (2) a Gaussian model of log-transformed percent cover data conditional on the presence (zeros removed), hereafter "conditional cover." Predictions from these models allowed us to consider separately occurrence and density, and, when multiplied together, produce predictions of percent cover.

FIGURE 1 Study sites and regional environmental conditions. (a) Map of Central British Columbia, Canada, and study area on the northwest coast of Calvert Island (inset). Locations of three lighthouses are marked on the map along with (b) time series showing sea surface temperature and air temperature anomalies relative to monthly means from 1970 to 2019. (c) Temperature data from these lighthouses were combined using principal components analysis (PCA; see Appendix S2). PCA axis 1 (black line) is shown along with mean climatology and the 10th and 90th percentiles (gray lines). Heatwaves and cold spells are shown with red and blue fill, respectively, and survey dates are denoted with vertical lines. (d) Duration of heatwaves expressed as cumulative heatwave days in the year and 5 years leading up to each survey. Note data missing in the temperature anomaly time series are denoted with an "X" in (b).

The hurdle approach was also helpful because of the highly zero-inflated abundances for many taxa. These phenomenological models allowed us to simultaneously address hypotheses about changes in abundance, diversity, and distribution across individual taxa and functional groups.

We included several nonlinear terms in the HMSC models because we observed that some species declined in cover and then rebounded during our surveys and because species in this system tend to have unimodal distributions across elevations. We modeled occurrence and log-transformed cover as quadratic functions of quadrat elevation and year (fixed effects). We allowed linear terms for elevation to interact with linear and quadratic terms for year, and we included site, transect, and quadrat as random intercepts (see Appendix S3 and Whalen, 2023).

We used functional group assignments to test how species responses to fixed effects were attributable to morpho-functional traits; starting with a prior assumption that species with similar traits have similar responses, the model uses information from common taxa to obtain more reliable parameter estimates for rarer ones. We included 47 well sampled taxa following an arbitrary requirement that each taxon must have occurred at least 48 times (six quadrats per year, on average; Appendix S3: Section S1, Table S1). The 70 rare taxa we removed accounted for 5% total cover, on average, but four of these taxa exceeded 50% cover in at least one quadrat (Appendix S3: Figure S1). Most taxa were modeled at the species level, but the variation in taxonomic resolution over time and the constraints of field identification required us to lump several taxa into genus or higher (Appendix S3: Section S1). We ran models using the following setup: chains = 4, thin = 100, transient = 12,500, samples = 250, for a total of 1000 posterior samples. We tested for convergence using Gelman's diagnostic scores and visual assessment of trace plots (Appendix S3: Section S2; Vehtari et al., 2021).

We drew several inferences from model posterior probabilities. To assess population changes over time, we tested for linear trends in occurrence, conditional cover, and cover (occurrence × conditional cover) for taxa and functional groups across the range of elevations, weighting by the sample frequency within eight elevation bins, greatly simplifying calculations. This produced 1000 slopes, which we summarized using medians and 50% and 95% credible intervals (CIs), using the latter as a threshold for significant deviation from zero. We further assessed linear trends in elevational distributions using the predicted elevation peak for each taxon in each year of the probit model, which we defined as the mean of elevations exceeding half the maximum probability of occurrence within the range of surveyed elevations. This approach increased our ability to detect elevational changes over time; the spatial distributions for many taxa exceeded the surveyed elevational range, especially toward the subtidal zone, resulting in a high frequency of cases in which maximum cover was predicted at the upper or, more typically, lower edge of surveyed elevations.

Aggregate changes in community structure and biodiversity

In order to further assess temporal changes in communities, including contributions of rarer taxa, we used the complete dataset of seaweeds and invertebrates (116 taxa after removing singletons) and analyzed transect-level cover data. We present the total annual cover of seaweeds and invertebrates averaged within transects and three diversity metrics for seaweeds calculated for each year (richness, Hill-Shannon, Hill-Simpson; Roswell et al., 2021). For each data aggregate, we tested for change over time using linear regression, including transect and year as fixed effects and using 95% confidence limits around least-squares means for slopes on each transect to infer statistical significance. Data were log-transformed to better satisfy model assumptions. We also ran models predicting species richness and cover as a function of heatwave duration to quantify the association between community change and environmental change. Because impacts from multiyear heatwaves may result from the accumulation of stress over time, we compared generalized linear models (Poisson link function) with predictor variables for total heatwave duration (heatwave days, based on PCA) measured 1 year and 5 years prior to the start of each survey (Figure 1c,d).

Statistical software

Data manipulation and analyses were performed in R version 3.6.3 (R Core Team, 2019), relying on packages *readxl* (Wickham & Bryan, 2019), *tidyverse* (Wickham et al., 2019), *Hmsc* (Tikhonov et al., 2021), and *heatwaveR* (Schlegel & Smit, 2018).

RESULTS

Species shifted in both abundance and vertical elevation

We documented significant shifts in the abundance and vertical distribution of species that began during the 2014–2016 marine heatwave. Conditions on the Central Coast of British Columbia were anomalously and

historically warm for prolonged periods from 2014 to 2019 as shown by temperatures from all three lighthouses (Figure 1). The survey period included 6 of the 10 years with the greatest total number of heatwave days recorded at Pine Island in 82 years (Table 2). Moreover, rock temperatures at Foggy Cover exceeded 30 and 35°C several times during the heatwave (Appendix S2: Figures S4 and S5). Ten of the 43 seaweed taxa that we modeled with HMSC declined in cover over the 8 years surveyed (based on 95% CIs), while only two significantly increased (15 out of 43 trended toward decrease and 10 out of 43 trended toward increase with 50% CIs) (Figure 2a; Appendix S3: Figures S3 and S4). We also observed greater proportional declines in cover among initially more abundant and common taxa ($r = -0.39$; Appendix S3: Figure S5).

Declines in seaweed cover were sometimes, but not always, accompanied by shifts in vertical distribution (Figure 2b). Seaweeds tended to shift toward lower elevations (median response $= -34.9$ cm, interquartile range $= -96$ to 0 cm), with significant shifts in peak elevation detected for 11 of 43 modeled seaweeds (downslope trends 22 of 43 based on 50% CIs; Figure 2). We detected no significant upslope shifts, consistent with the hypothesis that increasing abiotic stress would erode the upper margins of intertidal seaweed distributions. Importantly, shifts in cover and elevation were uncorrelated ($r = -0.05$), with cover declines and increases occurring across the range of sampled elevations (Appendix S3: Figure S5d). Nonetheless, peak elevation and cover both tended to decline; during the study period, modeled elevation peaks declined by 35 cm and cover declined by 25%, on average. However, the median predicted shifts in elevation and cover ranged from -122 to $+24$ cm and 97% loss to a six-fold increase, respectively, highlighting the diversity of responses across taxa.

Our analysis of shifts in occurrence, cover, and peak elevation focused on detecting linear trends over time, but we also detected nonlinear temporal trends for some taxa: quadratic parameters for the survey year were significant for 15 of 47 taxa in HMSC models. In some cases, these nonlinear temporal trajectories suggest greater changes than those summarized by linear trends, such as the loss and partial recovery of *Alaria marginata* (Figures 3b and 4) or the precipitous decline of *Palmaria hecatensis* (Figure 4g). Other cases, such as the abrupt crash observed for *Pyropia* spp. in 2016 (Figure 4h), were not captured by our HMSC models but are likely to represent acute responses to the heatwave.

Total seaweed cover declined

We observed major declines in total seaweed cover; prior to the 2014–2016 heatwave, average cover of all seaweeds

TABLE 2 Top 10 heatwave years based on total days warmer than the threshold water temperature (90th percentile of the seasonal trend) between 1937 and 2019 at Pine Island (Figure 1a,b).

Year[a]	Days above seasonal threshold	Maximum anomaly (°C)
2016	**300 (207)**	**3.5**
2014	**274 (11)**	**3.8**
2019	**198 (17)**	**3.9**
2015	**173 (161)**	**3.1**
2018	**170 (16)**	**2.6**
1997	131	4.3
1941	119	1.8
1998	116	2.2
2017	**102 (33)**	**2.9**
1992	83	2.9

Note: Total heatwave days are shown along with the maximum detected heatwave intensity, expressed as degrees Celsius above the threshold temperature. Years included in this study are shown in bold, and numbers in parentheses show the no. heatwave days leading up to each annual survey using principal components analysis (PCA) axis 1 (Figure 1c,d). The time series was interpolated linearly to fill gaps prior to calculations. See Appendix S2 for additional details.
[a]Four years featured higher maximum heatwave anomalies than those included here (1963 = 4.0°C, 2013 = 3.9°C, 1967 = 3.4°C, 1978 = 3.1°C).

along transects routinely exceeded 100% cover (including canopy-forming and understory species), but total seaweed cover declined significantly on all three high-shore transects and two midshore transects (ranging from 53%–83% observed decline; Figure 5b). Changes in seaweed cover and bare space were each predicted by the cumulative number of heatwave days for both one and 5 years leading up to each survey (Table 3), and models that included the five-year time window had stronger support than those that included only the previous year (ΔAIC >10). In contrast with seaweeds, sessile invertebrates increased in cover (Figures 2a and 5c), with *Mytilus* mussels increasing more than 20-fold (Figures 3d and 4f). The invertebrate cover change was positively associated with cumulative heatwave days over a 5-year time window (Table 3). The availability of bare rock substrate (i.e., habitat lacking seaweeds and sessile invertebrates) also increased significantly on four transects (Figure 5d): bare space was positively associated with heatwave duration (Table 3) and negatively correlated with total seaweed cover ($r = -0.63$, $p < 0.001$).

Functional groupings failed to capture species-specific responses

Of the five seaweed functional groups, only thin turfs declined linearly in occurrence over time while crusts
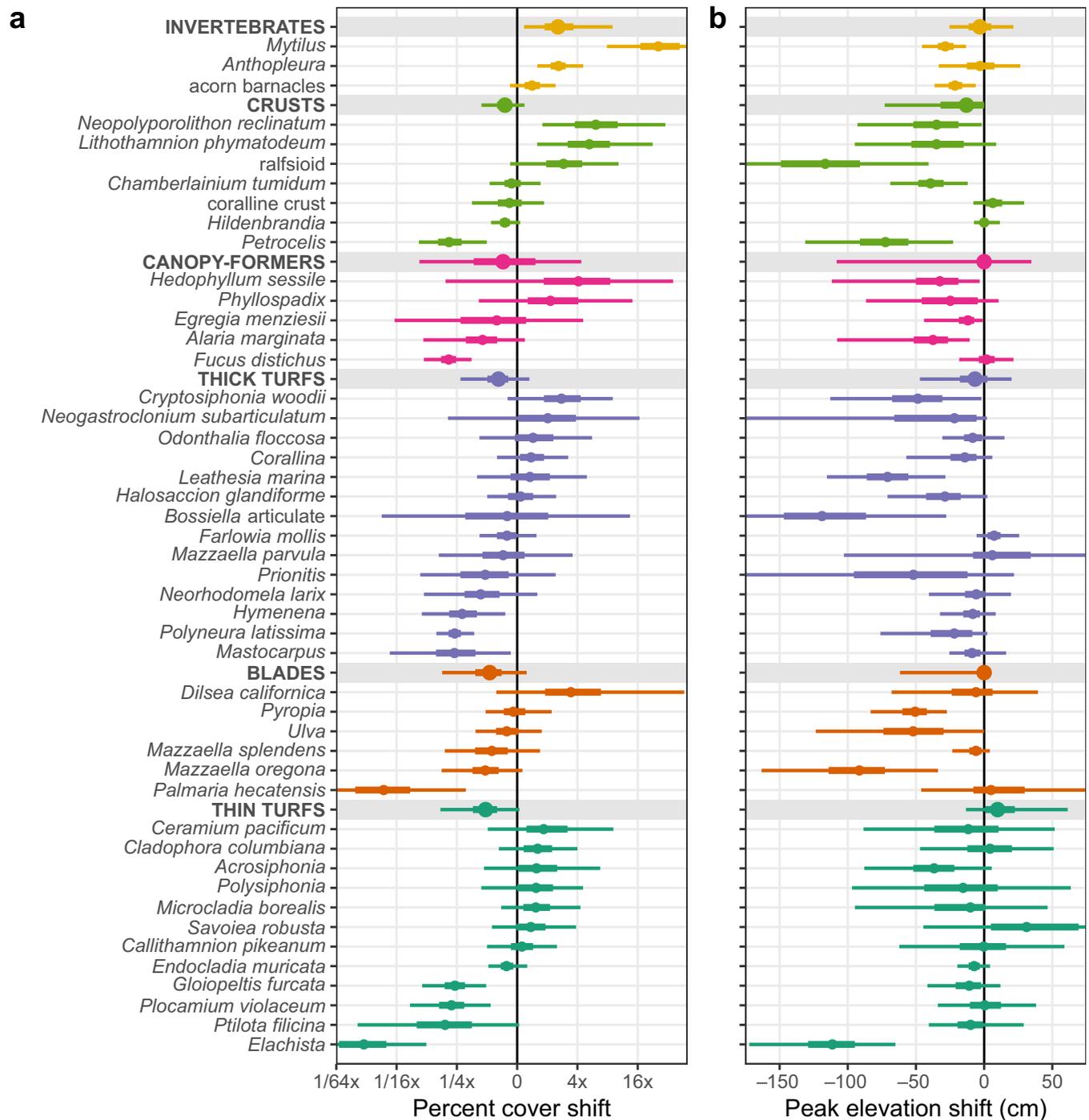
FIGURE 2 Shifts over time in (a) percent cover (fold change) and (b) peak elevation (cm) for the six functional groups and 47 taxa modeled using HMSC. Points are median shifts (i.e., linear change from 2012 to 2019) across 1000 posterior samples, and errors bars are 50% (thick bars) and 95% credible intervals (thin bars). Note that the scale on the horizontal axis does not include extreme values for all 95% credible intervals.

and sessile invertebrates occurred more frequently (Appendix S3: Figure S6). Thick turfs and crusts experienced losses in conditional cover, but these were offset by maintenance (for thick turfs) or increases (for crusts) in occurrence. We detected no significant shifts in cover for any seaweed functional group once we accounted for occurrence, and we detected no significant shifts in peak

elevation at the functional group level (Figure 2b). However, at least one member of every seaweed functional group shifted downslope significantly or lost significant cover. Wide variation in responses of canopy-formers was due to partial recovery following declines in the most intense periods of the heatwave and opposing patterns of occurrence and cover among different taxa (Figures 3 and 4).
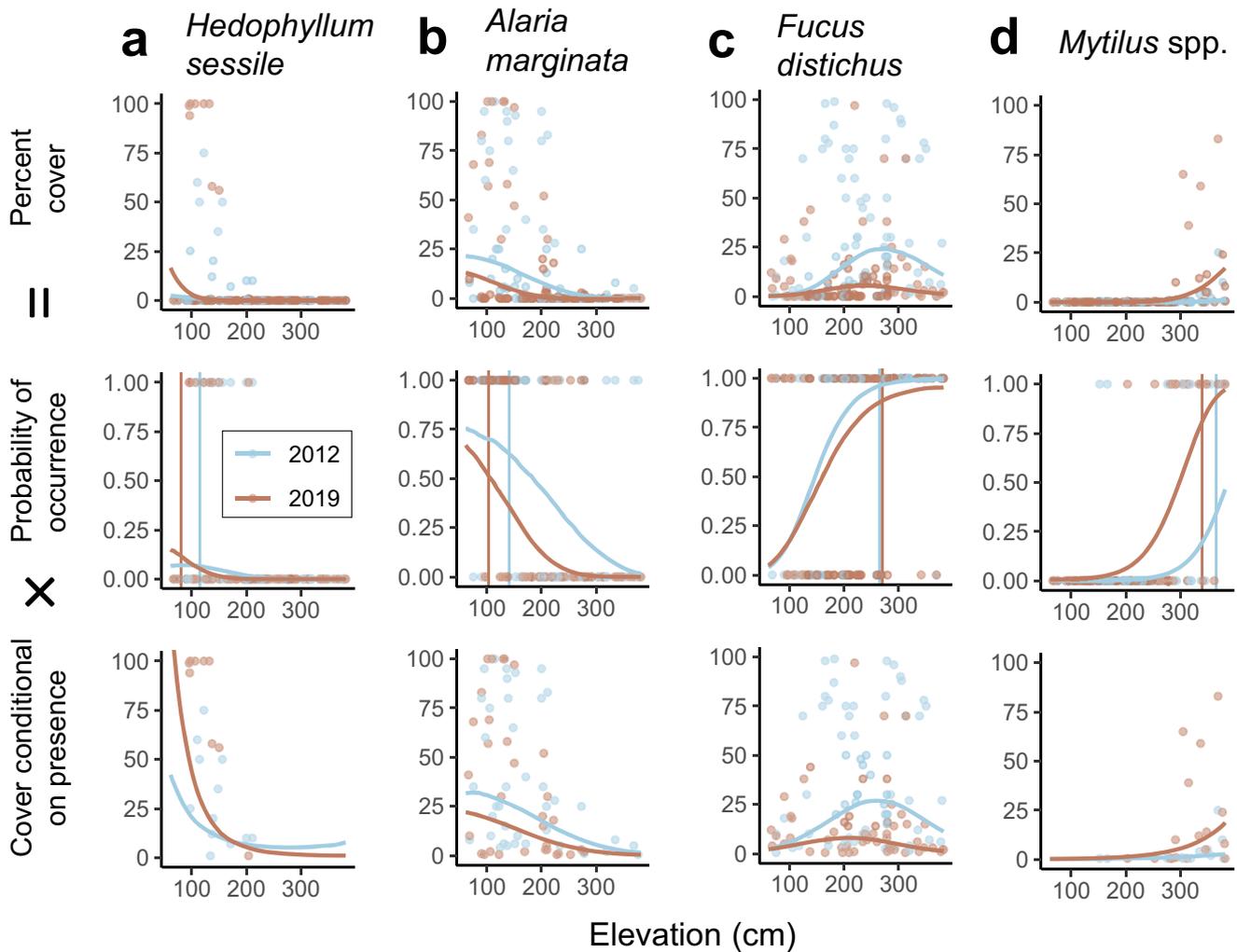
FIGURE 3 Abundance and distribution of select taxa at the beginning (2012, blue) and end (2019, red) of the survey period with HSMC predictions across elevations. Percent cover (top row) is the product of two sets of predictions in the rows below: a probit model predicting occurrence (middle row) and a log–linear model of cover conditional on presence (bottom row). Vertical lines in occurrence panels (middle row) show predicted elevation peak in each year calculated as mean elevations exceeding half the maximum probability of occurrence.

For example, while the winged kelp (*A. marginata*) trended toward decreases in cover over time (based on 50% CIs), sea cabbage (*Hedophyllum sessile*) and surfgrasses (*Phyllospadix* spp.) trended toward increases (Figures 2a and 4d). Together, these results indicate the limited ability of our seaweed functional groupings to capture the dynamics of constituent species, which were highly variable.

Species richness remained stable

Species richness along transects was largely stable over time (Figure 5a), although small, significant declines in diversity were detected when rare taxa were down-weighted, reflecting decreasing community evenness (i.e., the increasing dominance of particular taxa; Appendix S4: Figure S1, Table S1).

DISCUSSION

We leveraged a taxonomically well resolved time series of intertidal seaweed biodiversity to investigate how populations and communities changed across time and space during an unprecedented series of heatwaves. In doing so, we documented declines in occupancy, abundance, and vertical distribution of seaweeds coincident with rising temperatures. Declines in seaweed cover and occurrence resulted in an increased incidence of exposed bare rock, demonstrating the severity of ecosystem changes associated with the heatwave.

Shifts in abundance, distribution, and trophic structure in the intertidal zone may have conservation consequences given the high level of habitat specificity observed in this ecosystem. We estimate that 47% of taxa
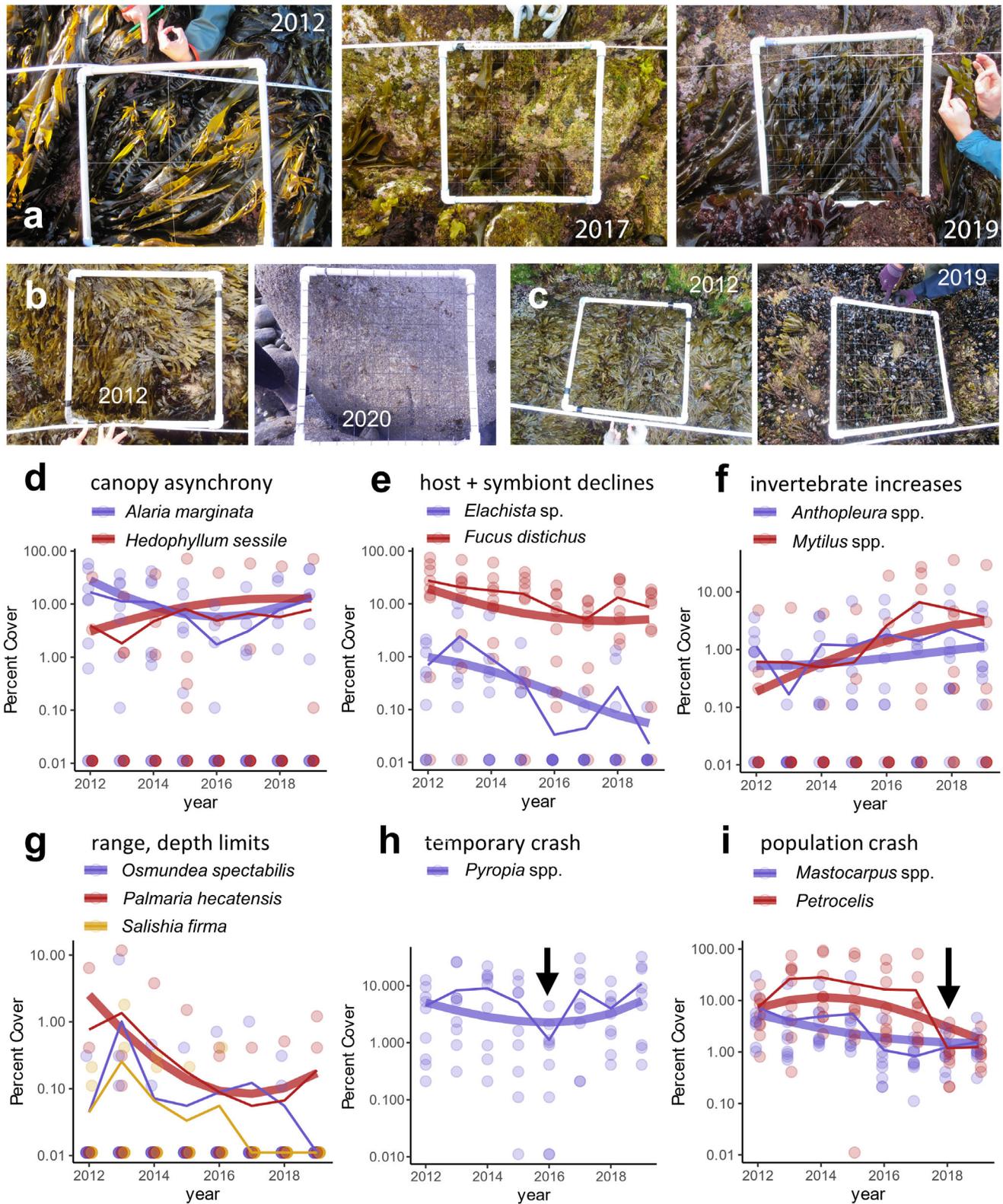
FIGURE 4 Examples of population and community change before and after the onset of the heatwave. (a–c) Photographic timeseries documenting (a) loss and partial recovery of *A. marginata* cover (low-shore transect, Fifth Beach), (b) loss of *F. distichus* cover and partial replacement by barnacles (midshore transect, Foggy Cove), and (c) partial replacement of *Fucus* by *Mytilus californianus* (high-shore transect, Fifth Beach). (d–i) Select time series of seaweed and invertebrate cover, illustrating the range of temporal change observed in the dataset. Thin lines connect empirical annual means averaged along each transect, and thick lines show HMSC predictions of median cover averaged over eight discrete elevations and weighted by their frequency of sampling. Note that some quadrats were revisited (Appendix S3: Figure S2), allowing limited comparison of photographs in different years. Photograph credits: P. T. Martone, S. C. Lindstrom, S. Starko.
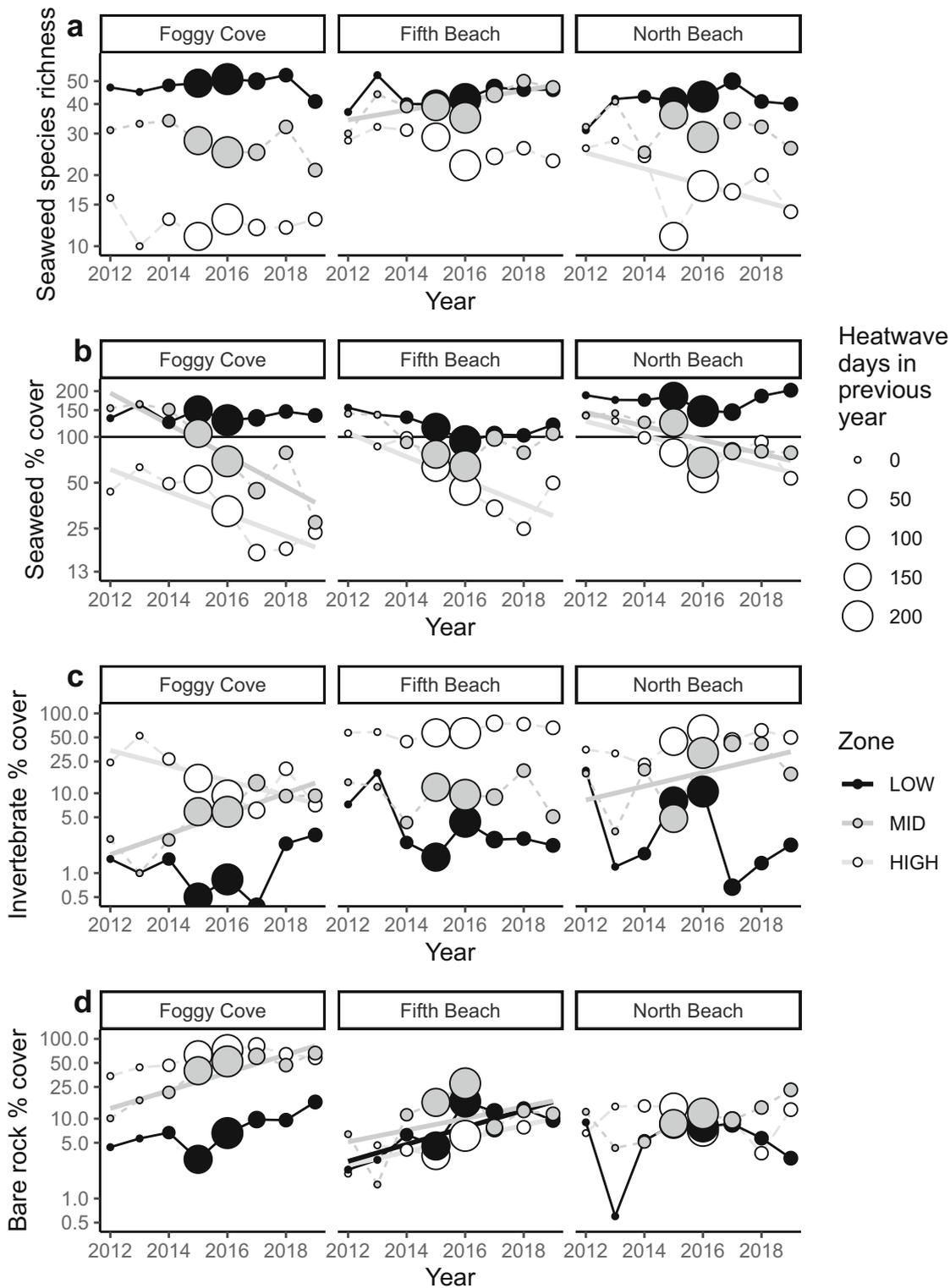
FIGURE 5 Timeseries of (a) observed seaweed species richness, (b) total seaweed percent cover, (c) total invertebrate percent cover, and (d) bare rock percent cover for each transect. Symbol colors denote elevational zones and symbol size is proportional to the total number of heatwave days in the year preceding each survey based on PCA axis 1 (Figure 1c). Regression lines are shown for transects with significant increases or decreases over time for each metric based on least-squares regression. Note the log-transformation and different ranges for *y*-axes.

(54 out of 116; Appendix S3: Table S1) are found predominantly or exclusively in the intertidal zone. While our understanding of fundamental and realized niches is incomplete for many species, this habitat specificity suggests that population persistence may be sensitive to the erosion of distribution limits.

T A B L E 3   Parameter estimates from generalized linear mixed effects models predicting transect-level species richness and cover changes as a function of total number of heatwave days in the year leading up to each survey or the total number of heatwave days in the 5 years leading up to each survey.

Response	Predictor: Total heatwave duration (1 year)					Predictor: Total heatwave duration (5 years)				
	λ (day^{-1})	SE	z-value	p-value	Predicted change 200 heatwave days	λ (day^{-1})	SE	z-value	p-value	Predicted change 500 heatwave days
Seaweed species richness	−3.0e-04	2.9e-04	−1.02	0.309	−1.8 species	−4.9e-05	1.0e-04	−0.49	0.624	−0.75 species
Seaweed cover	−2.0e-03	1.8e-04	−11.33	<0.001	−35.5% cover	−8.9e-04	5.7e-05	−15.66	<0.001	−41.9% cover
Invertebrate cover	2.7e-04	3.7e-04	0.73	0.466	+0.66% cover	4.6e-04	1.3e-04	3.57	<0.001	+2.8% cover
Bare rock cover	2.4e-03	3.6e-04	6.52	<0.001	+6.7% cover	1.3e-03	1.4e-04	9.51	<0.001	+8.6% cover

Note: Model used a Poisson link function with random intercepts for transect.

Understanding variation in seaweed responses

Seaweed cover and elevational peaks tended to decline over time, but these shifts were variable across taxa and functional groups, giving us an opportunity to consider how traits determine zonation and modulate transitions between community states (Connell, 1961; Petraitis & Latham, 1999; Sousa, 1979). Importantly, our functional groupings did not capture the dynamics of constituent species well; we observed cover increases, decreases, and maintenance across a diverse assemblage of seaweeds, but few significant responses at the functional group level (Appendix S3: Figure S6). While functional groups were hypothesized to reflect responses to stress, they were based on morphology, which is problematic when gross morphology does not reflect physiology and ecosystem functioning (Mauffrey et al., 2020; Padilla & Allen, 2000; Phillips et al., 1997). Thus, although functional groups are commonly used to assess community-level changes in seaweed responses to climate change and heatwaves (Filbee-Dexter & Wernberg, 2018; Smith et al., 2016), the range of population responses we report highlights the limitations of using coarse morphological categories in this regard.

In contrast with the limited utility of morpho-functional groups, life history traits may help explain the timing and magnitude of population changes (Figures 3–5), because they are known to mediate seaweed responses to fluctuating environments (Carney & Edwards, 2006; Lubchenco & Cubit, 1980). For instance, the culturally significant food resource, *Pyropia abbottiae*, was nearly absent in 2016 but reached the highest recorded levels in 2017 (Figure 4h). This pattern was not well captured in our modeling and may reflect a lack of environmental cues during warm winters required for maturation of the shell-boring microscopic phase (Appendix S2; Waaland et al., 1990). In such cases, the alternate life history phase may have provided resilience

to extreme stress. Conversely, declines in *F. distichus*, a dribble spawner with no alternate phase, and its obligate epiphyte, *Elachista* sp., were among those with the greatest loss in seaweed cover (Figure 4e), and both life history phases (crust and turf) of *Mastocarpus* spp. declined precipitously during the survey period (Figure 4i). These observations may indicate more lasting population-level impacts on taxa with solely macroscopic phases. While we lacked information to include additional traits in HMSC modeling, these examples suggest that the impacts of heatwaves on species depend on both stress tolerance and life history.

While species diversity was largely stable over time (see also Tekwa et al., 2022), some species turnover did occur. Variation in responses among taxa may reflect thermal performance differences at biogeographic and local scales (Figure 4g; see Kroeker & Sanford, 2022). For example, the northern red seaweed, *P. hecatensis*, finds its southern limit near the study area (Hawkes, 1985) and experienced significant cover declines during the study. Conversely, *Salishia firma* and *Osmundea spectabilis*, two geographically widespread but primarily subtidal species that only occur in the lowest part of the intertidal zone, were not encountered following the heatwave, from 2017 to 2019 and in 2019, respectively. Thus, accumulated stress imposed by the multiyear heatwave may have shifted habitable ranges outside of surveyed elevations.

Species interactions and trophic shifts

The timing of canopy population collapse and recovery suggests that species interactions mediate community-level impacts of extreme climate events. For example, while *A. marginata* collapsed in 2016 and partially recovered, *H. sessile* steadily increased in cover at low elevations (Figures 3 and 4), compensating for canopy loss. Although it may be surprising that *Hedophyllum*

increased in abundance given our understanding of how temperature impacts the ranges and physiologies of kelps (Lüning & Freshwater, 1988; Spiecker & Menge, 2022), opposing fluctuations of these two kelp species are likely to reflect known physiological tolerances and competitive interactions. *Alaria* is generally competitively dominant unless otherwise excluded (e.g., when grazers are rare; [Dayton, 1975; Paine, 2002; Widdowson, 1965]), yet it is also sensitive to acute warming, particularly during reproduction and recruitment (Muth et al., 2019). Thus, declines in *Alaria* are likely to open space for increased growth or recruitment of *Hedopyllum*. While we do not have robust data on mobile grazers, available data (Appendix S5: Figure S1) suggest an increase in the chiton, *Katharina tunicata*, on the low elevation transect where *Hedophyllum* increased most, which may have concentrated grazing pressure on *Alaria* and favored *Hedophyllum* recruitment. Remaining thick turfs (Figure 2a) may have also facilitated *Hedophyllum* settlement and recruitment at lower, potentially less stressful elevations (Figure 3a); on Calvert Island and elsewhere, *H. sessile* often recruits to articulated coralline red seaweeds, including *Corallina* spp., and rarely to bare rock (Barner et al., 2016; B. A. Twist & P. T. Martone, unpublished data). We speculate that differential impacts of the heatwave on reproduction, recruitment, and species interactions—both negative and positive—across life history phases contributed to observed increases in *Hedophyllum*. These results highlight how shifts in species-level thermal performance may not scale to the community level.

Higher up the shore, *F. distichus* was replaced by invertebrates at rocky bench sites, consistent with shifts observed in Alaska (Suryan et al., 2021; Weitzman et al., 2021). This pattern of increasing sessile invertebrate cover, however, was site-specific in our study; *Fucus* and other seaweeds declined synchronously at higher elevations at Foggy Cove and were not replaced, substantially increasing bare space (Figure 5d). Increases in invertebrates began after declines in seaweeds in response to open space and perhaps favorable oceanographic conditions (e.g., Menge et al., 2008). Collectively, these observations indicate the loss of primary production and shifts toward secondary production in more stressful environments that experience warming.

Our finding that initially more common and abundant taxa experienced greater cover loss (Appendix S3: Figure S5) may suggest that responses to heatwaves are governed by trade-offs between stress tolerance and competitive ability (Gilman et al., 2010). Importantly, this pattern involved cover losses of spatially dominant—and presumably competitively dominant—taxa at both higher and lower elevations, suggesting that abiotic conditions were stressful across elevations in ways relevant to the entire ecosystem. Conversely, increases in initially rarer taxa may be driven by competitive release following the loss of more dominant taxa, or by differences in thermal performance (i.e., an initially rare species may become more competitive closer to its thermal optimum).

Shifts from seaweed- to invertebrate-dominated communities at all three sites began directly after seaweed die-off but may have also been facilitated by reductions in keystone predators during the heatwave. Sea star wasting disease, probably exacerbated by increased water temperatures, drove declines in predatory sea stars across the Northeast Pacific (Burt et al., 2018; Harvell et al., 2019; Miner et al., 2018). Reductions in top-down pressure resulting from sea star mortality or emigration could reinforce the recruitment of barnacles and mussels, potentially facilitating the expansion of sessile invertebrates along midzone transects following seaweed die-off. However, limited data on sea star densities suggests that *Pisaster ochraceus*, a keystone predator of sessile invertebrates, was chronically rare on high-elevation transects where mussel cover increased most (Appendix S5). Reductions in predation pressure on molluscan grazers could have also had cascading effects on seaweed communities (Dethier & Duggins, 1988; Paine, 2002). While we lack appropriate data to investigate reciprocal interactions among seaweeds and sessile invertebrates or changes in top-down processes, these trophic explanations would not explain the erosion of the upper margins of seaweed distributions because mobile consumers should prioritize foraging at lower, less stressful elevations.

Attributing change

Attribution of change is difficult in ecological systems (Ferraro et al., 2019), especially when the disturbance is associated with co-occurring environmental changes, limiting our ability for the control needed in deductive study designs. The oceanographic and atmospheric responses during the heatwave (Figure 1) complicate our ability to precisely link abiotic change to physiological mechanisms (e.g., overheating, desiccation, photodamage, nutrient starvation). However, correlations between the change in seaweed cover and heatwave duration (Table 3) suggest acute and chronic impacts of intensified abiotic stress on seaweeds. An alternative hypothesis for observed declines in seaweed cover that we were unable to test involves nutrient depletion following warming-induced ocean stratification, which has been implicated in the severe decline in seaweeds associated with oceanographic regime shifts (e.g., Dayton & Tegner, 1984). Nutrient levels were depleted during the 2014–2016 heatwave south of the

study area (Dosser et al., 2021), but nutrient data for the areas around Calvert Island are not currently available. We suspect that elevated water and air temperatures, sun exposure, and desiccation, perhaps interacting with nutrient limitation, all played a role in driving responses in this intertidal ecosystem. For example, the nutrient limitation is known to influence the thermal tolerance of kelp species (Fernández et al., 2020; Gerard, 1997). These added stressors may interact synergistically with existing stress gradients to influence elevational limits, driving species down gradients toward reduced abiotic stress.

The history of intertidal ecology provides strong domain expertise for our inductive reasoning (Sagarin & Pauchard, 2010), and similar responses observed elsewhere bolster our inference; for example, declines in *F. distichus* and increases in mussels at multiple sites in the Gulf of Alaska (Suryan et al., 2021; Weitzman et al., 2021) suggests some consistency in impacts of the heatwave. While our analyses are correlative and we cannot fully determine causality, our results are consistent with direct physiological effects and indirect effects of intensifying abiotic stress on abundance and distribution that span populations to communities. Directional shifts in abundance and elevational distribution highlight the pervasive influence of heatwaves in this system. However, species richness did not change significantly over the survey period, and we speculate that seaweed diversity in this system may limit destabilizing effects of the heatwaves on communities (Miner et al., 2021, but see Menge et al., 2022).

Implications

Our study demonstrates the importance of local gradients for understanding community responses to extreme climate events. Indeed, abiotic gradients are central to understanding the impacts of extreme climate events across ecosystems (Bachman et al., 2022; Giraldo-Ospina et al., 2020; Hayashida et al., 2020; Hoiss et al., 2015; Magel et al., 2022; Starko et al., 2022; Suarez & Kitzberger, 2010). Species abundances and distributions shifted in different ways across the elevation gradient during the multiyear marine heatwave, producing substantial change at the community level. Shifts at both the population and community level also depended on initial abundances and probably also species diversity, so community responses to extreme events therefore depend on how environmental changes interact with existing abiotic and biotic gradients (Hoiss et al., 2015). Our findings of seaweed replacement by invertebrates and increased bare rock also suggest that extreme events can make ends of stress gradients uninhabitable for entire trophic guilds (Levin et al., 2009). With increasing temperatures across

the region, the habitable area for seaweeds shrank modestly, a pattern previously documented over horizontal spatial gradients (Harley, 2003, 2011; but see Barry et al., 1995). If an intertidal species is not viable against natural enemies in the subtidal zone or requires emersion for physiological or reproductive processes, then it may eventually run out of suitable habitat, similar to the "escalator to extinction" hypothesis on mountain slopes (Kelly & Goulden, 2008). Unlike on warming mountain slopes, where species move from areas of high to low diversity as environments become more favorable for strong competitors (Usinowicz & Levine, 2021), intertidal species shifted toward lower, more speciose elevations during warming, potentially intensifying species interactions and eroding upper edges of the ecotone between marine and terrestrial realms. Thus, our results suggest that gradients in stress and biodiversity, and their directionality relative to changing environmental conditions, mediate responses to climate extremes. Disentangling these factors remains an important challenge to our understanding of ecology in a changing world.

AUTHOR CONTRIBUTIONS

Patrick T. Martone and Sandra C. Lindstrom designed and coordinated the survey; Matthew A. Whalen analyzed the data; Matthew A. Whalen and Samuel Starko wrote the paper with substantial input from all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and code (Whalen, 2023) are available in Zenodo at https://doi.org/10.5281/zenodo.7671696.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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