ARTICLE

Microclimate predicts kelp forest extinction in the face of direct and indirect marine heatwave effects

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Abstract

Marine heatwaves threaten the persistence of kelp forests globally. However, the observed responses of kelp forests to these events have been highly variable on local scales. Here, we synthesize distribution data from an environmentally diverse region to examine spatial patterns of canopy kelp persistence through an unprecedented marine heatwave. We show that, although often overlooked, temperature variation occurring at fine spatial scales (i.e., a few kilometers or less) can be a critical driver of kelp forest persistence during these events. Specifically, though kelp forests nearly all persisted toward the cool outer coast, inshore areas were >3°C warmer at the surface and experienced extensive kelp loss. Although temperatures remained cool at depths below the thermocline, kelp persistence in these thermal refugia was strongly constrained by biotic interactions, specifically urchin populations that increased during the heatwave and drove transitions to urchin barrens in deeper rocky habitat. Urchins were, however, largely absent from mixed sand and cobble benthos, leading to an unexpected association between bottom substrate and kelp forest persistence at inshore sites with warm surface waters. Our findings demonstrate both that warm microclimates increase the risk of habitat loss during marine heatwaves and that biotic interactions modified by these events will modulate the capacity of cool microclimates to serve as thermal refugia.

KEYWORDS
biogenic habitat, canopy-forming kelp, climate change, historical ecology, Laminariales, marine heatwave, microclimate, regime shifts

INTRODUCTION

Climate change is amplifying marine heatwaves such that they are now considered a dominant threat to many coastal marine ecosystems (Hughes et al., 2018; Smale et al., 2019; Straub et al., 2019). In contrast to gradual warming—which may drive predictable shifts in species distributions—marine heatwaves are rapid, punctuated events that can perturb entire ecosystems with long-term ecological consequences (Coleman & Wernberg, 2020; Hughes et al., 2018; Smale et al., 2019). Through both direct physiological effects on organisms (Arias-Ortiz et al., 2018; Hughes et al., 2018; Smale et al., 2019; Straub et al., 2019) and indirect effects arising from altered species interactions (e.g., Burt et al., 2018; Vergés

et al., 2014, 2016), marine heatwaves have been responsible for driving rapid ecological change in both temperate and tropical waters (Filbee-Dexter & Wernberg, 2018; Hughes et al., 2018; Wernberg et al., 2016). Over the past few decades, marine heatwaves have become increasingly frequent and intense, leading to losses of key habitat-forming coastal species—including corals, mangroves, seagrasses and kelp forests—in ecosystems around the world (Arias-Ortiz et al., 2018; Babcock et al., 2019; Hughes et al., 2018; Smale et al., 2019; Wernberg et al., 2016). When marine heatwaves cause local conditions to exceed key physiological thresholds, they can drive mass mortality on vast scales (e.g., Arias-Ortiz et al., 2018; Hughes et al., 2018; Wernberg et al., 2016). At the same time, marine heatwaves can introduce novel taxa (Cavole et al., 2016; Vergés et al., 2014) or alter the relative abundance of species that are critical to the food web (Burt et al., 2018; Cavole et al., 2016; Hamilton et al., 2021; Harvell et al., 2019; von Biela et al., 2019), potentially shifting the trophic dynamics of ecosystems (Cavole et al., 2016). These combined effects have the potential to cause the local or regional extinction of key habitat-forming foundation species (Smale et al., 2019; Vergés et al., 2019), producing devastating economic consequences (Bennett et al., 2016) and driving regime shifts with cascading effects on the functioning of coastal ecosystems (Harley, 2011; Hughes et al., 2018; Smale et al., 2019; Vergés et al., 2019; Wernberg et al., 2016).

Predicting the impacts of heatwaves on marine habitats will be critical if we are to manage and preserve coastal ecosystems through the 21st century, given that these heatwaves are expected to continue increasing in frequency, duration, and intensity under climate change (Oliver et al., 2018, 2019). Although organisms experience and respond to their immediate environmental conditions, and most resource managers work at local, rather than broad, scales (Bates et al., 2018), much of our understanding about variation in species' responses to the direct and indirect effects of marine heatwaves is based on broad latitudinal comparisons (e.g., Cavanaugh et al., 2019; Vergés et al., 2016; Wernberg et al., 2016). Yet, in parts of the ocean, temperature and other environmental variables can vary considerably over short distances (e.g., millimeters to kilometers) and short time periods (e.g., minutes to hours) (Bates et al., 2018; Harley, 2011; Helmuth et al., 2002, 2014), indicating that latitude alone fails to capture much of the variation in conditions experienced by organisms through heatwave events (Bates et al., 2018; Woodson et al., 2019). This creates a major challenge when trying to understand how ecosystem processes such as carbon capture or habitat provisioning will change with future warming. Failure to address this spatial mismatch comes at our own peril because we must integrate local microclimatic variation (i.e., ocean weather) to accurately predict how marine ecosystems will respond to climate warming (Bates et al., 2018).

Of the coastal habitats currently most threatened by climate warming (Pörtner et al., 2019), kelp forests are the most globally widespread. Found across more than a third of the world's coastlines (Jayathilake & Costello, 2021), kelp (Laminariales) form three-dimensional habitats used by a wide range of fish, invertebrates, and other macroalgae (Graham, 2004; Steneck et al., 2002; Teagle et al., 2017). They include some of the fastest growing primary producers on Earth and play key roles in carbon and nutrient cycling (Filbee-Dexter & Wernberg, 2020; Wilmers et al., 2012). Kelp forests are critically threatened by warming in many areas (Berry et al., 2021; Filbee-Dexter & Wernberg, 2018; Smale, 2020; Smale et al., 2019), however, and declines in kelp forests can have cascading effects on ecosystems through losses of habitat (Filbee-Dexter & Wernberg, 2018) and productivity (Duggins et al., 1989), yielding negative consequences for fisheries, tourism, carbon capture, and other ecosystem services (Bennett et al., 2016). Marine heatwaves are now considered to be the dominant threat to kelp forests (Pörtner et al., 2019), along with changes in trophic structure that are often exacerbated by extreme warming (Johnson et al., 2011; Ling, 2008; Ling et al., 2015; Vergés et al., 2016; Watson et al., 2021). Yet, these drivers can have highly variable effects on kelp forest ecosystems (Burt et al., 2018; Krumhansl et al., 2016; Smale, 2020; Wernberg et al., 2019), and the local-scale factors that determine how kelp forests respond remain poorly understood.

Our current lack of understanding about local drivers of kelp resilience is especially problematic because coastal ecosystems experience highly variable environmental conditions across narrow spatial and temporal distances (Bates et al., 2018; Harley, 2011; Helmuth et al., 2002, 2014), which may drive variation in resilience on a range of spatial scales. Although there is some evidence from other systems that fine-scale temperature gradients can mediate the responses of habitat-forming species to heatwaves (e.g., Palumbi et al., 2014; Verdura et al., 2021), the importance for kelp forests remains unclear. Yet these types of gradients are especially common in fjords, bays, and inlets on temperate coastlines, where kelp forests represent the most common coastal biome (Jayathilake & Costello, 2021). This may help to explain why the responses of kelp forests have also been highly variable in the face of past heatwaves (Cavanaugh et al., 2019; Hamilton et al., 2019; Krumhansl et al., 2016; Reed et al., 2016; Smale, 2020; Straub et al., 2019).

Between 2014 and 2016, the Northeast Pacific experienced the longest sustained marine heatwave on record globally (Bond et al., 2015; Levine & McPhaden, 2016). Driven initially by a persistent high-pressure system and further extended by the unusually strong 2015–2016 El Niño, this event lasted multiple years and had far-reaching effects on coastal ecosystems, driving major

alterations in trophic dynamics. Anomalously high sea surface temperatures (SSTs) exacerbated the ongoing sea star wasting disease epidemic that had already been decimating sea star populations across the coast (Harvell et al., 2019; Kohl et al., 2016; Montecino-Latorre et al., 2016). This resulted in the functional extinction of *Pycnopodia helianthoides*—an important predator of sea urchins—from most of the Northeast Pacific (Hamilton et al., 2021; Harvell et al., 2019). At the same time, anomalously high temperatures drove direct kelp mortality toward species' latitudinal range limits (Arafeh-Dalmau et al., 2019; Cavanaugh et al., 2019; Finger et al., 2021; Rogers-Bennett & Catton, 2019) and likely made kelp forests more susceptible to increased grazing pressure across their ranges (McPherson et al., 2021; Rogers-Bennett & Catton, 2019). Yet the effects of direct and indirect drivers are challenging to disentangle and have been variable across Northeast Pacific kelp forests (Beas-Luna et al., 2020; Burt et al., 2018; Hamilton et al., 2019; Rogers-Bennett & Catton, 2019; Schultz et al., 2016). Though kelp forests near their southern limits (i.e., warm-edge) experienced losses from low latitudes (Arafeh-Dalmau et al., 2019; Beas-Luna et al., 2020; Cavanaugh et al., 2019)—as seen with past heatwaves in other systems (Filbee-Dexter, Feehan et al., 2020; Filbee-Dexter, Wernberg et al., 2020; Vergés et al., 2016; Wernberg et al., 2016)—kelp populations toward their range centers have shown highly variable responses (from no impact to severe kelp loss: Reed et al., 2016; Hamilton et al., 2019; Schroeder et al., 2020; Smith et al., 2021; Beas-Luna et al., 2020). This suggests that local or regional factors play key roles in mediating kelp forest resilience across much of their range.

Here we synthesize historical and recent data sources to evaluate the role of fine-scale environmental variation (i.e., microclimate) in dictating the indirect and direct impacts of the 2014–2016 marine heatwave on the Northeast Pacific's two major canopy-forming kelp species. Focusing on a coastal fjord system with high local temperature variation and a legacy of kelp research (Barkley Sound, British Columbia), we reconstructed the historical distribution back to the 1970s of the two largest Northeast Pacific kelp forest species, *Macrocystis pyrifera* and *Nereocystis luetkeana*, and conducted resurveys across a local-scale temperature gradient of more than 3°C on average to test whether microclimate influenced kelp forest persistence through the 2014–2016 marine heatwave. We hypothesized that (1) the probability of local kelp forest extinction would vary significantly across this microclimatic gradient, with warmer sites being less persistent; (2) during anomalously warm conditions, warm microclimates would be sufficiently stressful to cause direct physiological damage to the kelp; and (3) deeper habitats could serve as thermal refugia in warm microclimates

only where newly increasing subtidal urchin populations were not locally abundant. Overall, we establish that, although the distribution of kelp forests across Barkley Sound prior to the 2014–2016 marine heatwave was stable for at least four decades, this unprecedented marine heatwave event triggered persistent losses relative to historical baselines. Moreover, patterns of kelp loss reflect a strong link between the resilience of kelp forests and pre-existing environmental gradients that can buffer or exacerbate the impacts of ecosystem-level perturbation.

METHODS

Study system

Barkley Sound is a coastal fjord in British Columbia, Canada, that opens to the Pacific Ocean at its southwest edge. Barkley Sound lacks persistent sea otter (*Enhydra lutris*) populations, which have been functionally absent since their extirpation in the mid to late 19th century (Markel & Shurin, 2015; Watson & Estes, 2011), meaning that *P. helianthoides* is the dominant predator of sea urchins (Burt et al., 2018) in the region. We conducted our study on the Northeast Pacific canopy-forming species *Macrocystis pyrifera* form *integrifolia* (giant kelp) and *Nereocystis luetkeana* (bull kelp), which are the largest and among the most ecologically important kelp taxa globally (Graham, 2004; Teagle et al., 2017).

Direct environmental effects of heatwave

We collected and compiled environmental data with two aims: first, to quantify temporal changes in temperature at a broad scale and, second, to assess how variation in these variables is distributed across Barkley Sound. To characterize temporal patterns of temperature, we analyzed in situ data from $n = 3$ sites. The longest of these time series is that of SST from Amphitrite Point Lighthouse on the outer edge of Barkley Sound (1936–2021) from which temperature anomalies were calculated. The other two are subtidal stations where temperature has been monitored since 1999 (at ~6 and ~10 m depth see Appendix S1: Figure S1) and were used as additional lines of evidence for temporal trends in temperature.

Our second aim was to capture local spatial variation in temperature to better understand heterogeneity in the environment over which broad-scale changes are superimposed. To characterize spatial variation in temperature, we deployed temperature loggers in 2019 and 2020 at varying distances (1–16 km) from the outer coast and at varying depths (~0.1–8 m or intertidal). We

defined the outer coast as a line between Cape Beale and Amphitrite lighthouses (Appendix S1: Figure S1). Temperature measurements taken in 2019 occurred while long-term station temperatures exceeded baseline averages, only about 0.5–1°C less than 2014–2016 on average, suggesting that spatial patterns reflected those that occurred during the marine heatwave. We also compared temperatures from iButton loggers installed at two inshore sites in the summers of 2015 and 2016 (Iwabuchi & Gosselin, 2019) to temperatures collected at the Amphitrite lighthouse on the outer coast. To explore spatial variation in dissolved nitrogen (specifically nitrate and nitrite) availability, we analyzed an unpublished data set by one of the authors (L. Druehl; available at doi: 10.5281/zenodo.6397743) collected between 1979 and 1982 ($n = 18$ time points, $n = 7$ sites) and two depths (1 and 4 m below surface). We also collected comparable data at 1 and 5 m in August 2021 ($n = 2$ time points; $n = 6$ sites). In both cases, nitrate and nitrite were combined for analysis. Though differences in methodology and exact location varied by time point, we tested whether nitrogen varied with distance from the outer coast by fitting nonlinear decay models separately to each depth for each data set. We note that, though low salinity is an important limiting variable for kelp in the broader region (Druehl, 1978), data collected by Druehl et al. (1988) indicated little predictable variation in salinity across the study area (which varies from ~30 to 27 ppt seasonally). Specific information on different in situ measurements are provided in Appendix S1: Section S1.

Indirect top-down effects

To test whether regional declines in the sunflower sea star, *P. helianthoides* (described by Harvell et al., 2019; Hamilton et al., 2019), have led to an increase in regional urchin abundances—potentially increasing grazing pressure on kelp forests—we analyzed subtidal scuba diver data collected from 2013 to 2016 by Parks Canada at sites ($n = 6$) in the Broken Group Islands at depths of 5–12 m. These data include abundances of *P. helianthoides*, *Mesocentrotus franciscanus* (red urchins), and *Macrocystis pyrifera* along transects sampled at each site ($n = 4$ to 6 per year), allowing us to directly test whether sea star wasting disease led to a trophic cascade that has limited kelp abundance in rocky subtidal areas (Appendix S1: Section S1). To test for differences in abundance between years, we conducted generalized linear mixed-effects models (fixed = year, random = site), varying the error distribution depending on the data set. For survey data on urchin and *Pycnopodia* abundances, we used a negative binomial distribution, which is appropriate for count data where variance is substantially greater than the mean. For

data on kelp abundance (where average count per quadrat was the response), we used a gamma distribution, which is appropriate for right-skewed, continuous data.

Characterizing changes in kelp distributions

To test whether direct and indirect effects of the 2014–2016 marine heatwave have altered the distribution of kelp forests across space, we assembled all known relevant historical and modern data sets spanning from 1971 to 2016 (summarized in Appendix S1: Table S1). Synthesizing these various data sources gave us a detailed record of kelp forest presence-absence before and during the 2014–2016 marine heatwave, giving us a reliable baseline with which we could compare postheatwave distributions. These data included aerial and satellite imagery, hand-drawn and computer-generated maps, and site- or kelp-bed-level survey data. We conducted a series of resurveys between 2017 and 2021 aimed at determining changes in the distribution of each species relative to preheatwave baselines.

For one stretch of coastline that spans the entire 16-km microclimatic gradient and had especially high data coverage (including a low elevation flyover from 2007), we used a "shoreline segment" method to compare across time points. We assigned shoreline segments (mean length = 32 m) based on coastal features (e.g., distinct rocky outcroppings or points) that were recognizable from both imagery and a boat. Within each shoreline segment, we noted whether canopy kelp was present or absent both in the historical imagery and our postheatwave in situ surveys (see Appendix S1: Section S1 for more information on shoreline unit assignments and classification). For satellite imagery and high-altitude aerial imagery, species assignment was not possible, and thus data on both kelp species were grouped. For comparisons between 2007 low-elevation flyovers and modern resurveys, species were treated separately due to the high-resolution of images. Owing to uncertainty in the resolution at which hand-drawn maps were originally produced, we did not quantitatively compare them to modern distributions; instead, we reproduced these maps digitally by georectifying the original images and producing a spatial layer matching the original drawings. This allowed us to make qualitative comparisons between original hand-drawn maps and those produced from postheatwave surveys using the same basemap.

We also resurveyed individual kelp beds and rocky shore sites that were depicted in maps and survey data. Kelp beds and sites were treated the same way, and each one was revisited based on geographical information, photos, or detailed site descriptions. These data sets (from 1993 to 1995 and 2008) included a haphazard selection of

the kelp forests that were present across Barkley Sound during historical survey periods. Although the definition of a kelp bed can vary by surveyor, we considered a bed to be present if at least a single plant was still found in the vicinity of a historically mapped bed. We used logistic regression to test whether the probability of kelp forest extirpation from sites or segments was dependent on distance from open coast. To compare data from 1993 to 1995 (Appendix S1: Table S1) with modern resurveys (2017–2020), each of which included multiple years, we randomly selected one pre- and one postheatwave time point for each site.

Kelp growth measurements and condition assessments

To infer whether kelp from warmer areas were physiologically stressed in shallow waters during marine heatwaves, we measured the growth of tagged *Macrocystis* plants at four sites along the microclimatic gradient during the summer of 2020, a subsequent year of anomalously warm temperatures (Chen et al., 2021). We also measured health metrics of both *Macrocystis* ($n = 5$ sites) and *Nereocystis* ($n = 7$ sites) believed to be indicative of stress (namely: bleaching and blade length; see Appendix S1: Section S1). Growth experiments and health measurements were conducted between 2 and 12 July 2020. Though wave exposure likely also plays a factor in morphological features, like blade length, and generally becomes reduced moving inshore, we intentionally aimed to collect measurements from sheltered bays along the temperature gradient to minimize these effects (Appendix S1: Section S1). In situ temperature measurements from Amphitrite Point indicated that this time window was on average $0.8°C$ above historical averages and even reached temperatures exceeding the 90th percentile of historical measurements (indicative of marine heatwave conditions) (Hobday et al., 2016) for 2 days. This is further corroborated by data from Taylor Islet, showing July 2020 as a month of unusually warm temperatures compared to previous years. We used linear models (on site-level averages) to test for the effect of distance from open coast (a proxy of microclimate; see *Results*) on each health metric. We also used an analysis of variance (ANOVA) and Tukey post hoc test to compare mean frond and blade growth rates across two inner and two outer coast sites.

ROV transects and photoquadrats

To supplement our surface surveys and to better understand the factors influencing the persistence or disappearance of kelp forests, we conducted a series of remotely operated vehicle (ROV) surveys. In Barkley Sound, the lower limit of kelp is generally set by either sea urchins (usually *Strongylocentrotus purpuratus* or *Mesocentrotus franciscanus*) or by the lack of rocky substrate (e.g., sand or silt) (Druehl, 1978). To characterize the drivers of kelp lower limits across the environmental gradient, we conducted ROV surveys using the Trident Underwater Drone (Sofar Ocean, San Francisco, CA). We used a stratified random sampling approach to select points along the shoreline ($n = 35$) and then conducted vertical ROV surveys from below the lowest macroalgae in toward shore at the start of each unit. From this underwater imagery we extracted the depth below datum of the lowest macroalgae, the depth of the highest urchin (if present), and then the substrate below the lowest macroalgae. We also estimated a qualitative score of urchin abundance based on perceived percentage cover of urchins on the benthos in the ROV videos ($0 = $ absent, $1 \leq 6\%$, $2 = 6\%–20\%$, $3 \geq 20\%$). This measure was taken from their vertical band of greatest abundance, provided it was within 2 m elevation of lowest macroalgae depth. In addition to randomly chosen survey sites, we conducted several additional haphazard surveys with the goal of detecting *Macrocystis* beds not visible from the surface, a phenomenon previously reported in Barkley Sound (Druehl, 1978) and elsewhere along the west coast of North America (Ladah et al., 1999). In one location previously described has having a submerged bed (Sharp, 1974), we conducted a ~500-m horizontal ROV survey along the shore. For this survey, the ROV was sent to the bottom and followed by the boat. The survey was conducted in a zigzag manner across depths in order to assess the continuity of the bed.

We tested for an effect of substrate and distance from open coast on kelp presence using a binomial logistic regression. To test for an effect of these same fixed effects on maximum seaweed depth and urchin abundance score, we conducted an analysis of covariance (ANCOVA) and a Kruskal-Wallis test, respectively. In addition to our ROV surveys, we conducted surveys using a photoquadrat dropped from the surface to quantify urchin density and percentage foliose algae cover across depths at some sites (see Appendix S1: Section S1).

Statistical analysis and visualization software

All analyses were conducted in R version 4.1.2 using the following packages: tidyverse (Wickham et al., 2019), lme4 (Bates et al., 2015, 4), nlme (Pinheiro et al., 2017), and glmmTMB (Brooks et al., 2017). Visualizations were performed using ggplot2 (Wickham, 2011) and ArcMap (ESRI, Redlands, CA).

RESULTS

During the 2014–2016 Northeast Pacific marine heatwave, kelp forests went locally extinct at roughly 40% of the sites (41 out of 102, or 40%) or shoreline segments (125 out of 290, or 43%) that we resurveyed, with most losses occurring at inshore sites that experienced the warmest temperatures.

Remarkably, SSTs varied by more than 3°C on average across the 16-km gradient from the outer coast to the inner sound, even during nonheatwave years (Figure 1, Appendix S1: Figures S1–S3), such that surface waters at inshore sites commonly reached temperatures that far surpassed those typical of either kelp species' midrange. Instead, summer temperatures experienced at inshore sites
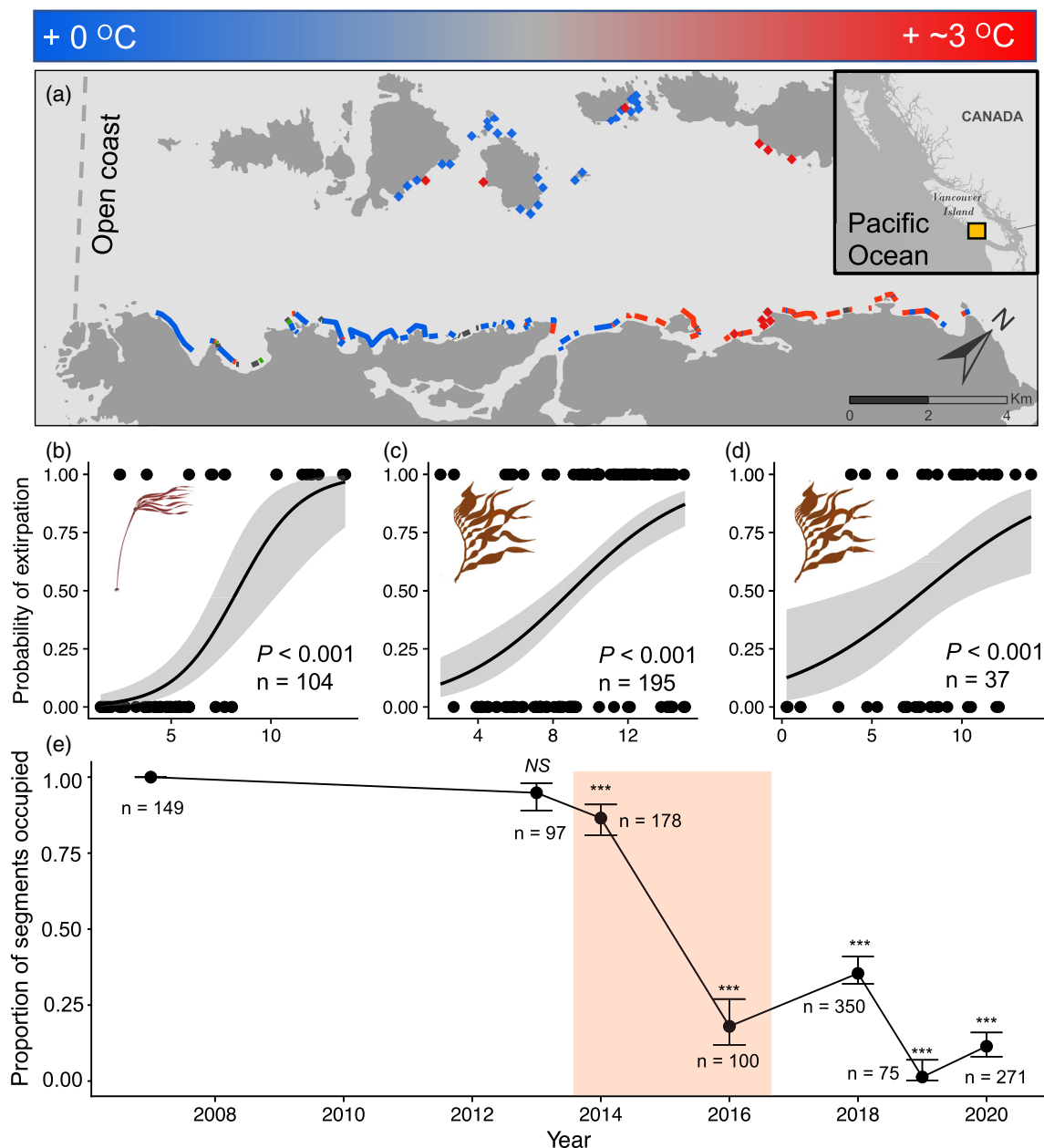

FIGURE 1 Changes in distribution of canopy-forming kelp species along a temperature gradient. (a) Map of change in distribution of two canopy-forming kelp species in Trevor Channel, Barkley Sound, 2007–2018/2019 (red = extirpation, blue = persistence, green = colonization, gray = never occupied). Both shoreline segments (lines; first sampled 2007) and 2008 survey sites (diamonds) are shown. The colored bar above the map indicates the position of sites along an average summer sea surface temperature (SST) gradient as measured in 2019. (b–d) Probability of extirpation at a particular segment or site as a function of its distance from the open coast, for (b) *Nereocystis*, (c) *Macrocystis* (both from shoreline segment data), (d) *Macrocystis* (2008 site data); (e) proportion of inshore shoreline segments (>8 km from open coast) occupied by canopy kelp at each time point between 2007 and 2020. Asterisks indicate significant differences from the initial 2007 survey (***$p < 0.001$); n indicates number of segments sampled each year.

were typically more similar to those experienced at ~10°–15° latitude further south. Warmer inshore sites were also found to be generally more nitrate depleted in the summer (Appendix S1: Figure S4), which is known to further impair the thermal tolerance of canopy kelp (Fernández et al., 2020). Synthesizing multiple data sets, we found clear evidence that both kelp species were present along this entire gradient in every data set from the four decades prior to the heatwave (1971–2014). Then, beginning in 2014, kelp forests experienced temperatures at least 1.5–2°C warmer than historical baselines, conditions that persisted for several

years with one monthly temperature anomaly lasting 21 consecutive months (Figure 2a). Though temperatures toward the outer coast of Barkley Sound remained close to optimal growth temperatures (~15°C), surface waters 12 km inshore regularly reached temperatures >18°C (Figure 2), exceeding the optimal thermal range of both focal species (Fernández et al., 2020; Supratya et al., 2020). In both 2015 and 2016, short-term surface temperatures as high as ~22°C were recorded at inshore sites (Figure 2, Appendix S1: Figure S4), 5°C warmer than the warmest temperature recorded at a long-term station on the outer
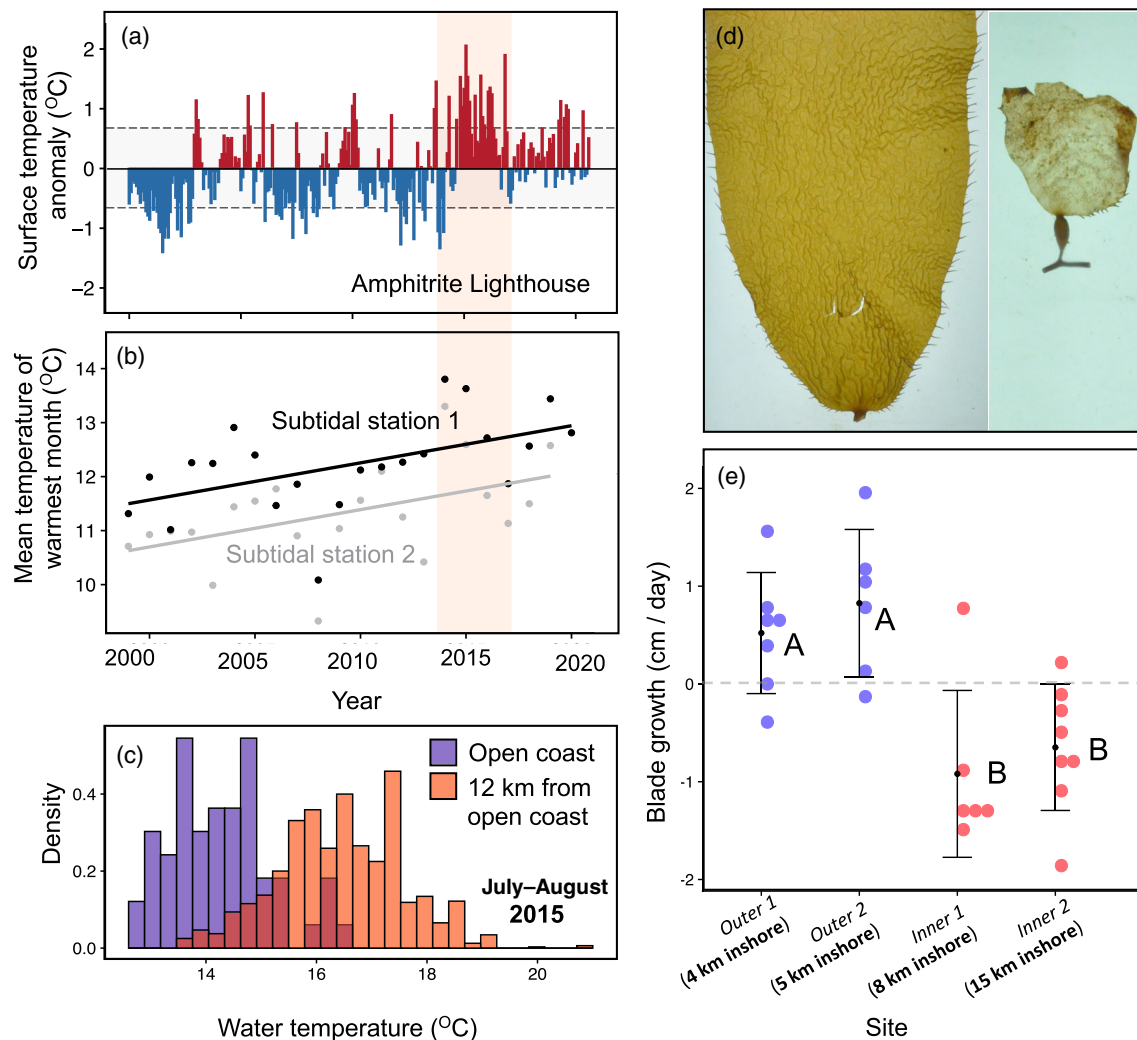

FIGURE 2 Environmental change and kelp fitness consequences in Barkley Sound. Shown are monthly temperature anomalies between 2006 and 2020 (calculated relative to 35-year monthly average) at (a) Amphitrite Point Lighthouse on outer edge of Barkley Sound, temperature of warmest month at two long-term sites in Barkley Sound through time (linear model: Station 1—$F = 7.6934$, df = 21, $p = 0.0132$; Station 2—$F = 5.7463$, df = 20, $p = 0.0270$). (b) The 2014–2016 marine heatwave is highlighted in pink. (c) Relative frequency of in situ temperature measurements from summer of 2015 at Amphitrite Point (open coast; surface temperature) and Fleming Island (~12 km inshore; 1–1.5 m depth); (d, e) growth rate and blade bleaching of *Macrocystis pyrifera* along a microclimatic gradient. (d) Examples of kelp blades growing at the surface at an outer coastal site (outer 1) and an inshore site (inner 2); (e) blade growth of *Macrocystis* blades at inshore ($n = 2$) and outer shore ($n = 2$) sites measured in July 2020. Letters indicate significant differences between means as determined by a Tukey's post hoc test.

coast of Barkley Sound. During this time, kelp forests were extirpated at most sites located more than 8 km inshore (Figure 1a, Appendix S1: Figures S5–S10).

We found strong support for the hypothesis that kelp from warmer inshore waters were more likely to have been extirpated than those toward the cooler outer shore when compared to all earlier time points (1993–1995, 2007, 2008, 2013, 2014; logistic regressions: $p < 0.01$ in all comparisons; Figure 1b–d, Table 1, Appendix S1: Table S1). This spatial pattern of kelp loss was further reflected in qualitative comparisons to hand-drawn maps from the 1970s, which indicate the historical presence of kelp forests along the entire temperature gradient at that time (Appendix S1: Figure S7). This pattern was consistent regardless of data collection methodology or historical year of comparison, indicating that changes in kelp forest distribution far surpass typical interannual variation. Moreover, one historical data set (Appendix S1: Table S1) was restricted to intertidal areas, but others were more inclusive subtidal surveys (that included any canopy kelp visible from the surface, regardless of depth). Thus, kelp extirpations captured across all survey types provide strong evidence that canopy kelp forests have declined across their previous vertical distribution on the shore.

Kelp losses have persisted for several years since the heatwave (i.e., from 2017 to 2021), and remaining kelp have continued to decline in some inshore areas (Appendix S1: Figures S7 and S8), coinciding with persistent temperature anomalies (Figure 1), which may hinder recovery and drive further mortality. In particular, there was a secondary marine heatwave in 2019–2020 (Chen et al., 2021), which was a period associated with further declines in kelp extent in Barkley Sound (Appendix S1: Figure S7). We leveraged this sustained warming to test the effect of anomalously warm water on kelp growth and health and found evidence that inshore surface waters were physiologically stressful for kelp during summer conditions that approached those experienced during the marine heatwave. We found that inshore *Macrocystis* kelp had reduced frond (ANOVA: $F = 71.62$, $p < 0.001$) and net blade (ANOVA: $F = 9.35$, $p < 0.001$) growth rates (Figure 2e) and increased blade bleaching (linear mode: $F = 40.12$, $p < 0.01$, df = 5, Appendix S1: Figure S11) relative to populations near the open coast. Though *Macrocystis* blades from outer sites grew ~0.7 cm/day on average, inshore kelp blade did not grow at all over the several days of monitoring and had negative net blade growth (Figure 2d, Appendix S1: Figure S11), indicating that tissue was fragmenting faster than it was growing. Kelp from inshore sites also had reduced blade length in both species (*Macrocystis*: ~0.2 m versus ~0.3 m on average; ANOVA: $F = 5.471$, $p < 0.01$; *Nereocystis*: ~0.7 m to >1.9 m on average; linear model: $F = 40.12$, $p = 0.001$; longest: $F = 19.07$, $p < 0.01$, Appendix S1: Figure S11).

Subtidal surveys conducted between 2013 and 2016 (at $n = 6$ sites) by scuba reveal that the abundance of the sea star, *P. helianthoides*, dropped significantly during the heatwave (Figure 3a; $\chi^2 = 22.51$, $p < 0.001$), from more than two individuals per transect before the heatwave to ~0.5 per transect in 2016. During this same time period, the abundance of the red sea urchin, *Mesocentrotus franciscanus* (Figure 3b; $\chi^2 = 51.751$, $p < 0.001$) also increased approximately 10-fold across these sites from ~5 individuals per transect on average before the heatwave to more than 50 in 2016. This increase in urchin abundances was associated with losses of kelp at these deeper subtidal (<5 m) depths (Figure 3c; $\chi^2 = 32.487$, $p < 0.001$). Though from 2013 to 2015 *Macrocystis* was found at a density of

TABLE 1 Results of binomial regression testing for a relationship between distance from open coast and extirpation probability.

Data source	Species	Historical years	Resurvey years	Sample size (n)	Coefficient	df	Z-statistic
Aerial flyover (segments)	Both species	1981	2018	254	1.029***	253	8.52
Parks Canada intertidal surveys (sites)	*Macrocystis*	1993–1995	2017–2020	49	0.281**	48	2.69
ShoreZone Aerial flyover (segments)	*Macrocystis*	2007	2018	195	0.325***	194	5.63
	Nereocystis	2007	2018	104	0.681***	103	4.32
	Both species	2007	2018	297	0.435***	296	8.78
Google Earth imagery (segments)	Both species	2013	2018	131	0.641***	130	5.48
Aerial flyover (segments)	Both species	2014	2018	293	0.326***	292	7.78
Bamfield Marine Sciences Centre student kelp forest maps (sites)	*Macrocystis*	2008	2019	37	0.909**	36	2.91

Note: Significant F-statistics are shown in bold with asterisks indicating significance value (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).
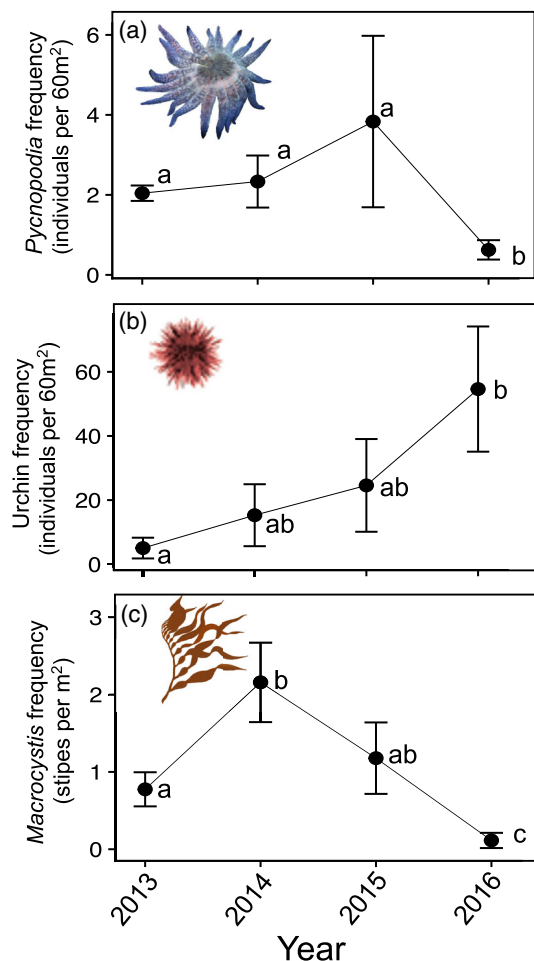
FIGURE 3 Trophic cascade impacts the abundance of subtidal kelp forests. Shown are scuba survey data depicting average abundance (±SE) of (a) sunflower star, *Pycnopodia helianthoides*, (b) red urchin *Mesocentrotus franciscanus*, and (c) giant kelp, *Macrocystis pyrifera*, at subtidal sites (*n* = 6) in Barkley Sound spanning 2014–2016 marine heatwave and sea star die-off. Letters indicate significant differences between individual means.

~1–2 stipes/m^2, four out of six sites had no *Macrocystis* in 2016, with an average of only 0.1 stipes/m^2 across all sites. This pattern of change across trophic levels is consistent with a top-down trophic cascade caused by drastic decreases in the abundance of predatory sea stars. Thus, changes in trophic dynamics in deeper waters have likely contributed to patterns of kelp loss, threatening forests in deeper habitats that are typically cooler (Appendix S1: Figures S12 and S13) and more nutrient rich (Appendix S1: Figure S4).

Underwater surveys conducted with a ROV across our study region (in October 2020, Figure 4, Appendix S1: Figure S14) revealed sharp transitions between fleshy macroalgae-dominated communities and urchin barrens, mostly lacking fleshy algae, corroborating past work that

urchins set the lower depth limit of kelp forests in Barkley Sound (e.g., Druehl, 1978; Markel & Shurin, 2015). Sea urchins reached their upper limits within a few meters of the maximum depth of fleshy seaweeds at all rocky sites, and these transitions always occurred subtidally (between 0 and 5 m below chart datum: mean lower low water large tide; Figure 4, Appendix S1: Figure S15). Sea urchin upper depth limits had a similar range for sites with and without kelp (Appendix S1: Figure S16), strongly suggesting that urchins alone do not explain the complete loss of fringing kelp beds right up into the intertidal zone. Moreover, we recorded kelp losses at multiple sites from warm inshore areas that appeared to lack urchins and were not replaced by urchin barrens. Instead, other macroalgae, including red turfy seaweeds, other kelp species, *Desmarestia* spp., or *Sargassum muticum*, have replaced some of the lost forests at inshore sites (Appendix S1: Section S2).

Despite extirpation of kelp forests in many inshore areas, some stretches of inshore coastline with unstable substrate did retain kelp, illustrating the potential for local refugia. ROV surveys revealed that, somewhat surprisingly, bottom substrate played a key role in determining this kelp forest persistence: communities at sites with unstable substrate (>50% sand/sediment and cobble; hereafter "sandy") lacked urchins at all but one site (Figure 4; Kruskall-Wallis on urchin abundance score: $\chi^2 = 26.257$, df = 2, $p < 0.0001$; Appendix S1: Figure S17) and seaweeds extended to greater depths than at predominantly rocky sites (<50% sand/sediment/cobble; hereafter "rocky") (Figure 4). This pattern was reflected in a significant interaction between substrate type (two levels: sandy, rocky) and distance from open coast on maximum seaweed depth (Figure 4b; ANCOVA: $t = -4.029$, $p < 0.001$, df = 34). The absence of urchins in sandy areas was further associated with increased probability of canopy kelp presence but only further from the open coast (logistic regression; substrate × distance interaction: $z = 3.349$, $p < 0.001$, df = 34), such that sandy areas inshore tended to retain kelp in the absence of urchins.

Remarkably, some of these deeper sandy coves had extensive populations of *Macrocystis* (mixed with understory kelp) even in areas of locally warm surface waters. These forests extended to depths of ~10–14 m below datum, deeper than is typical in Barkley Sound (Druehl, 1978; Markel & Shurin, 2015). In some cases, these forests were barely visible from the surface, except for a relatively small number of individuals that were sometimes visible in the shallows. In fact, toward the deeper limit of these beds, *Macrocystis* plants had an unusual prostrate morphology. They had large blades relative to each float (sometimes several meters) and mostly lay flat along the bottom (Figure 4f). This morphology was described by Lobban (1978), Sharp (1974), and
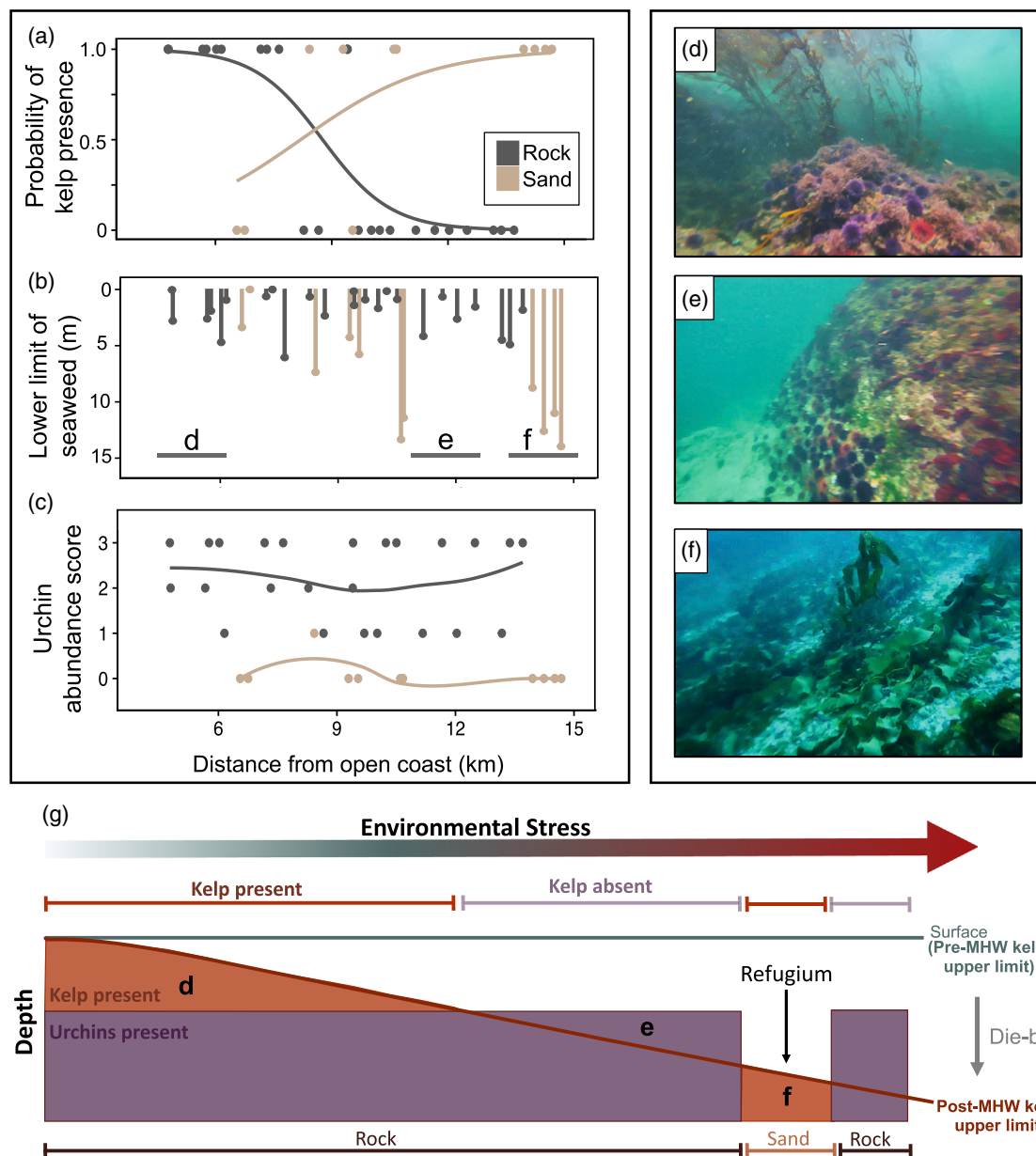
FIGURE 4 Spatial patterns and local drivers of kelp loss and resilience. (a–c) Results of vertical remotely operated vehicle surveys at random sites ($n = 35$) at increasing distances from the open coast. Panels shows the probability of (a) kelp occupancy, (b) lower depth limit of fleshy seaweeds, and (c) urchin abundance score as a function of both substrate and distance from open coast. (d–f) Example images from different scenarios shown in panel (b): (d) a fringing *Macrocystis* forest and (e) macroalgae reef interfacing with urchin barrens at rocky sites, as well as (f) a sandy site with a submerged *Macrocystis* forest. (g) Conceptual model that explains how substrate and local environmental stress predict spatial patterns of kelp loss. Prior to heatwave, kelp was present along the entire gradient. During the marine heatwave, kelp died back from the surface and were extirpated from sites where habitable water conditions were only available below the lower depth of urchins. Sandy habitats then provide deep refugia by limiting urchin abundances. Scenarios shown in (d–f) are also depicted in (g). MHW, marine heatwave.

Druehl (1978) from these same coves but seldom recorded elsewhere for this species (but see the somewhat similar record from New Zealand: Gerard & Kirkman, 1984). We tracked the largest of these submerged forests for over 500 m and did not locate either end of the continuous bed (Video S1). Though kelp at these depths were visibly

healthy, shallow fronds in this mostly submerged forest were sampled during our growth survey and showed a lack of growth capacity at the surface (Figure 2d, Appendix S1: Figure S11), suggesting that the persistence of these *Macrocystis* plants is only viable due to the availability of habitat below the thermocline.

DISCUSSION

Marine habitats are threatened globally by climate change, including gradual and acute temperature increases, and other human-mediated changes to the physical and biological environment (Filbee-Dexter & Wernberg, 2018; Wernberg et al., 2019). However, regional and local environmental heterogeneity has led to wide variation in the responses of habitat-forming foundation species to these ongoing stressors (Claar et al., 2020; Krumhansl et al., 2016; Palumbi et al., 2014; Pfister et al., 2018; Smale, 2020). Understanding the fine-scale factors that drive this variation is essential if we are to make accurate predictions about future ecosystems in a changing ocean (Bates et al., 2018). Here, we investigated the role of microclimate in mediating the local responses of kelp forests to multiple abiotic and biotic stressors experienced throughout the Northeast Pacific at a broad scale (Bond et al., 2015; Cavanaugh et al., 2019; Cavole et al., 2016; Harvell et al., 2019; Rogers-Bennett & Catton, 2019). We did so by leveraging a persistent spatial gradient of summer SSTs that exposes kelp further from the open coast to temperatures comparable to those felt ~2000 km further south. We demonstrated that kelp forests in locally warm microclimates were less likely to persist through a major marine heatwave. Though kelp occupancy toward the open coast has remained largely unchanged for decades (<4% loss in the outermost 8 km), we detected a >70% decline in kelp occupancy from inshore (≥8 km) shoreline segments that occurred during the 2014–2016 marine heatwave (Figure 1e). Though this correlation with local microclimate might imply that direct physiological stress is the main driver of kelp forest extinction, our data suggest that this pattern reflects a complex interaction between direct and indirect (i.e., abiotic and biotic) drivers.

Drivers of kelp loss

We documented kelp forest losses up into the intertidal zone (above urchin limits in our study area; Figure 4a) and in some shallow sandy bays that appear to lack urchins (with remnant kelp populations showing signs of physiological stress or surface dieback; Appendix S1: Section S2; Figures S18–S22). This provides direct evidence that environmental drivers are responsible for kelp declines in shallow waters. In addition to warmer temperatures, the heatwave was associated with reduced nitrate content off the coast of Barkley Sound (Peña et al., 2019), an issue that may have been exacerbated toward the warm edge of the gradient where nitrate availability is generally lower (Appendix S1: Figure S4). However, canopy kelp forests commonly experience low nitrogen levels during regular seasonal cycles (e.g., Hurd et al., 2000; Smith et al., 1983; Smith et al., 2018). For example, Dixon Island in Barkley Sound (which lost kelp during the heatwave; Appendix S1: Figure S5) commonly has very low nitrate in the summer (Druehl et al., 1988; Hurd et al., 1994, 2000) but consistently had kelp prior to the heatwave. There is direct experimental evidence that nitrogen limitation negatively impacts kelp thermal tolerance (Fernández et al., 2020; Gerard, 1997). Thus, we propose that, although temperature was the principal driver of kelp loss, interactions with local nutrient regimes may have been important in determining the temperature threshold at which kelp mortality occurred.

The direct physiological effects of temperature and reduced nutrients are exemplified by our surveys of kelp growth and metrics of health. Not only was growth reduced at inshore sites during the warm summer conditions of 2020, but blade growth was negative, indicating a net loss of tissue. Blade bleaching likely directly reflects a stress response to environmental conditions, and shorter blades at sites further from the open coast may also be a consequence of weaker tissues and increased dissolution in the presence of low nutrient levels or high temperature (Simonson et al., 2015; Stephens & Hepburn, 2016; Filbee-Dexter, Feehan et al., 2020). Other factors, such as waves and currents, can also strongly influence blade length, and though we attempted to limit these confounding factors by sampling only in protected coves, we cannot fully rule out these potential drivers. However, given the direct observation of net tissue loss and the magnitude of variation between sites (~1.9 vs. ~0.7 m on average for *Nereocystis*), we strongly suspect that temperature and nutrients contribute to this variation in blade length. The lack of difference in blade number indicates that variation in blade length is likely not a consequence of differences in kelp age or phenology. Overall, these growth data and health metrics indicate that the surface water conditions further from the open coast are unsuitable for kelp forest persistence during anomalously high summer temperatures.

Cooler, nutrient-rich water below the thermocline may offer a refuge for kelp forests (Giraldo-Ospina et al., 2020; Graham et al., 2007). However, urchin predation can limit the maximum depth of kelp forests by grazing at their seaward edges (Markel & Shurin, 2015), potentially preventing kelp populations from establishing or persisting in these thermal refugia. Along the entire Northeast Pacific coastline, sustained warm temperatures during the 2014–2016 heatwave indirectly enhanced the spread of marine disease, leading to the functional extinction of the sunflower star *Pycnopodia* and subsequent increases in urchin abundance (Harvell et al., 2019). Barkley Sound was no exception. As expected, subtidal surveys spanning the heatwave revealed a trophic

cascade in which the loss of the predatory sea star, *P. helianthoides*, was associated with a sharp increase in urchin abundance and losses of kelp in deeper subtidal areas. The timing of this increase in urchins parallels an independent data set from a long-term inshore subtidal site in Barkley Sound monitored between 1990 and 2020, where red urchins rapidly increased following 2015 (see fig. 5 in Watson et al., 2021), consistent with the timing of sea star wasting disease. Increases in urchins, possibly along with calmer seas during periods of warming (Watson et al., 2021), may have facilitated the movement of urchins upshore (Markel & Shurin, 2015), thereby reducing the availability of deeper, subtidal habitats. Thus, high temperatures and abundant urchins impacted kelp forests across different parts of their depth range, together driving losses in warmer areas.

We present a conceptual framework outlining how microclimate and grazing pressure may interact to influence kelp forest occupancy in our system (Figure 4g), derived from ecological theory about how climate change can differentially impact the zonation patterns of interacting species, and lead to local extinctions (Harley, 2003, 2011). We propose that environmentally stressful conditions excluded kelp forests from shallow waters in local "hotspots" while having limited direct impact on outer coast kelp forests or those in deeper areas below the thermocline. These outer-shore or deeper kelp forests experience the cool temperatures typical of those expected at midrange for these species and, like other midrange outer-coast kelp populations (Hamilton et al., 2019), were largely resilient in the face of increased temperatures. Simultaneously, urchin populations have expanded, likely also becoming more aggressive (i.e., less time hiding) following predation release, as their main predator was lost from the system (Smith et al., 2021). Urchins set a lower depth limit for kelp on rocky shores and their increases have likely driven kelp further up the shore (Markel & Shurin, 2015) or reinforced existing boundaries of fringing kelp forests, eliminating those deeper than a few meters below the surf line. Moreover, Watson et al. (2021) hypothesized that upshore movement in urchins could have also been facilitated by calmer conditions during the marine heatwave, allowing urchins to graze shallower than usual. In areas where urchins and warm surface conditions co-occur, kelp forests have been "squeezed out" by these combined effects (Figure 4g). In contrast, in the absence of either one of these stressors, kelp forests were largely persistent, remaining as shallow fringing forests in the cool waters of the outer coast or as deeper, largely submerged forests in the absence of urchins at inshore sandy sites (Figure 4g). The tendency for multiple drivers to influence organisms in nonlinear ways is an increasingly recognized phenomenon in

ecology and conservation (Brook et al., 2008). Our results highlight that one mechanism for such interactive effects of multiple drivers is through the differential impacts of individual drivers on different types of microhabitats (in this case depth). This squeezing effect by multiple drivers has been documented in other systems where stressors are vertically graded. In particular, the intertidal alga *Mazzaella parksii* can be excluded from communities if stress from aerial exposure pushes them below the upper limit of their gastropod grazers (Harley, 2003). Similarly, the interacting effects of deoxygenation and ocean acidification are expected to reduce the vertical distribution of Humboldt Squid within the water column (Rosa & Seibel, 2008). Together these patterns illustrate that variation between horizontal and vertical drivers will play an important role in driving the future distributions of marine taxa.

Although not directly responsible for kelp forest losses, biotic interactions with other seaweeds may influence the capability of kelp to recolonize these coastlines (Filbee-Dexter & Wernberg, 2018). The warmth-tolerant invasive seaweed *Sargassum muticum*, for example, has increased in abundance in Barkley Sound over the past two and half decades (Starko et al., 2019) but is restricted to wave-sheltered sites. Many of the kelp forests that were lost at inshore sites were not replaced by *Sargassum*, but for those that were, dense *Sargassum* beds may limit recruitment of canopy kelp through competition for space and light. Other seaweeds to replace canopy kelp include foliose red algae (e.g., *Prionitis* spp., *Chondracanthus* spp.) and *Desmarestia* spp. Little is known about how competition for space with these seaweeds limits the capacity for recolonization by *Macrocystis* or *Nereocystis* in the Northeast Pacific, but work elsewhere has shown that competition with primary space holders may be a key factor limiting the recovery of kelp forest ecosystems once they have collapsed to a degraded state (Filbee-Dexter et al., 2016; Filbee-Dexter & Wernberg, 2018; Fredriksen et al., 2020).

Subsurface refugia

We identified several areas in Barkley Sound where surface waters were warm, but the absence of urchins allowed kelp to grow to greater depths. Urchins have been shown to largely avoid sand, strongly decreasing the strength of kelp–urchin interactions in sandy areas (Ferrario et al., 2021; Laur et al., 1986). Our ROV surveys revealed an interacting effect of benthic substrate and distance from open coast on kelp presence. Sandy sites toward the open coast tend to be wave-exposed beaches and are therefore unsuitable habitat for kelp forests

owing to the movement of unconsolidated substrate. However, sandy habitats in sheltered coves further inshore likely experience little water movement, enabling the establishment of kelp populations on small pebbles or cobble in the sand while eliminating urchins (Laur et al., 1986). Together these results indicate that, in the absence of urchins, deeper waters may act as refugia in the face of warm surface conditions. Moreover, local substrate condition may limit urchin populations, potentially offering fine-scale local refugia in the face of herbivore booms.

The role of deep-water kelp forests as thermal refugia is well documented globally (Giraldo-Ospina et al., 2020; Ladah et al., 1999). For example, diebacks of the surface canopy occur in *Macrocystis* populations from Southern and Baja California during El Niño years (Ladah et al., 1999), facilitating long-term forest persistence. In Australia, deeper forests had higher survival through the 2011 marine heatwave than did shallow-water kelp (Giraldo-Ospina et al., 2020). Spatial refugia also play an essential role in global kelp biogeography (Bolton, 2010), such as those in deep tropical waters (much deeper than in this study), despite the warm, eutrophic surface waters (Graham et al., 2007), or those in the Arctic below seasonal ice cover (Filbee-Dexter et al., 2019). Our results contribute additional evidence for the general importance of subsurface thermal refugia and further demonstrate that the availability of these refugia can strongly depend on biotic interactions. Overgrazing by urchins caused by predator extirpation is common throughout the Northeast Pacific and is likely to strongly limit the availability of deep habitats for kelp. However, local conditions can also limit urchin abundance or influence the efficacy of their grazing (Figure 4d–f), potentially making way for a natural mosaic of habitable refugia.

Some of the remaining kelp forests at the warm edge of the local temperature gradient were nearly or entirely submerged below the surface. Though the extent to which these mostly submerged *Macrocystis* populations are distributed across protected bays in the Northeast Pacific remains unclear, submerged beds in locally warm areas have been anecdotally reported in California and Chile (Edwards, 2004; Gerard & Kirkman, 1984; Ladah et al., 1999; Mora-Soto et al., 2020). In these cases, the submerged form has often been associated with persistently high temperatures (e.g., 17–18°C; Mora-Soto et al., 2020), comparable to those we recorded at inshore sites in Barkley Sound. The presence of submerged kelp forests may bias data collected through surveys conducted at the surface or through analysis satellite or aerial imagery (Mora-Soto et al., 2020). Thus, understanding the conditions that lead to subsurface kelp forests will be an important step in ground-truthing the use of remote sensing data for kelp monitoring. However, our results show that by coupling in situ surveys with remotely sensed imagery, novel insights into the processes driving patterns of kelp forest loss can be gained.

CONCLUSIONS

Although drivers of resilience to climate perturbations are often studied in similar habitats over broad latitudinal gradients (e.g., Cavanaugh et al., 2019; Wernberg et al., 2016), here we demonstrated that local-scale variation could be instrumental in mediating the responses of species and ecosystems to global change. We showed that the position of kelp forests along a microclimatic gradient of ~16 km strongly influenced their probability of persistence through the 2014–2016 marine heatwave. Although the impacts of marine heatwaves are likely to be most acute at low latitudes, coastlines tend to become more geographically complex at higher latitudes with substantially more wave-sheltered, inshore coastline (Starko et al., 2019). Inshore waters in bays and fjords may experience disproportionate climate variability relative to the open coast, where latitude may better predict the temperatures experienced each season. Yet, complex, fjord-laden coastlines make up a substantial proportion of the kelp forest habitat on Earth (Jayathilake & Costello, 2021), a pattern that may create large pockets of unexpected rapid change owing to the exacerbated effects of shifting environmental conditions. Midlatitude, fjord-laden shores represent immense stretches of coastline (e.g., ~60,000 km in British Columbia alone vs. ~1000 km of linear coastline along the outer coast of Washington and Oregon combined). Losses of kelp forests from these immense areas could have profound effects on coastwide productivity, habitat connectivity, and carbon drawdown. Understanding how this fine-scale variation contributes to the spatial resilience of marine foundation species in the face of abiotic and biotic perturbations will be essential if we are to meaningfully scale up predictions about how global change will impact marine habitats to the broadest spatial scales.

The effective management of kelp forest ecosystems will depend on our ability to understand and mitigate the stressors limiting their resilience and distributions (Hollarsmith et al., 2022); our data contribute critical insights in this regard. Our study illustrates how variation within even a relatively small region could lead to substantially different levels of resilience across local kelp forest habitats, and this should be considered when designing monitoring schemes or interpreting monitoring data. Moreover, inshore habitat that experiences greater environmental variation should be specifically targeted

for monitoring and conservation actions in order to identify local or regional areas of vulnerability. Our results also suggest that, at least in the short term, the suppression of urchin populations (e.g., through otter introductions or active urchin removals) could enable kelp forests to extend to greater depths, thereby increasing their resilience to environmental stress at the surface. This adds to the growing evidence that mitigation of destructive urchin grazing should be a management priority in the Northeast Pacific despite its inherent challenges (Gregr et al., 2020; Wilmers et al., 2012). Short-term reduction in grazing pressure could also provide time to identify heat-resistant kelp genotypes (Coleman & Goold, 2019; Wernberg et al., 2018) or refine emerging scalable kelp restoration tools to further support kelp forest recovery (Coleman et al., 2020; Fredriksen et al., 2020).

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST

The authors have no competing interests to disclose.

DATA AVAILABILITY STATEMENT

Data and code (Starko and chrisjneufeld, 2022) are available on Zenodo at https://doi.org/10.5281/zenodo.6397743.

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