

# Multi-scale stability of an intertidal kelp (*Postelsia palmaeformis*) near its northern range edge through a period of prolonged heatwaves

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## Abstract:

- **Background and Aims:** Climate change, including gradual changes and extreme weather events, is driving widespread species losses and range shifts. These climatic changes are felt acutely in intertidal ecosystems, where many organisms live close to their thermal limits and experience the extremes of both marine and terrestrial environments. A recent series of multi-year heatwaves in the northeast Pacific Ocean may have impacted species even toward their cooler, northern range edges. Amongst them, the high intertidal kelp *Postelsia palmaeformis*, has traits that may make it particularly vulnerable to climate change, but it is critically understudied.
- **Methods:** In 2021 and 2022, we replicated in-situ and aerial *P. palmaeformis* surveys that were originally conducted in 2006 and 2007 to assess the state of northern populations following recent heatwaves. Changes in *P. palmaeformis* distribution, extent, density, and morphometrics were assessed between these two time points over three spatial scales, ranging from 250-m grid cells across the entire 167-km study region, to within grid-cells, and the individual patch.
- **Results:** We found evidence consistent with population stability at all three scales: *P. palmaeformis* remained present in all 250-m grid-cells in the study region where it was previously found, and neither extent within-cells or patch density changed significantly between time points. However, there was evidence of slight distributional expansion, increased blade lengths, and a shift to earlier reproductive timing.
- **Conclusions:** We suggest that apparent long-term stability of *P. palmaeformis* may be due to thermal buffering near its northern range edge as well as from the wave-exposed coastlines it inhabits, which may have decreased heatwave impacts. Our results highlight the importance of multi-scale assessments when examining changes within species and

populations, and the importance of dispersal capability and local conditions in regulating species' responses to climate change.

**Keywords:** biogeography; climate change; species distributions; kelp; heatwave; multi-scale analysis; leading range edge; phenological shifts; *Postelsia palmaeformis*; stability

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## INTRODUCTION

Climate change is reorganizing ecological communities, with changes occurring across scales, from individual organisms to whole ecosystems (Cooley *et al.*, 2022; Parmesan *et al.*, 2022). Gradual warming is driving phenological changes, abundance declines, and species range shifts over time (Poloczanska *et al.*, 2013; Pecl *et al.*, 2017; Cohen *et al.*, 2018), while more frequent, intense, and prolonged heatwaves (Oliver *et al.*, 2018) cause more rapid changes (Wernberg *et al.*, 2016; Smale *et al.*, 2019; Straub *et al.*, 2019). At broad scales, warming often leads to range contractions at species' trailing (equatorward) range edges, when thermal safety margins are exceeded (Wernberg *et al.*, 2016; Pinsky *et al.*, 2019), and range expansions at their leading (poleward) range edges as new habitat becomes suitable for colonization (Pinsky *et al.*, 2013; Sanford *et al.*, 2019). However, local adaptation can make populations equally vulnerable to warming throughout a species' range (Bennett *et al.*, 2015, 2022), and other fine-scale environmental variables and species traits can modulate exposure or sensitivity, leading to more complex or seemingly counterintuitive responses (Sunday *et al.*, 2015; Parmesan and Hanley, 2015; Fuchs *et al.*, 2020). Evaluating how species respond to climate change requires baseline data from which change can be inferred (Brown *et al.*, 2011; Berry *et al.*, 2021). While long time-series data are lacking for the world's many data deficient species and ecosystems, the importance of evaluating climate change impacts necessitates using and carefully scrutinizing alternate data sources, including historical datasets and mixed-method approaches, if we are to broadly understand species' vulnerability to future change, the stability of the ecosystems they support, the long-term sustainability of the ecosystem services they provide, and required conservation actions (Brown *et al.*, 2011; Pecl *et al.*, 2017).

Organisms living in the marine intertidal zone are vulnerable to gradual warming and heatwaves as they often experience temperatures near their upper thermal tolerance limits when exposed at low tide (Helmuth *et al.*, 2002; Harley, 2011; Amstutz *et al.*, 2021). This is especially true for non-motile species in the high intertidal zone where communities are the most vulnerable to extreme conditions during heatwaves (Whalen *et al.*, 2023). Additionally, common traits such as sessile adult life-stage, specific habitat requirements, and poor dispersal mean that many intertidal species have limited capacity to shift their ranges in response to warming (Sunday *et al.*, 2015; Årevall *et al.*, 2018; Fuchs *et al.*, 2020), and are also unable to escape the impacts of heatwaves (Weitzman *et al.*, 2021). Although this can lead to widespread local extinctions (Thomsen *et al.*, 2019), these may not be well-predicted by latitude because of factors including regional variation in the timing of low tides, local variation in wave exposure, and different site aspects, which together create high levels of fine-scale spatial variation in intertidal temperatures (Helmuth *et al.*, 2002, 2006; Seabra *et al.*, 2011; Amstutz *et al.*, 2021). As such, it is important to evaluate the climate-change response of intertidal species throughout their range at multiple scales.

Amongst intertidal organisms, the sea palm kelp *Postelsia palmaeformis* (hereafter, *Postelsia*) may be quite vulnerable to heatwaves because of its specific habitat requirements (Paine, 1988; Nielsen *et al.*, 2006), disturbance-mediated method of population maintenance (Paine *et al.*, 2017), and poor dispersal capabilities (Coyer *et al.*, 1997; Kusumo *et al.*, 2006). *Postelsia* occurs in the wave-exposed rocky intertidal zone from Central California, USA, to northern Vancouver Island, British Columbia (BC), Canada where its vertical and horizontal distributions are limited by multiple abiotic and biotic factors including wave exposure, thermal stress, light availability, and interspecific competition (Figure 1; Abbott and Hollenberg 1976; Paine 1979, 1988; Holbrook *et al.* 1991; Blanchette 1996; Nielsen *et al.* 2006). Occurring higher in the intertidal zone than any other canopy-forming seaweed, *Postelsia* forms secondary structure for an associated community of organisms

(Teagle *et al.*, 2017) and contributes to intertidal productivity through its rapid growth (Leigh *et al.*, 1987). Understanding the status of this foundation species is thus important for assessing changes in intertidal productivity and associated ecosystem services (Straub *et al.*, 2019; Hanley *et al.*, 2020). As an annual kelp, *Postelsia* patches are maintained through the local dispersal of spores; however, these often settle no further than 5 m from their parent plant, and patches >20 m apart can exhibit strongly distinct genetic structure (Coyer *et al.*, 1997; Kusumo *et al.*, 2006; Paine *et al.*, 2017). Long-distance dispersal of *Postelsia*, which relies on the transport of dislodged reproductive sporophytes, only occurs rarely, according to experimental studies and dispersal models (Paine *et al.*, 2017). Thus, while *Postelsia*'s annual life history may result in fluctuations in extent and cover at a patch scale, its method of long-distance dispersal likely sets strong constraints on the variability of its large-scale geographic distribution (Paine *et al.*, 2017).

Between 2014 and 2016, the northeast Pacific Ocean experienced an unprecedented, multi-year marine heatwave (Di Lorenzo and Mantua, 2016; Gentemann *et al.*, 2017; Tseng *et al.*, 2017) that resulted in losses of intertidal and subtidal kelp in many places (Cavanaugh *et al.*, 2019; Starko *et al.*, 2019, 2023; Rogers-Bennett and Catton, 2019; Whalen *et al.*, 2023). Water and air temperature anomalies persisted throughout this period (Figure 2), and though not as extreme, warm temperatures continued in the years following due to smaller marine heatwaves in 2019 and 2020 (Barkhordarian *et al.*, 2022), and an unprecedented atmospheric heatwave in June 2021 (Qian *et al.*, 2022). Although these heatwaves spanned the entire geographic range of *Postelsia* and may have significantly impacted its species-level distribution and abundance, there are no published studies comparing its populations before and after this period of extreme environmental change. While unpublished data from California and Oregon suggest dramatic declines in abundance (87–100% in 2015) occurred in all monitored populations, with slow recovery since (Lohse *et al.* 2020, WSN, unpubl. res.), impacts elsewhere remain unknown.

Here we leveraged rare *Postelsia* data collected prior to recent heatwaves (2006–2007), and re-surveyed the same area (2021–2022) to quantify population change across 167 km of coastline near the species' northern range edge. Although such two-timepoint analyses lack the temporal resolution to assess interannual variability, they can identify broad changes in data-poor species that help avoid shifting baselines (Baum and Myers, 2004; McClenachan *et al.*, 2012), and have previously been used to quantify climate change impacts in terrestrial forests (Danby and Hik, 2007), marine intertidal ecosystems (Barry *et al.*, 1995; Harley, 2011), and variable systems including subtidal and intertidal kelp forests (Starko *et al.*, 2019; Mulders *et al.*, 2022). In this study, we examined *Postelsia* at three different spatial scales: regional distribution via presence-absence in 250-m grid cells across a broad stretch of coastline on southwestern Vancouver Island; linear shoreline extent, within these 250-m cells; and individual patch metrics, via density and individual morphometrics in a patch near the northwest edge of our study region. We tested two competing hypotheses about the status of *Postelsia* near its northern range edge: (1) the effects of prolonged heatwaves will be neutral to beneficial at or near species' leading range edges. In this case, *Postelsia* populations would remain stable due to thermal buffering or potentially expand due to improved habitat suitability near its northern range edge; (2) due to fine-scale variation of intertidal temperature poorly associated with latitude (Bates *et al.*, 2018), intertidal species will decline at hotspots throughout their ranges during prolonged heatwaves. As such, northern *Postelsia* populations could experience patchy distributional losses and extent/density loss at sites with particularly stressful local conditions.

## MATERIALS AND METHODS

### *Study Area*

We focused on a 167-km stretch of shoreline along the southwestern coast of Vancouver Island, BC, Canada that is largely protected under the Canadian National and Provincial Park systems [Supplementary information Figure S1A], because it is one of the few regions with high-quality baseline data collected prior to recent northeast Pacific heatwaves. This region of coast, spanning from Cape Beale in the northwest (48.80°N, -125.21°W) to Sombrio Beach in the southeast (48.50°N, -124.33°W), is within 230 km of the northern range edge of *Postelsia*, and still within the species contiguous range. Moreover, Sombrio Beach is located near the entrance to the Strait of Juan de Fuca (part of the Salish Sea) and is the furthest into the Salish Sea that *Postelsia* is known to occur. Therefore, this region captures the most sheltered range boundary of *Postelsia* on Vancouver Island. Northwest of Sombrio Beach, most of the study region is defined by exposed rocky shorelines which are optimal *Postelsia* habitat (Paine, 1988; Nielsen *et al.*, 2006). Baseline data allowed us to accurately compare current and past *Postelsia* distributions at multiple scales, providing a rare snapshot into how this species has responded to a period of significant heatwaves in its Canadian range.

### *Regional Air and Water Temperature*

We analyzed air and sea surface temperature (SST) using long-term time series datasets from nearby lighthouses to provide context on how gradual warming and large temperature anomalies such as the 2014–16 heatwave influenced the thermal conditions of our study region. Marine and terrestrial heatwaves are defined as periods where water or air temperatures exceed the long-term 90<sup>th</sup> percentile for a minimum of five or three days, respectively (Perkins and Alexander, 2013; Hobday *et al.*, 2016; Oliver *et al.*, 2018). Average monthly temperature anomaly was calculated as the degrees Celsius above or below a 34-year historical monthly average (dating to 1988 and calculated from daily temperature readings taken at the lighthouses). Air temperature was taken from the Cape Beale Lighthouse at the north-western edge of our study region, and SST data were taken from the Amphitrite Lighthouse (~27 km northwest of Cape Beale). While the Amphitrite Lighthouse is just outside of our study region, it is the closest available location with a continuous long-term SST dataset and is located on the exposed west coast of Vancouver Island like much of our study region.

### *Low Altitude Oblique Coastal Image Data*

We quantified *Postelsia*'s presence-absence and linear extent within 250-m cells along the coast using a publicly available dataset (ShoreZone; Howes *et al.* 1994; Cook *et al.* 2017; <https://mcori.maps.arcgis.com>) of oblique photographs. The 2270 images analyzed for this study were collected from a helicopter flying at low altitude (<100 m) to ensure an image scale of around 1:2500 to 1:5000 [Supplementary information Figure S1B]. Flights were all completed at low tides, with a focus on collecting data when tides were lower than 0.7 m above Canadian chart datum to ensure much of the mid and high intertidal was exposed. Flights were initially completed in August 2007 (13–14 Aug 2007) and we commissioned new flights in 2021 to match the initial timing (8–9 August 2021), when many of the larger *Postelsia* individuals in a patch would be near their maximum size for the season and potentially reproductive (Thompson *et al.*, 2010). Within the dataset available for our study area (n = 2270 images), photographs are of high quality and provide a largely continuous view of the coastline, often overlapping. To determine the distribution of *Postelsia*, we matched geographic

features visible in ShoreZone and Google Earth satellite imagery to georeference *Postelsia* observations.

### *Imagery Data Processing*

To assess changes in the distribution of *Postelsia*, we compared its presence and absence along the length of the study region in 2007 and 2021. To do so, we first overlaid Google Earth satellite imagery of the study region with a grid of 250-m by 250-m cells in ArcGIS Pro and selected cells containing coastline within Google Earth satellite imagery. This resulted in the division of our study area into 839 cells. Multiple ShoreZone images often depicted the same cell from different vantages, allowing a full view of the cell and thus the determination of true *Postelsia* presence or absence. However, due to slight differences in the paths and/or images from ShoreZone flights, only ~84% (n = 706) of the cells had high-quality overlapping data for both years, allowing comparisons over time. The 250-m scale was chosen because it would become increasingly more difficult to distinguish cell boundaries from the imagery at smaller scales. We identified cell boundaries in the aerial imagery by visually matching distinct shoreline features evident in the satellite imagery to those same distinct features in the aerial photos from the two time points. We then located every patch of *Postelsia* in the imagery and associated it with the correct cell by carefully and repeatedly examining each ShoreZone image [Supplementary information Figure S2]. We denoted the presence (1) or absence (0) of *Postelsia* in each cell for each year and assessed change over time using the ArcGIS Pro raster calculator to combine the two layers. Any cells containing a value of one in the resulting layer (denoting *Postelsia* presence in only one of the two years) were inspected to identify if *Postelsia* was only present in 2007 (loss) or in 2021 (colonization). The visual inspection process, from identification of cell boundaries to inspection for *Postelsia* occurrence, was time consuming and made possible by the availability of high-resolution images (300 DPI) and the fact that *Postelsia* is very distinct in the mid to high intertidal zone, being the only golden-coloured canopy-forming algal species that occurs in this zone within our study region. To test for differences in the distribution of *Postelsia* between years, we conducted a binomial generalized linear mixed effect model (GLMM; fixed: year (factor); random: cell; Brooks *et al.* 2017). All statistical analyses were carried out in R version 4.1.3 (R Core Team, 2022).

While our regional (250-m grid cells over 167 km) scale presence-absence analysis assessed large-scale changes in *Postelsia* distribution, we also examined finer-scale (within grid-cell) changes in linear patch extent. To perform this analysis, we compared oblique and satellite imagery, using distinct shoreline features to trace the linear extent of *Postelsia* patches onto the satellite imagery for a randomly selected subset (n=25) of cells that contained *Postelsia* in both time points (~19% of all such cells) [Supplementary information Figure S3]. We summed the length of all patches within a cell to find the linear extent of *Postelsia* in each year and compared linear extent between years to calculate the percent increase or decrease. As this process was potentially dependent on an observer's interpretation of the shoreline features between multiple sets of aerial and satellite imagery, all analyses were carried out by a single individual (M. Csordas). To ensure inconsistency in shoreline tracing introduced by analyst interpretation and differences in the aerial imagery available for each time point was not being interpreted as change in linear patch extent, a representative cell (one out of the 25) was selected to undergo this process twenty separate times. A 95% measure of methodological error was determined for this cell by taking the range of percent linear change for the 19 closest estimates (95% of the twenty separate tracings). This value was determined to be 18.7% and changes in percent linear extent below this threshold could potentially arise through artifacts of methodological error. Results from this scale will also have to be interpreted carefully due to the large

potential for interannual fluctuations in *Postelsia* patch extent (Paine *et al.*, 2017) but should nicely compliment our larger-scale regional analysis. To test for differences in *Postelsia* extent between years, we conducted a GLMM (fixed: year (factor); random: cell (factor)) assuming a Gaussian distribution.

The fine-scale analysis was also performed on all five cells where colonization occurred by using the ShoreZone and satellite imagery to trace the available shoreline in each cell [Supplementary information Figure S3]. Available shoreline was defined as any shoreline at the same tidal height as the *Postelsia* patch within the oblique imagery and was traced onto the satellite imagery by visual inspection of shoreline features. After this, we separately traced the linear extent of the *Postelsia* patch. From these two lengths (available shoreline and *Postelsia* extent), we calculated the percent of available shoreline that was colonized to assess the scale of colonization that had occurred.

### *Patch-Level Density, Reproductive Status, and Individual Size Metrics*

At the finest scale, we quantified changes in the density, reproductive status, and individual morphometrics of *Postelsia* in a single patch located off the southern point of Cape Beale (48.7810 °N, 125.2100 °W) near the north-western end of our study region. Declines in *Postelsia* abundance and size have previously been associated with stressful conditions (Nielsen *et al.*, 2006; Thompson *et al.*, 2010), making them potential fine-scale indicators of heatwave impacts. In each year, density counts were completed in at least ten 0.25-m<sup>2</sup> quadrats (n = 10 in 2006, n = 14 in 2021, n = 15 in 2022) randomly placed along a transect through the middle of the *Postelsia* zone (defined as the halfway point between the high and low intertidal limits of the *Postelsia* patch). Within each quadrat, we haphazardly selected ten individuals (or as many as possible if there were fewer than ten in the quadrat) and recorded their basal stipe diameter, stipe height, number of blades, and reproductive status (judged by whether sori were visible on any blades). For each of these individuals, three blades were haphazardly selected to have their basal width and total length measured. Basal width was measured just above the meristematic tissue and length was recorded from this point to the tip of the blade. This scale of analysis was limited by the available historical data which was originally collected on 11 July 2006 in a singular patch at Cape Beale. We repeated these surveys using the same protocols in 2021 (25–26 July 2021), and density and reproductive status data were also recollected in 2022 (15 July 2022). Due to the small number of years data was collected in, results are interpreted while considering the large amount of interannual variation that would be expected in these metrics (Paine *et al.*, 2017).

To determine if there were differences in density, reproductive status, or morphometrics between years, we fit generalized linear models (GLMs) to the data. An average value for each metric was calculated per quadrat and Shapiro-Wilk tests and histograms were used to test for normality. Distributions for the GLMs were selected to provide the best fit based on data type, normality test results, and model residual plots. Analysis of deviance for GLM fits were performed to examine the significance of the effect size of year (Fox and Weisberg, 2019). Where there was a significant effect estimated marginal means were plotted to determine if there had been a significant increase or decrease in the metric between timepoints (Searle *et al.*, 1980; Lenth *et al.*, 2022).



## RESULTS

### *Regional Temperature Profiles*

Both air temperature and SST reached abnormal highs since the initial surveys occurred in 2006 and 2007; air temperature and SST measurements reflect several heatwaves and sustained warm conditions after 2013. During the 2014–2016 marine heatwave and following, air temperatures reached  $> 3^{\circ}\text{C}$  and SSTs reached  $> 2^{\circ}\text{C}$  above their respective long-term averages and both measures stayed anomalously high for several years. Prior to this heatwave and the initial surveys, temperatures in the region steadily fluctuated around long-term average temperatures as seen from the one-year moving averages for temperature anomalies (Figure 2). Since 2013, these moving averages have largely remained above the long-term average, indicating that the climatic conditions experienced by *Postelsia* have changed between survey years.

### Postelsia Distribution and Extent

In our region-wide presence-absence analysis, we found no significant influence of year on *Postelsia* occurrence (Binomial GLMM:  $X^2 = 2.3266$ ,  $df = 1409$ ,  $p > 0.127$ ), confirming that distributions were not significantly different between 2007 and 2021 [Supplementary information Figure S4]. In 2021 *Postelsia* occurred in every cell it did in 2007 and five additional cells representing long-distance expansions ( $>250$  m) to new areas; there was no evidence of losses at this coarse scale (Figure 3). For cells where expansion occurred, shoreline tracing revealed that new *Postelsia* patches were extremely small, with the largest having only colonized  $\sim 2\%$  of the available shoreline within its cell and having a linear extent of only  $\sim 7.3$  m (Figure 3). The small scale of these expansions was despite much of the *Postelsia*-free shoreline in these cells appearing to be suitable rocky habitat. Overall, cells containing *Postelsia* appear to be spatially aggregated, with cells containing the species seldom occurring alone. *Postelsia* also appeared to be more prevalent near the northwestern end of our study region (Figure 3), as somewhat expected due to known distributional patterns of this kelp species into the Salish Sea.

Within- 250-m grid-cells, we found that 12 of 25 cells showed losses in the linear extent of *Postelsia*, while 13 showed increases (Figure 4). Only four increases and five decreases exceeded our estimated methodological error (Figure 4B) and statistical tests found no significant effect of year on extent within *Postelsia* patches ( $X^2 = 0.526$ ,  $df = 46$ ,  $p > 0.468$ ). To further examine the nine cells where extent changes exceeded our methodological error threshold, the maximum *Postelsia* extent was plotted in comparison to the average patch extent of all 25 randomly selected cells (Figure 4C). Six out of nine of these cells were well under the average extent, suggesting that substantial fluctuations in linear extent largely occurred in small patches where stochastic effects would be expected to cause more interannual variability (Wootton and Pfister, 2013). There were no obvious spatial patterns dictating where extent increases and decreases occurred within the study region (Figure 4A) and overall, our analysis suggests little difference in *Postelsia* extent and distribution between 2007 and 2021.

### Postelsia Density at Cape Beale

Resurveying the individual kelp patch at Cape Beale revealed no significant change in *Postelsia* density between 2006 and 2021. However, data from resurveys in 2022 showed a significantly higher density than either of the previous years (Figure 5A), leading to a significant effect of year overall (GLM:  $X^2 = 47.141$ ,  $df = 36$ ,  $p < 0.001$ ).

## Size Metrics and Reproductive Phenology

Stipe diameter (GLM:  $X^2 = 0.10398$ ,  $df = 22$ ,  $p > 0.747$ ), stipe height (GLM:  $X^2 = 0.06938$ ,  $df = 22$ ,  $p > 0.792$ ), blade density (GLM:  $X^2 = 0.45896$ ,  $df = 22$ ,  $p > 0.498$ ), and blade width (GLM:  $X^2 = 1.2499$ ,  $df = 22$ ,  $p > 0.263$ ) were all similar and statistically indistinguishable between 2006 and 2021 (Figure 5D-G). However, blade length was significantly different in the two years (GLM:  $X^2 = 4.07$ ,  $df = 22$ ,  $p < 0.0437$ ) with the estimated marginal means revealing that, on average, blades were 2.8 cm (~20%) longer in 2021 (Figure 5C). An ANCOVA modeling blade length as a function of blade width, year, and an interaction term concluded year to be the only significant predictor of blade length (Blade width ( $F = 2.1429$ ,  $p > 0.1587$ ); Year ( $F = 7.3295$ ,  $p < 0.0136$ ); Interaction term ( $F = 4.2389$ ,  $p > 0.0527$ ), confirming that blades were growing longer independent of their width. Wide blades reached similar lengths in 2006 and 2021, while thinner blades were longer in 2021, likely driving the overall trend of longer average length (Figure 5H). The proportion of reproductive individuals also differed between years (GLM:  $X^2 = 4.07$ ,  $df = 22$ ,  $p < 0.0437$ ), with more reproductive individuals in 2021 and 2022 than in 2006 despite all surveys being done around the same time of year (Figure 5B).

## DISCUSSION

### *Stability at the Distributional Scale*

*Postelsia*'s distributional stability suggests that the populations we studied were thermally buffered from the worst impacts of recent heatwaves, either because of their location near the species' leading range edge or due to finer-scale environmental conditions. *Postelsia* cannot complete its lifecycle at or above water temperatures of 18°C (Muth *et al.*, 2019), and previous studies suggest that sporophytes are unable to withstand prolonged water temperatures over 15°C (Lüning and Freshwater, 1988). In our 15-year study span, water temperatures at the local Amphitrite Point Light Station never exceeded 17°C (and barely exceeded 16°C), making it unlikely that the thermal tolerance threshold required to locally eradicate *Postelsia* from entire cells was reached. Less is known about the effects of air temperature on *Postelsia*, especially given that intraspecific interactions within tightly aggregated *Postelsia* patches likely influence the environment experienced by each individual when emersed (Holbrook *et al.*, 1991), and thus we can't determine if thresholds were surpassed in this regard. Alternatively, thermal buffering may have been provided by fine-scale wave exposure, given that *Postelsia*'s populations are restricted to highly exposed outer coasts (Nielsen *et al.*, 2006). In the northeast Pacific, differences in wave exposure can cause intertidal temperatures to vary greatly at fine scales (Helmuth *et al.*, 2002, 2006), which can shape intertidal communities and their response to heatwaves (Starko *et al.*, 2019). Our study region largely faces the direction of oncoming swell (Ban *et al.*, 2016) and the entire shoreline where *Postelsia* was found is classified by ShoreZone as semi-exposed or higher [Supplementary information Figure S5]. This, and mixing associated with large tidal currents, keeps ocean temperatures cool throughout this region (Ban *et al.*, 2016) and could contribute to making this a regional "cold spot" within *Postelsia*'s range (Helmuth *et al.*, 2006).

Although with only two time points of sampling it is possible that distributional losses occurred during heatwaves and *Postelsia* have since recovered, available evidence suggests this is unlikely. *Postelsia* metapopulation models parameterized from data collected on nearby Tatoosh Island, Washington (approx. 22 km from our study region), show only a 4% probability of colonization at a >10-m distance and predict only five long-distance expansions over 136 years (Paine *et al.*, 2017). Moreover, one experimentally cleared patch separated by 39 m remained clear for 27 years (Paine *et al.*, 2017). Thus, losses at our 250-m scale are unlikely to have recovered by long-distance dispersal

within the studied time period. Another possibility is that the disappearance of adult sporophytes during heatwaves was missed due to quick recovery facilitated by a microscopic propagule bank of *Postelsia* gametophytes and microscopic sporophytes. As with many intertidal species, *Postelsia* maintains a microscopic propagule bank in the intertidal zone as part of its annual lifecycle (Santelices *et al.*, 1995; Blanchette, 1996), but little is known about how long this propagule bank can persist, or if it is more thermally tolerant than macroscopic *Postelsia* sporophytes. Even if microscopic gametophytes and sporophytes were able to survive heatwaves (where adult sporophytes could not) and promote recovery, this would still be considered distributional stability over our 15-year study timespan.

Thus, overall our results are consistent with our first hypothesis, suggesting marine species like *Postelsia* have a larger thermal safety margins towards their leading range edges (Comte and Olden, 2017; Pinsky *et al.*, 2019). Although our study could not disentangle this from the hypothesis that the species' stability was driven by a local mediating factor (i.e. wave exposure), our methods, applied to other locations with varying oceanographic conditions throughout the northern range of *Postelsia*, could do so.

### *Limited Distributional Expansion*

The lack of significant expansion seen in our study may be explained by the specific habitat requirements of *Postelsia*, or its limited dispersal capabilities (Dayton, 1973; Paine, 1988; Nielsen *et al.*, 2006). While wave exposed, [Supplementary information Figure S5], rocky shores in this region may not all receive a disturbance regime suitable for *Postelsia* establishment (Paine, 1979; Blanchette, 1996), and differences in bathymetry and aspect may influence exposure and thermal regime on small scales not quantified by ShoreZone exposure class, thus impacting habitat suitability (Nielsen *et al.*, 2006; Hill *et al.*, 2010; Amstutz *et al.*, 2021). Additionally, little is known about what limits *Postelsia* at its northern range edge. Like some other autotrophs, its growth and recruitment may be light or temperature limited at higher latitudes (Manuel *et al.*, 2013; Filbee-Dexter *et al.*, 2019; Greiser *et al.*, 2020); however, this has yet to be shown for *Postelsia*, and its northern range edge could easily be defined by its poor dispersal capabilities alone (Paine *et al.*, 2017). Indeed, the five long-distance expansions in our study, while not significant at a distributional scale, are already more than would be predicted by existing models (Paine *et al.*, 2017). Coupled with declines in southern populations (Lohse *et al.* 2020, WSN, unpubl. res.), this lack of significant distributional expansion in the northern 12% of *Postelsia*'s range raises concerns about the risk of future range contractions.

### *Patch Level Changes at Cape Beale*

Within the single *Postelsia* patch at Cape Beale, density and individual characteristics were similar between timepoints. We suspect that the significant density increase in 2022 reflects the interannual variability *Postelsia* is prone to at this scale (Paine 1979, Blanchette 1996, Paine et al. 2017), rather than long-term population change, especially given that we were unable to detect a significant difference between 2006 and 2021. Of the morphometrics, only blade length was significantly different between surveys, with greater lengths in 2021 than in 2006. *Postelsia* blades grow outwards from meristematic tissue and overall length is determined by the meristematic growth rate balanced against blade tissue loss through a combination of senescence, sloughing, and erosion (Kalvass, 1994; Thompson *et al.*, 2010). Without further quantifying these processes, it is hard to say what caused increased lengths. Finally, the proportion of reproductive individuals at Cape Beale was significantly higher in 2021 and 2022 than in 2006 despite all surveys occurring within the same nearly two-week

period (July 11–26). This may hint at a phenological shift in reproductive timing, a phenomenon which is common due to climate change driven advancement of spring conditions (Poloczanska *et al.*, 2016; Cohen *et al.*, 2018). Consistent positive temperature anomalies in our study region since 2014 (Figure 2) could have driven early onset of reproduction (Moore *et al.*, 2011; Fuchs *et al.*, 2020). However, we lack sufficient temporal coverage in our dataset to test this hypothesis fully and it is yet unclear what impacts this could have on *Postelsia* in our study region.

Overall, our results suggest that *Postelsia* has remained stable for 15 years at multiple scales near its leading range edge through a period with prolonged heatwaves. These findings are in stark contrast to data from California and Oregon, which showed the complete loss of monitored *Postelsia* populations during the 2014–2016 heatwave and limited recovery thereafter (Lohse *et al.* 2020, WSN, unpubl. res.). Our findings highlight the importance of multi-scale assessments when examining changes within species and populations, and although they are consistent with the general trend of species being thermally buffered near their leading range edge, they also highlight the potential importance of factors such as dispersal capability and local environmental conditions in modulating a species' response to climate change. Future monitoring of this understudied species should be conducted at its true leading range edge as well as in other parts of its range with contrasting environmental characteristics to advance understanding of the species overall status and its responses to rapidly advancing climate change.

## SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Figure S1: A map of the study region in the context of the northeast Pacific coastline and an example of a ShoreZone photo with *Postelsia* encircled in the high intertidal zone. Figure S2: A visualization of the methodology for pairing features in satellite and aerial imagery to determine cell borders within the aerial images. Figure S3: A visualization of the methods for tracing available shoreline extent and *Postelsia* patches onto satellite imagery. Figure S4: Maps of *Postelsia* distributions from each timepoint. Figure S5: Map of wave exposure classes for the study region.

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## Conflict of Interest

We have no conflict of interest to declare.

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## Literature Cited

**Abbott IA, Hollenberg GJ. 1976.** *Marine algae of California*. Stanford, California: Stanford University Press.

**Amstutz A, Firth LB, Spicer JI, Hanley ME. 2021.** Facing up to climate change: Community composition varies with aspect and surface temperature in the rocky intertidal. *Marine Environmental Research* **172**: 105482. doi: 10.1016/j.marenvres.2021.105482.

**Årevall J, Early R, Estrada A, Wennergren U, Eklöf AC. 2018.** Conditions for successful range shifts under climate change: The role of species dispersal and landscape configuration. *Diversity and Distributions* **24**: 1598–1611. doi: 10.1111/ddi.12793.

**Ban SS, Alidina HM, Okey TA, Gregg RM, Ban NC. 2016.** Identifying potential marine climate change refugia: A case study in Canada's Pacific marine ecosystems. *Global Ecology and Conservation* **8**: 41–54. doi: 10.1016/j.gecco.2016.07.004.

**Barkhordarian A, Nielsen DM, Baehr J. 2022.** Recent marine heatwaves in the North Pacific warming pool can be attributed to rising atmospheric levels of greenhouse gases. *Communications Earth & Environment* **3**: 131. doi: 10.1038/s43247-022-00461-2.

**Barry JP, Baxter CH, Sagarin RD, Gilman SE. 1995.** Climate-related, long-term faunal changes in a California rocky intertidal community. *Science (New York, N.Y.)* **267**: 672–675. doi: 10.1126/science.267.5198.672.

**Bates AE, Helmuth B, Burrows MT, et al. 2018.** Biologists ignore ocean weather at their peril. *Nature* **560**: 299–301. doi: 10.1038/d41586-018-05869-5.

**Baum JK, Myers RA. 2004.** Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters* **7**: 135–145. doi: 10.1111/j.1461-0248.2003.00564.x.

**Bennett S, Wernberg T, Arackal Joy B, de Bettignies T, Campbell AH. 2015.** Central and rear-edge populations can be equally vulnerable to warming. *Nature Communications* **6**: 10280. doi: 10.1038/ncomms10280.

**Bennett S, Alcoverro T, Kletou D, et al. 2022.** Resilience of seagrass populations to thermal stress does not reflect regional differences in ocean climate. *New Phytologist* **233**: 1657–1666. doi: 10.1111/nph.17885.

**Berry HD, Mumford TF, Christiaen B, et al. 2021.** Long-term changes in kelp forests in an inner basin of the Salish Sea. *PLOS ONE* **16**: e0229703. doi: 10.1371/journal.pone.0229703.

**Blanchette CA. 1996.** Seasonal patterns of disturbance influence recruitment of the sea palm, *Postelsia palmaeformis*. *Journal of Experimental Marine Biology and Ecology* **197**: 1–14. doi: 10.1016/0022-0981(95)00141-7.

**Brooks ME, Kristensen K, Benthem KJ van, et al. 2017.** glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* **9**: 378–400. doi: 10.32614/RJ-2017-066.

**Brown CJ, Schoeman DS, Sydeman WJ, et al. 2011.** Quantitative approaches in climate change ecology. *Global Change Biology* **17**: 3697–3713. doi: 10.1111/j.1365-2486.2011.02531.x.

**Cavanaugh KC, Reed DC, Bell TW, Castorani MCN, Beas-Luna R. 2019.** Spatial Variability in the Resistance and Resilience of Giant Kelp in Southern and Baja California to a Multiyear Heatwave. *Frontiers in Marine Science* **6**: 413. doi: 10.3389/fmars.2019.00413/full.

- Cohen JM, Lajeunesse MJ, Rohr JR. 2018.** A global synthesis of animal phenological responses to climate change. *Nature Climate Change* **8**: 224–228. doi: 10.1038/s41558-018-0067-3.
- Comte L, Olden JD. 2017.** Climatic vulnerability of the world's freshwater and marine fishes. *Nature Climate Change* **7**: 718–722. doi: 10.1038/nclimate3382.
- Cook S, Daley S, Morrow K, Ward S. 2017.** *ShoreZone Coastal Imaging and Habitat Mapping Protocol*. Victoria, B.C., Canada: Coastal and Ocean Resources.
- Cooley, S., D. Schoeman, L. Bopp, P. Boyd, S. Donner et al. 2022.** Oceans and Coastal Ecosystems and Their Services. In: *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, et al (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 379-550, doi:10.1017/9781009325844.005.
- Coyer JA, Olsen JL, Stam WT. 1997.** Genetic Variability and spatial separation in the sea palm kelp *Postelsia palmaeformis* (Phaeophyceae) assessed with M13 fingerprints and RAPDS. *Journal of Phycology* **33**: 561–568. doi: 10.1111/j.0022-3646.1997.00561.x.
- Danby RK, Hik DS. 2007.** Evidence of Recent Treeline Dynamics in Southwest Yukon from Aerial Photographs. *ARCTIC* **60**: 411–420. doi: 10.14430/arctic198.
- Dayton PK. 1973.** Dispersion, Dispersal, and Persistence of the Annual Intertidal Alga, *Postelsia Palmaeformis* Ruprecht. *Ecology* **54**: 433–438. doi: 10.2307/1934353.
- Di Lorenzo E, Mantua N. 2016.** Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nature Climate Change* **6**: 1042–1047. doi: 10.1038/nclimate3082.



**Filbee-Dexter K, Wernberg T, Fredriksen S, Norderhaug KM, Pedersen MF. 2019.**

Arctic kelp forests: Diversity, resilience and future. *Global and Planetary Change* **172**: 1–14.

doi: 10.1016/j.gloplacha.2018.09.005.

**Fox J, Weisberg S. 2019.** *An R Companion to Applied Regression*. Thousand Oaks,

California: Sage Publications.

**Fuchs HL, Chant RJ, Hunter EJ, Curchitser EN, Gerbi GP, Chen EY. 2020.** Wrong-way

migrations of benthic species driven by ocean warming and larval transport. *Nature Climate*

*Change* **10**: 1052–1056. doi: 10.1038/s41558-020-0894-x.

**Gentemann CL, Fewings MR, García-Reyes M. 2017.** Satellite sea surface temperatures

along the West Coast of the United States during the 2014-2016 northeast Pacific marine heat

wave: Coastal SSTs During “the Blob.” *Geophysical Research Letters* **44**: 312–319. doi:

10.1002/2016GL071039.

**Greiser C, Hylander K, Meineri E, Luoto M, Ehrlén J. 2020.** Climate limitation at the

cold edge: contrasting perspectives from species distribution modelling and a transplant

experiment. *Ecography* **43**: 637–647. doi: 10.1111/ecog.04490.

**Hanley ME, Bouma TJ, Mossman HL. 2020.** The gathering storm: optimizing management

of coastal ecosystems in the face of a climate-driven threat. *Annals of Botany* **125**: 197–212.

doi: 10.1093/aob/mcz204.

**Harley CDG. 2011.** Climate Change, Keystone Predation, and Biodiversity Loss. *Science*

**334**: 1124–1127. doi: 10.1126/science.1210199.

**Helmuth B, Harley CDG, Halpin PM, O'Donnell M, Hofmann GE, Blanchette CA.**

**2002.** Climate Change and Latitudinal Patterns of Intertidal Thermal Stress. *Science* **298**: 1015–1017. doi: 10.1126/science.1076814.

**Helmuth B, Broitman BR, Blanchette CA, et al. 2006.** Mosaic patterns of thermal stress in the rocky intertidal zone: Implications for climate change. *Ecological Monographs* **76**: 461–479. doi: 10.1890/0012-9615(2006)076[0461:MPOTSI]2.0.CO;2.

**Hill N, Pepper A, Puotinen M, et al. 2010.** Quantifying wave exposure in shallow temperate reef systems: applicability of fetch models for predicting algal biodiversity. *Marine Ecology Progress Series* **417**: 83–95. doi: 10.3354/meps08815.

**Hobday AJ, Alexander LV, Perkins SE, et al. 2016.** A hierarchical approach to defining marine heatwaves. *Progress in Oceanography* **141**: 227–238. doi: 10.1016/j.pocean.2015.12.014.

**Holbrook MN, Denny MW, Koehl MAR. 1991.** Intertidal “trees”: consequences of aggregation on the mechanical and photosynthetic properties of sea-palms *Postelsia palmaeformis* Ruprecht. *Journal of Experimental Marine Biology and Ecology* **146**: 39–67. doi: 10.1016/0022-0981(91)90254-T.

**Howes D, Harper JR, Owens EH. 1994.** Physical shore-zone mapping system for British Columbia.

**Kalvass PE. 1994.** The effect of different harvest methods on sea palm (*Postelsia palmaeformis*) sporophyll growth. *California Fish and Game* **80**: 57–67.

**Kusumo HT, Pfister CA, Wootton JT. 2006.** Small-scale genetic structure in the sea palm *Postelsia palmaeformis* Ruprecht (Phaeophyceae). *Marine Biology* **149**: 731–742. doi: 10.1007/s00227-006-0254-z.

**Leigh EG, Paine RT, Quinn JF, Suchanek TH. 1987.** Wave energy and intertidal productivity. *Proceedings of the National Academy of Sciences* **84**: 1314–1318. doi: 10.1073/pnas.84.5.1314.

**Lenth RV, Buerkner P, Giné-Vázquez I, et al. 2022.** *emmeans: Estimated Marginal Means, aka Least-Squares Means*. <https://cran.r-project.org/web/packages/emmeans/index.html>. 6 Dec. 2022.

**Lohse D, Raimondi P, Ammann K. 2020.** The effects of a recent marine heatwave on the sea palm *Postelsia palmaeformis*.

**Lüning K, Freshwater W. 1988.** Temperature Tolerance of Northeast Pacific Marine Algae. *Journal of Phycology* **24**: 310–315. doi: 10.1111/j.1529-8817.1988.tb04471.x.

**Manuel SA, Coates KA, Kenworthy WJ, Fourqurean JW. 2013.** Tropical species at the northern limit of their range: composition and distribution in Bermuda’s benthic habitats in relation to depth and light availability. *Marine Environmental Research* **89**: 63–75. doi: 10.1016/j.marenvres.2013.05.003.

**McClenachan L, Ferretti F, Baum JK. 2012.** From archives to conservation: why historical data are needed to set baselines for marine animals and ecosystems. *Conservation Letters* **5**: 349–359. doi: 10.1111/j.1755-263X.2012.00253.x.

- Moore PJ, Thompson RC, Hawkins SJ. 2011.** Phenological changes in intertidal con-specific gastropods in response to climate warming. *Global Change Biology* **17**: 709–719. doi: 10.1111/j.1365-2486.2010.02270.x.
- Mulders Y, Mattio L, Phillips J, Lavery P, Kendrick G, Wernberg T. 2022.** Patch dynamics driven by wave exposure in subtidal temperate seaweeds are exacerbated by warming oceans. *Marine Ecology Progress Series* **685**: 85–95. doi: 10.3354/meps13989.
- Muth AF, Graham MH, Lane CE, Harley CDG. 2019.** Recruitment tolerance to increased temperature present across multiple kelp clades. *Ecology* **100**: e02594. doi: 10.1002/ecy.2594.
- Nielsen KJ, Blanchette CA, Menge BA, Lubchenco J. 2006.** Physiological snapshots reflect ecological performance of the sea palm, *Postelsia palmaeformis* (Phaeophyceae) across intertidal elevation and exposure gradients. *Journal of Phycology* **42**: 548–559. doi: 10.1111/j.1529-8817.2006.00223.x.
- Oliver ECJ, Donat MG, Burrows MT, et al. 2018.** Longer and more frequent marine heatwaves over the past century. *Nature Communications* **9**: 1324. doi: 10.1038/s41467-018-03732-9.
- Paine RT. 1979.** Disaster, Catastrophe, and Local Persistence of the Sea Palm *Postelsia palmaeformis*. *Science* **205**: 685–687. doi: 10.1126/science.205.4407.685.
- Paine RT. 1988.** Habitat Suitability and Local Population Persistence of the Sea Palm *Postelsia Palmaeformis*. *Ecology* **69**: 1787–1794. doi: 10.2307/1941157.

**Paine RT, Buhle ER, Levin SA, Kareiva P. 2017.** Short-range dispersal maintains a volatile marine metapopulation: the brown alga *Postelsia palmaeformis*. *Ecology* **98**: 1560–1573. doi: 10.1002/ecy.1798.

**Parmesan C, Hanley ME. 2015.** Plants and climate change: complexities and surprises. *Annals of Botany* **116**: 849–864. doi: 10.1093/aob/mcv169.

**Parmesan, C., M.D. Morecroft, Y. Trisurat, R. Adrian, G.Z. Anshari, et al. 2022.** Terrestrial and Freshwater Ecosystems and Their Services. In: *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, et al (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp. 197-377, doi:10.1017/9781009325844.004.

**Pecl GT, Araújo MB, Bell JD, et al. 2017.** Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* **355**: eaai9214. doi: 10.1126/science.aai9214.

**Perkins SE, Alexander LV. 2013.** On the Measurement of Heat Waves. *Journal of Climate* **26**: 4500–4517. doi: 10.1175/JCLI-D-12-00383.1.

**Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA. 2013.** Marine Taxa Track Local Climate Velocities. *Science* **341**: 1239–1242. doi: 10.1126/science.1239352.

**Pinsky ML, Eikeset AM, McCauley DJ, Payne JL, Sunday JM. 2019.** Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature* **569**: 108–111. doi: 10.1038/s41586-019-1132-4.

**Poloczanska ES, Brown CJ, Sydeman WJ, et al. 2013.** Global imprint of climate change on marine life. *Nature Climate Change* **3**: 919–925. doi: 10.1038/nclimate1958.

**Poloczanska ES, Burrows MT, Brown CJ, et al. 2016.** Responses of Marine Organisms to Climate Change across Oceans. *Frontiers in Marine Science* **3**: 62. doi: 10.3389/fmars.2016.00062.

**Qian Y, Hsu P-C, Yuan J, Zhu Z, Wang H, Duan M. 2022.** Effects of Subseasonal Variation in the East Asian Monsoon System on the Summertime Heat Wave in Western North America in 2021. *Geophysical Research Letters* **49**: e2021GL097659. doi: 10.1029/2021GL097659.

**R Core Team. 2022.** R: A language for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

**Rogers-Bennett L, Catton CA. 2019.** Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. *Scientific Reports* **9**: 15050. doi: 10.1038/s41598-019-51114-y.

**Sanford E, Sones JL, García-Reyes M, Goddard JHR, Largier JL. 2019.** Widespread shifts in the coastal biota of northern California during the 2014–2016 marine heatwaves. *Scientific Reports* **9**: 4216. doi: 10.1038/s41598-019-40784-3.

**Santelices B, Hoffmann A, Aedo D, Bobadilla M, Otaíza R. 1995.** A bank of microscopic forms on disturbed boulders and stones in tide pools. *Marine Ecology Progress Series* **129**: 215–228. doi: 10.3354/meps129215.

**Seabra R, Wethey DS, Santos AM, Lima FP. 2011.** Side matters: Microhabitat influence on intertidal heat stress over a large geographical scale. *Journal of Experimental Marine Biology and Ecology* **400**: 200–208. doi: 10.1016/j.jembe.2011.02.010.

**Searle SR, Speed FM, Milliken GA. 1980.** Population Marginal Means in the Linear Model: An Alternative to Least Squares Means. *The American Statistician* **34**: 216–221. doi: 10.1080/00031305.1980.10483031.

**Smale DA, Wernberg T, Oliver ECJ, et al. 2019.** Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change* **9**: 306–312. doi: 10.1038/s41558-019-0412-1.

**Starko S, Bailey LA, Creviston E, et al. 2019.** Environmental heterogeneity mediates scale-dependent declines in kelp diversity on intertidal rocky shores (J Hewitt, Ed.). *PLOS ONE* **14**: e0213191. doi: 10.1371/journal.pone.0213191.

**Starko S, Timmer B, Reshitnyk L, et al. 2023.** Temperature and food chain length, but not latitude, explain region-specific kelp forest responses to an unprecedented heatwave. *bioRxiv. Marine Ecology Progress Series*, in press. doi: 10.1101/2023.01.07.523109.

**Straub SC, Wernberg T, Thomsen MS, et al. 2019.** Resistance, Extinction, and Everything in Between – The Diverse Responses of Seaweeds to Marine Heatwaves. *Frontiers in Marine Science* **6**: 763. doi: 10.3389/fmars.2019.00763.

**Sunday JM, Pecl GT, Frusher S, et al. 2015.** Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters* **18**: 944–953. doi: 10.1111/ele.12474.

**Teagle H, Hawkins SJ, Moore PJ, Smale DA. 2017.** The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology* **492**: 81–98. doi: 10.1016/j.jembe.2017.01.017.

**Thompson S, Knoll H, Blanchette C, Nielsen K. 2010.** Population consequences of biomass loss due to commercial collection of the wild seaweed *Postelsia palmaeformis*. *Marine Ecology Progress Series* **413**: 17–32. doi: 10.3354/meps08705.

**Thomsen MS, Mondardini L, Alestra T, et al. 2019.** Local Extinction of Bull Kelp (*Durvillaea* spp.) Due to a Marine Heatwave. *Frontiers in Marine Science* **6**.

**Tseng Y-H, Ding R, Huang X. 2017.** The warm Blob in the northeast Pacific—the bridge leading to the 2015/16 El Niño. *Environmental Research Letters* **12**: 054019. doi: 10.1088/1748-9326/aa67c3.

**Weitzman B, Konar B, Iken K, et al. 2021.** Changes in Rocky Intertidal Community Structure During a Marine Heatwave in the Northern Gulf of Alaska. *Frontiers in Marine Science* **8**: 556820. doi: 10.3389/fmars.2021.556820.

**Wernberg T, Bennett S, Babcock RC, et al. 2016.** Climate-driven regime shift of a temperate marine ecosystem. *Science* **353**: 169–172. doi: 10.1126/science.aad8745.

**Whalen MA, Starko S, Lindstrom SC, Martone PT. 2023.** Heatwave restructures marine intertidal communities across a stress gradient. *Ecology* **n/a**: e4027. doi: 10.1002/ecy.4027.

**Wootton JT, Pfister CA. 2013.** Experimental separation of genetic and demographic factors on extinction risk in wild populations. *Ecology* **94**: 2117–2123. doi: 10.1890/12-1828.1.



## FIGURES

**Figure 1.** Conceptual model of abiotic and biotic factors influencing *Postelsia*'s geographical range and intertidal limits, due to high (red) or low (blue) values at the corresponding extremes. Grey symbols mean this variable has not been shown to limit *Postelsia* at the corresponding extremes. Note that high temperatures are limiting at both the southern range edge and upper intertidal limit.

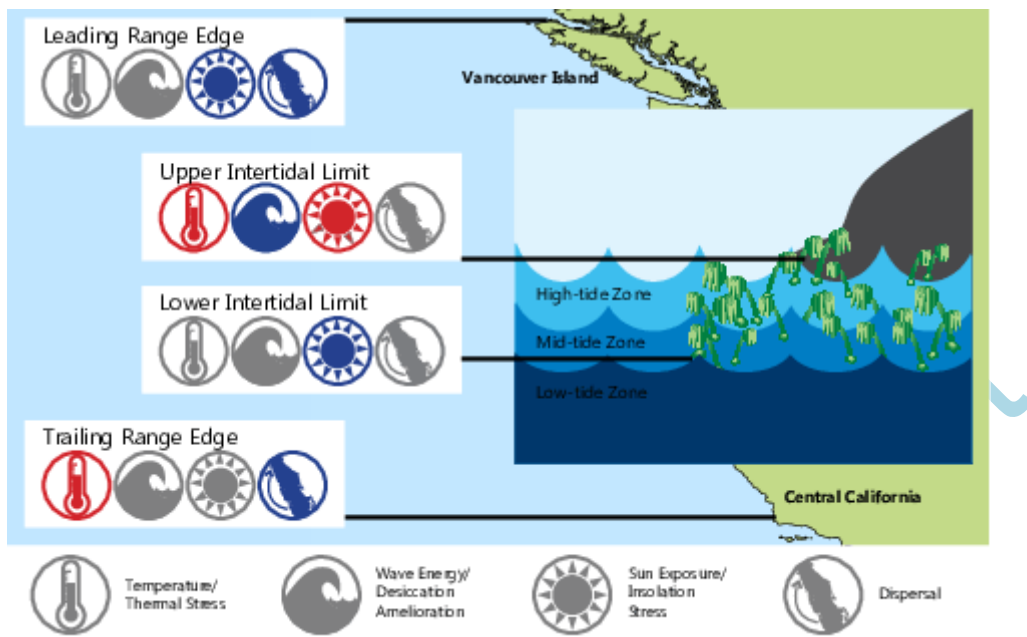
**Figure 2.** Temperature anomalies between 1990 and 2022 for (A) air and (B) sea surface temperature (SST) with survey timing and heatwave noted above the plots. Data were taken from lighthouses on the exposed coast within or near the study area and anomalies were calculated based on 34-year historical averages (dating to 1988). One-year moving averages of temperature anomaly are shown as solid black lines.

**Figure 3.** Map depicting changes in the distribution of *Postelsia* between 2007 and 2021 at a 250 m scale (blue = present both years, red = present in 2021, black = absent in both years). Each of the five expansion cases (red) has been displayed at a larger scale and labelled with the percent of available shoreline that was colonized. There were no cells where loss occurred (presence in 2007 with and absence in 2021) and missing cells are due to a lack of data for one of the two years.

**Figure 4.** (A) Map depicting the percent linear increase or decrease in *Postelsia* extent between 2007 and 2021 in 25 randomly selected cells. Changes larger than our methodological error threshold are marked with an asterisk (\*). (B) Percent linear increase and decrease for each of the 25 cells. The dashed horizontal lines represent the percent change required for increases/decreases to be considered beyond the threshold for human error. (C) The maximum patch extent for each cell with a significant increase/decrease relative to the average patch extent from all 25 cells (dashed red line).

**Figure 5.** Patch-level and individual measurements of *Postelsia* at Cape Beale for surveys completed in 2006, 2021, and 2022. Box plot comparisons between (A) density, (B) the percent of reproductive individuals, (C) blade length, (D) blade width, (E) stipe diameter, (F) stipe height, and (G) blade density are plotted with significant differences marked using asterisks ( $***p < 0.001$ ,  $**p < 0.01$ ,  $*p < 0.05$ ). Notably, there were differences in reproductive state, blade length, and blade width between years. (H) The relationship between blade length and blade width was plotted for quadrat level average values in 2006 and 2021 with linear regressions and associated 95% confidence intervals fitted to the trend displayed in each year.

Figure 1



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Figure 2

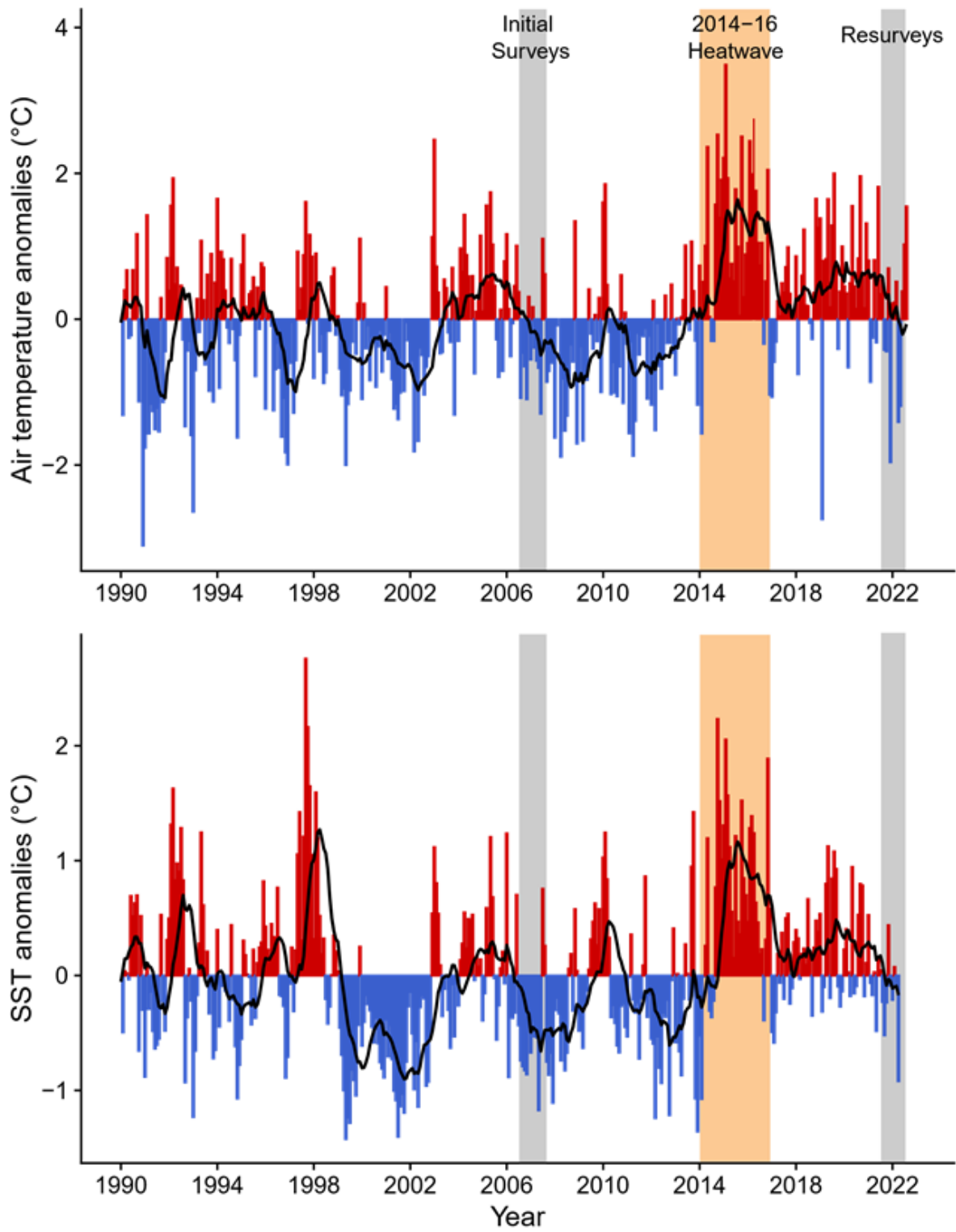


Figure 3

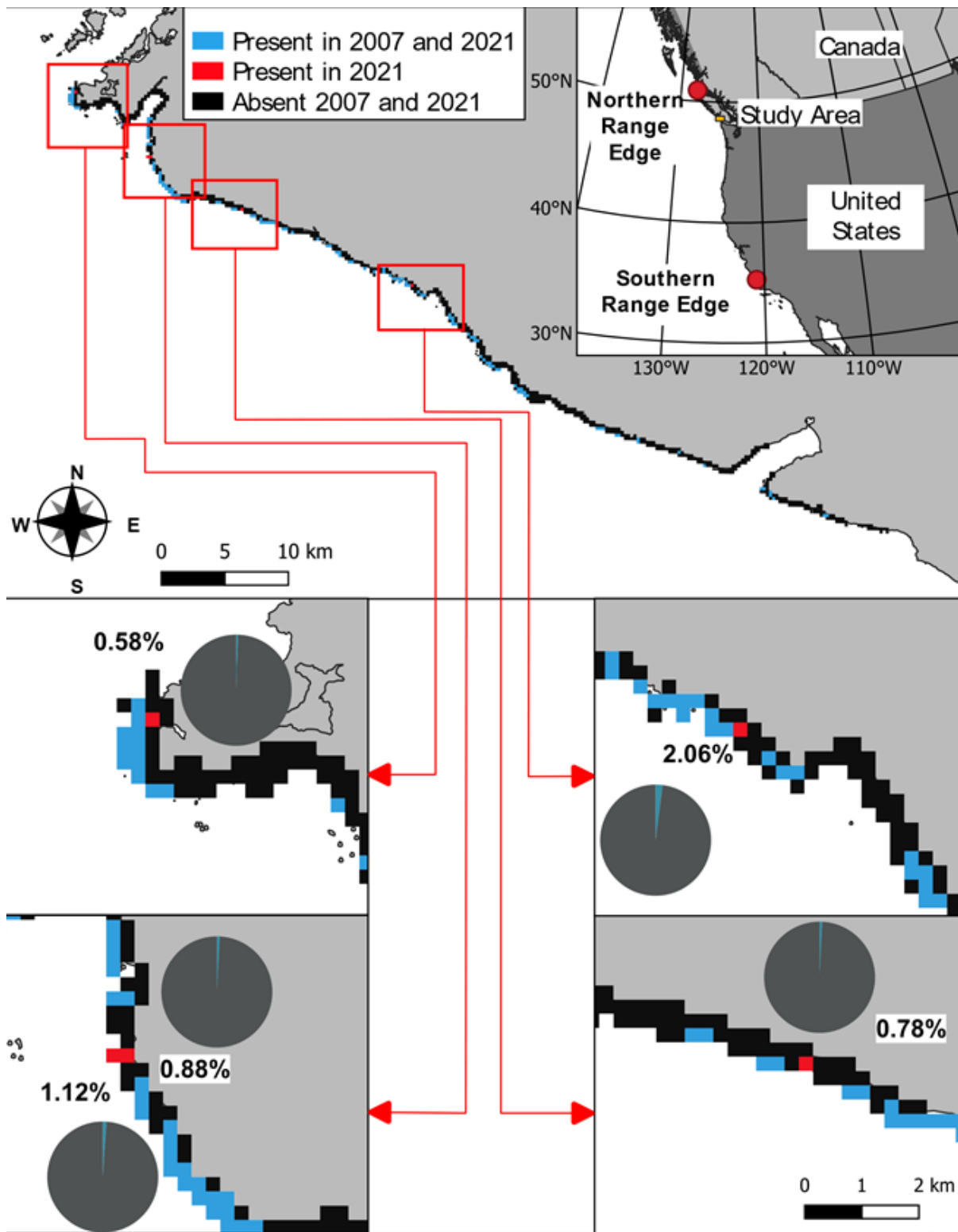
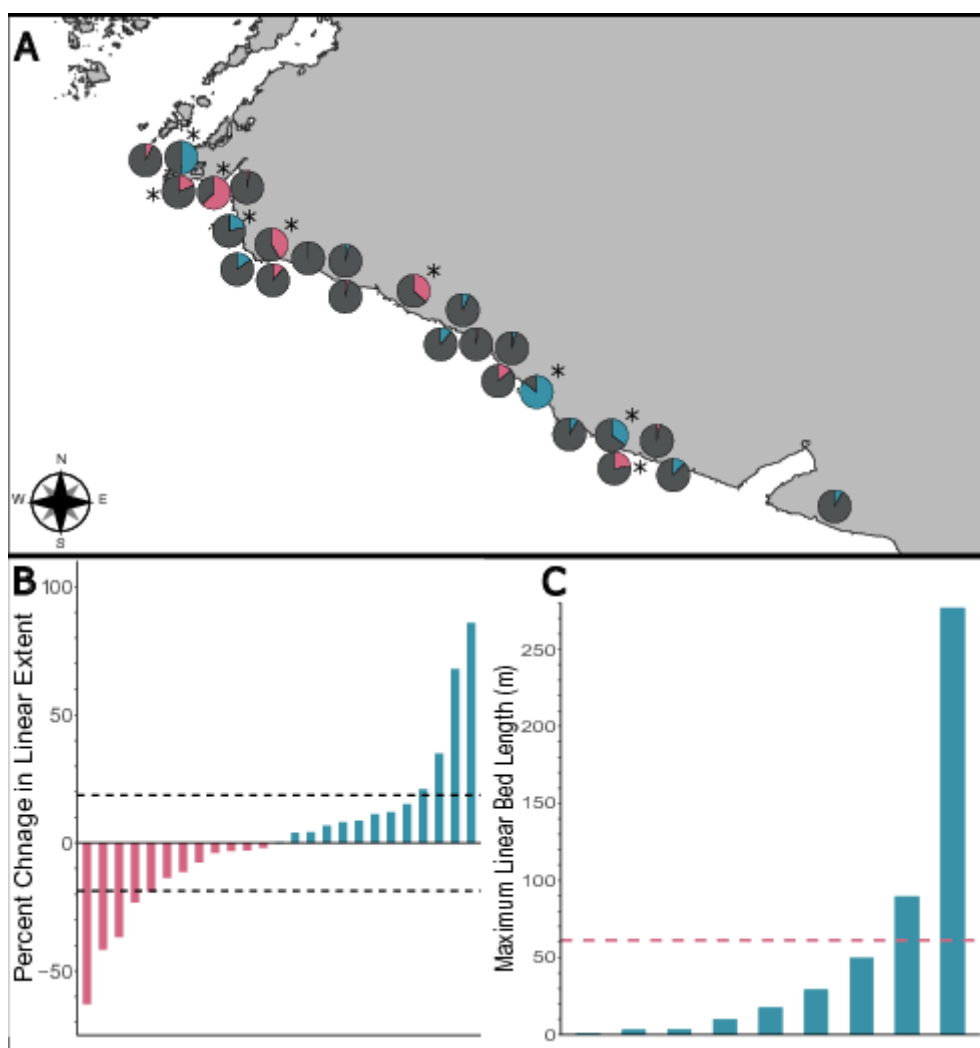
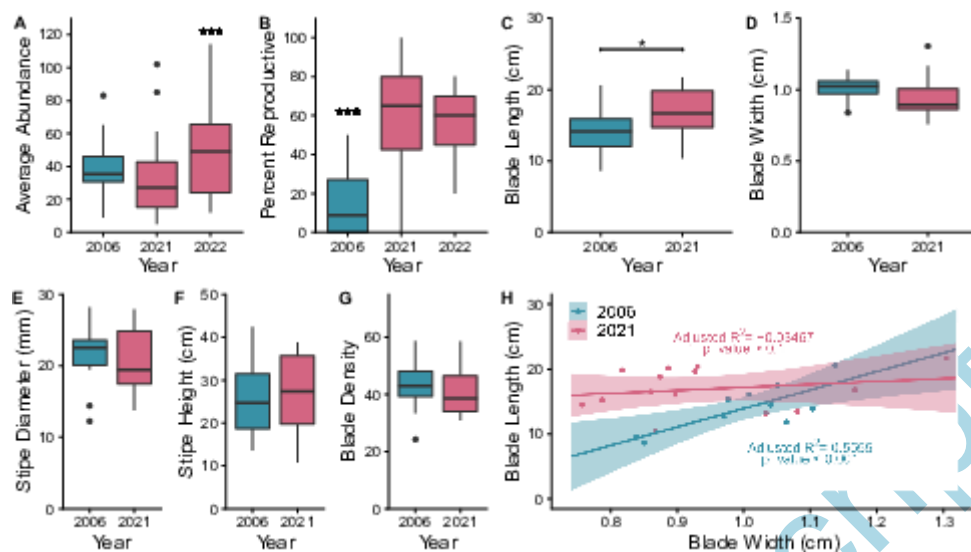


Figure 4



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Figure 5



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