

SPECIAL ISSUE: MACROALGAE IN A CHANGING WORLD

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

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- **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 multiyear heatwaves in the northeast Pacific Ocean might have impacted species even towards their cooler, northern range edges. Among them, the high intertidal kelp *Postelsia palmaeformis* has traits that could 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 conducted originally in 2006 and 2007, in order 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.
- **Key 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 the extent within cells nor the 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* might be attributable to thermal buffering near its northern range edge and from the wave-exposed coastlines it inhabits, which may have decreased the impacts of heatwaves. Our results highlight the importance of multiscale assessments when examining changes within species and populations, in addition to the importance of dispersal capability and local conditions in regulating the responses of species to climate change.

**Key words:** Biogeography, climate change, species distributions, kelp, heatwave, multiscale analysis, leading range edge, phenological shifts, *Postelsia palmaeformis*, stability.

## 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 (Parmesan and Hanley, 2015; Sunday *et al.*, 2015; Fuchs *et al.*, 2020). Evaluation of how species respond to climate change requires baseline data from which change can be inferred (Brown *et al.*, 2011; Berry *et al.*, 2021). Although long time-series data are lacking for the many data-deficient species and ecosystems in the world, the importance of evaluating the impacts of climate change necessitates the use and careful scrutiny of alternative data sources, including historical datasets and mixed-method approaches, if we are to gain a broad understanding of the vulnerability of species to future change, the stability of the ecosystems they support, the long-term sustainability of the ecosystem services they provide and the required conservation actions (Brown *et al.*, 2011; Pecl *et al.*, 2017).

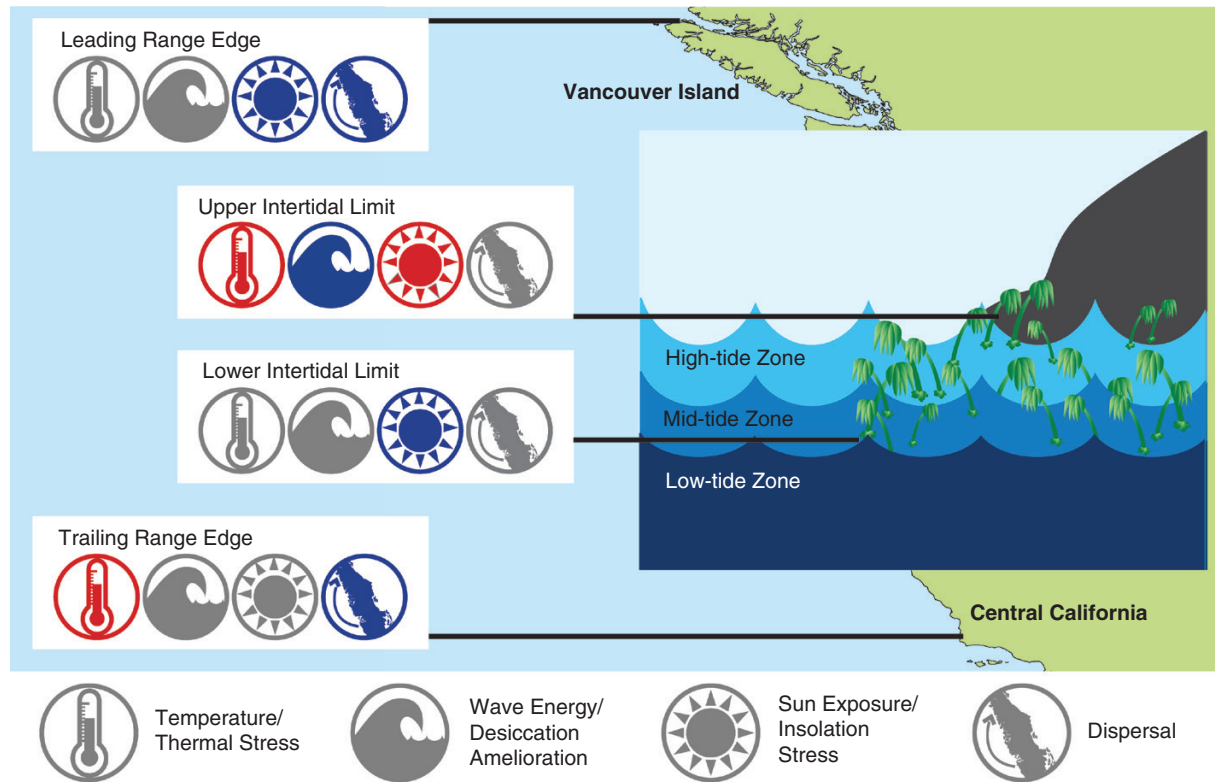


FIG. 1. Conceptual model of abiotic and biotic factors influencing the geographical range and intertidal limits of *Postelsia*, owing to high (red) or low (blue) values at the corresponding extremes. Grey symbols mean that this variable has not been shown to limit *Postelsia* at the corresponding extremes.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

Organisms living in the marine intertidal zone are vulnerable to gradual warming and heatwaves because 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 might not be predicted well 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*) might be 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 (Fig. 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, occurs only rarely according to experimental studies and dispersal models (Paine *et al.*, 2017). Thus, although the annual life history of *Postelsia* 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 geographical distributions (Paine *et al.*, 2017).

Between 2014 and 2016, the northeast Pacific Ocean experienced an unprecedented, multiyear 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; Rogers-Bennett and Catton, 2019; Starko *et al.*, 2019, 2023; Whalen *et al.*, 2023). Water and air temperature anomalies persisted throughout this period (Fig. 2), and although not as extreme, warm temperatures continued in subsequent years owing 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 geographical range of *Postelsia* and may have impacted its species-level distribution and abundance significantly, 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, Western Society

of Naturalists 101st Meeting, unpublished research), impacts elsewhere remain unknown.

Here, we leveraged rare *Postelsia* data collected before the recent heatwaves (2006–07), and resurveyed the same area (2021–22) to quantify population change across 167 km of coastline near the species' northern range edge. Although such two-time-point analyses lack the temporal resolution to assess interannual variability, they can identify broad changes in data-poor species that help to avoid shifting baselines (Baum and Myers, 2004; McClenachan *et al.*, 2012), and have been used previously to quantify the impacts of climate change 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

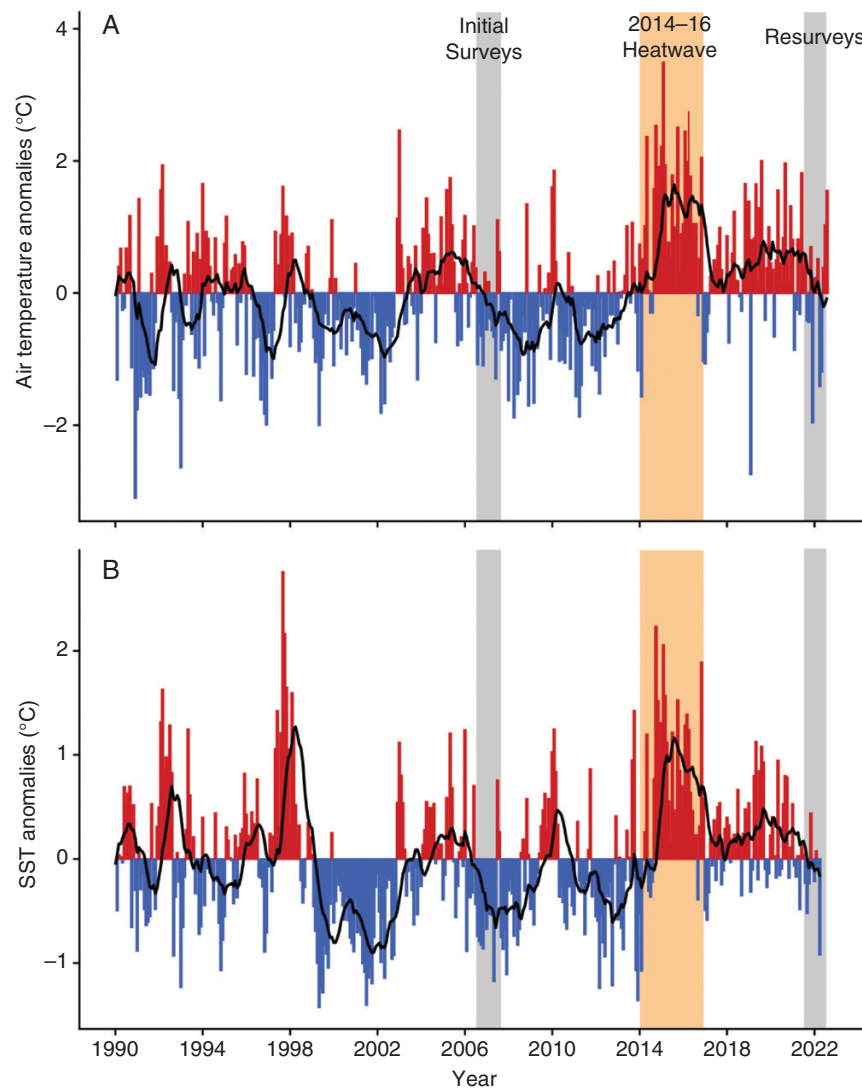


FIG. 2. Temperature anomalies between 1990 and 2022 for (A) air and (B) sea surface temperature (SST), with survey timing and the large 2014–16 heatwave noted above the plots. Data were taken from lighthouses on the exposed coast within or near the study area, and anomalies were calculated based on 34-year historical averages (dating to 1988). One-year moving averages of temperature anomaly are shown as continuous black lines.

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 leading range edges of the species, in which case, *Postelsia* populations would remain stable owing to thermal buffering or, potentially, expand owing to improved habitat suitability near its northern range edge; and (2) owing 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, in which case, 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 Data Fig. S1A), because it is one of the few regions with high-quality baseline data collected before the 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 contiguous range of the species. 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 make an accurate comparison of 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 analysed 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 when water or air temperatures exceed the long-term 90th percentile for a minimum of 5 or 3 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 northwestern edge of our study region, and SST data were

taken from the Amphitrite Lighthouse (~27 km northwest of Cape Beale). Although the Amphitrite Lighthouse is slightly outside 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 the presence–absence and linear extent of *Postelsia* within 250 m cells along the coast using a publicly available dataset (ShoreZone; Howes *et al.*, 1994; Cook *et al.*, 2017; <https://www.shorezone.org/interactive-shorezone-maps/>) of oblique photographs. The 2270 images analysed for this study were collected from a helicopter flying at low altitude (<100 m) to ensure an image scale of approximately 1:2500 to 1:5000 (Supplementary Data Fig. S1B). Flights were all completed at low tides, with a focus on collecting data when tides were <0.7 m above Canadian chart datum to ensure that much of the mid- and high intertidal was exposed. Flights were completed initially in August 2007 (13–14 August 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 geographical features visible in ShoreZone and Google Earth satellite imagery to georeference *Postelsia* observations.

### Data processing of imagery

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 × 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, owing 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 photographs 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 Data Fig. 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 whether *Postelsia* was present only in 2007 (loss) or only 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 v.4.1.3 (R Core Team, 2022).

Although our regional scale (250 m grid cells over 167 km) 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* at both time points (~19 % of all such cells; Supplementary Data Fig. S3). We summed the length of all patches within a cell to find the linear extent of *Postelsia* in each year and compared the linear extent between years to calculate the percentage increase or decrease. Given that 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 that inconsistency in shoreline tracing introduced by the analyst's 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 (1 of 25) was selected to undergo this process 20 separate times. A 95 % measure of methodological error was determined for this cell by taking the range of percentage linear change for the 19 closest estimates (95 % of the 20 separate tracings). This value was determined to be 18.7 %, and changes in percentage linear extent below this threshold could potentially arise through artefacts of methodological error. Results from this scale will also have to be interpreted carefully owing to the large potential for interannual fluctuations in *Postelsia* patch extent (Paine *et al.*, 2017) but should nicely complement 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 Data Fig. 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 traced the linear extent of the *Postelsia* patch separately. From these two lengths (available shoreline and *Postelsia* extent), we calculated the percentage 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 northwestern 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 immediately 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 that were collected originally on 11 July 2006 in a single 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). Owing to the small number of years in which data were collected, the results are interpreted while considering the large amount of interannual variation that would be expected in these metrics (Paine *et al.*, 2017).

To determine whether there were differences in the 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. Analyses of deviance for GLM fits were performed to examine the significance of the effect size of year (Fox and Weisberg, 2019). When there was a significant effect, estimated marginal means were plotted to determine whether there had been a significant increase or decrease in the metric between time points (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 afterwards, air temperatures reached >3 °C and SSTs reached >2 °C above their respective long-term averages, and both measures stayed anomalously high for several years. Before this heatwave and the initial surveys, temperatures in the region fluctuated steadily around long-term average

temperatures, as seen from the 1-year moving averages for temperature anomalies (Fig. 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:  $\chi^2 = 2.3266$ , d.f. = 1409,  $P > 0.127$ ), confirming that distributions were not significantly different between 2007 and 2021 (Supplementary Data Fig. 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 (Fig. 3). For cells where expansion occurred, shoreline tracing revealed that new *Postelsia* patches were extremely small, with the largest having colonized only ~2 % of the available shoreline within its cell and having a linear extent of only ~7.3 m (Fig. 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* appeared to be aggregated spatially, with cells containing the species seldom occurring alone. *Postelsia* also appeared to be more prevalent near the northwestern end of our study region (Fig. 3), as somewhat expected owing 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*, whereas 13 showed increases (Fig. 4). Only four increases and five decreases exceeded our estimated methodological error (Fig. 4B), and statistical tests found no significant effect of year on extent within *Postelsia* patches ( $\chi^2 = 0.526$ , d.f. = 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 (Fig. 4C). Six out of nine of these cells were well under the average extent, suggesting that substantial fluctuations in linear extent occurred largely 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 (Fig. 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 in either of the previous years (Fig. 5A), leading to a significant effect of year overall (GLM:  $\chi^2 = 47.141$ , d.f. = 36,  $P < 0.001$ ).

#### Size metrics and reproductive phenology

Stipe diameter (GLM:  $\chi^2 = 0.10398$ , d.f. = 22,  $P > 0.747$ ), stipe height (GLM:  $\chi^2 = 0.06938$ , d.f. = 22,  $P > 0.792$ ), blade density (GLM:  $\chi^2 = 0.45896$ , d.f. = 22,  $P > 0.498$ ) and blade width (GLM:  $\chi^2 = 1.2499$ , d.f. = 22,  $P > 0.263$ ) were all similar and statistically indistinguishable between 2006 and 2021

(Fig. 5D–G). However, blade length was significantly different in the two years (GLM:  $\chi^2 = 4.07$ , d.f. = 22,  $P < 0.0437$ ), with the estimated marginal means revealing that, on average, blades were 2.8 cm (~20 %) longer in 2021 (Fig. 5C). An ANCOVA modelling 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, whereas thinner blades were longer in 2021, probably driving the overall trend of longer average length (Fig. 5H). The proportion of reproductive individuals also differed between years (GLM:  $\chi^2 = 4.07$ , d.f. = 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 (Fig. 5B).

## DISCUSSION

### *Stability at the distributional scale*

The distributional stability of *Postelsia* suggests that the populations we studied were thermally buffered from the worst impacts of recent heatwaves, either because of their location near the leading range edge of the species or owing 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 >15 °C (Lüning and Freshwater, 1988). In our study span of 15 years, 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 eradicate *Postelsia* locally 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 are likely to influence the environment experienced by each individual when emersed (Holbrook et al., 1991), and thus we cannot determine whether thresholds were surpassed in this regard. Alternatively, thermal buffering might have been provided by fine-scale wave exposure, given that populations of *Postelsia* 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 Data Fig. 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 the range of *Postelsia* (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 that this is unlikely. *Postelsia* metapopulation models parameterized

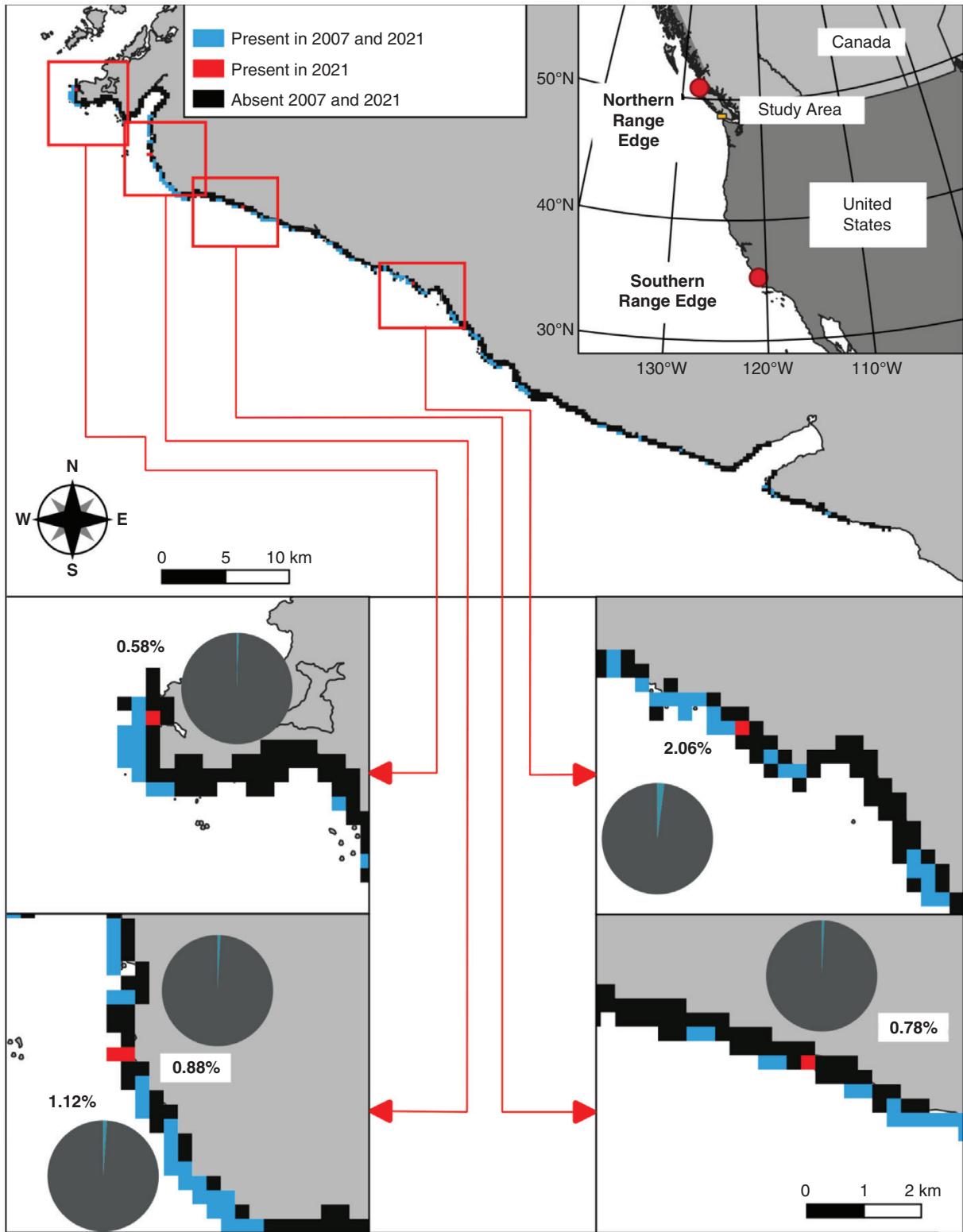


FIG. 3. Map depicting changes in the distribution of *Postelsia* between 2007 and 2021 at a scale of 250 m (blue = present both years, red = present in 2021, black = absent in both years). Each of the five cases of expansion (red) has been displayed at a larger scale and labelled with the percentage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

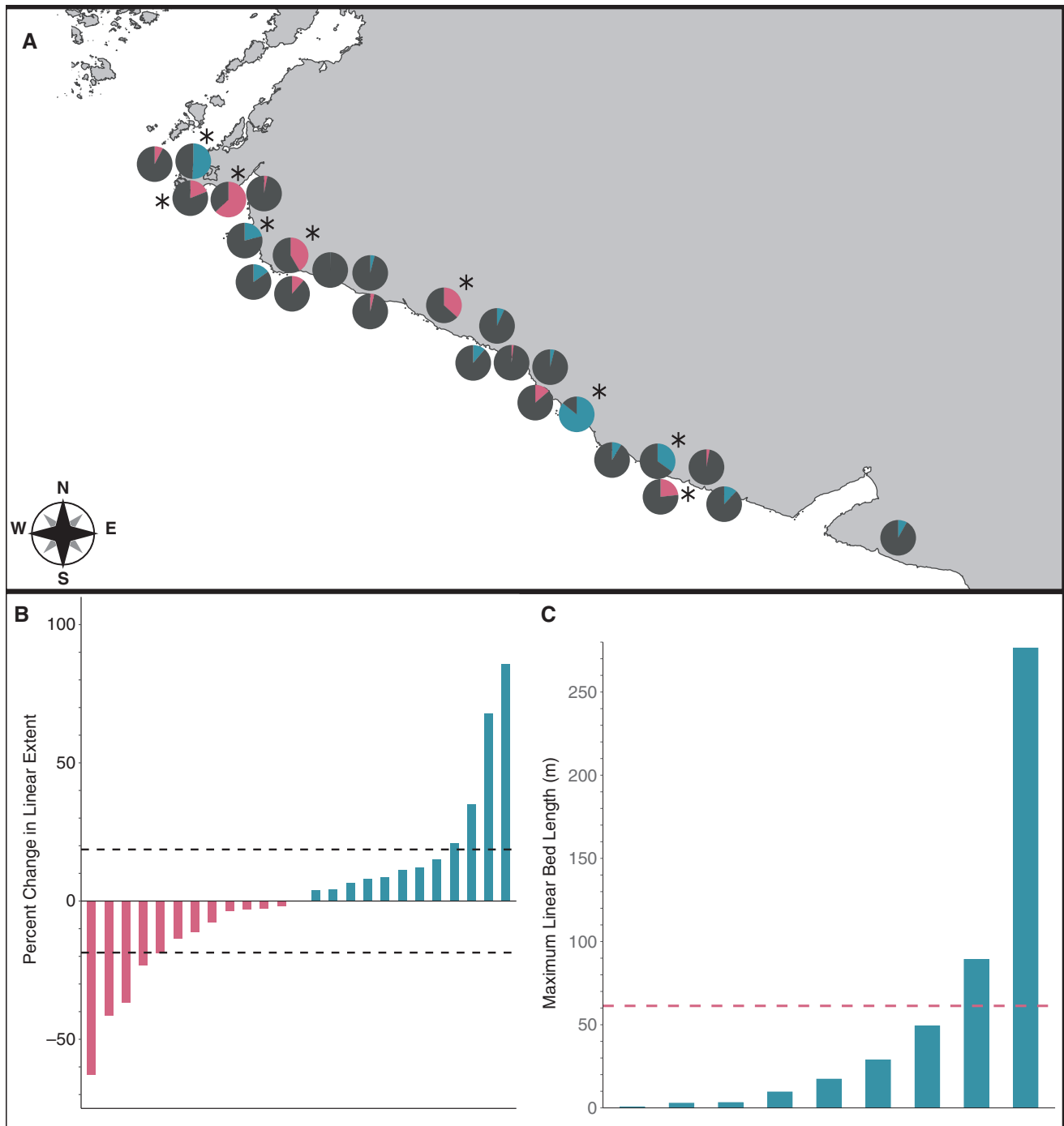


FIG. 4. (A) Map depicting the percentage linear increase (blue) or decrease (red) in the extent of *Postelsia* between 2007 and 2021 in 25 randomly selected cells. Changes larger than our methodological error threshold are marked with an asterisk (\*). (B) Percentage linear increase and decrease for each of the 25 cells. The dashed horizontal lines represent the percentage 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).

from data collected on nearby Tatoosh Island, Washington (~22 km from our study region), show only a 4 % probability of colonization at a distance of >10 m 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 owing 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,



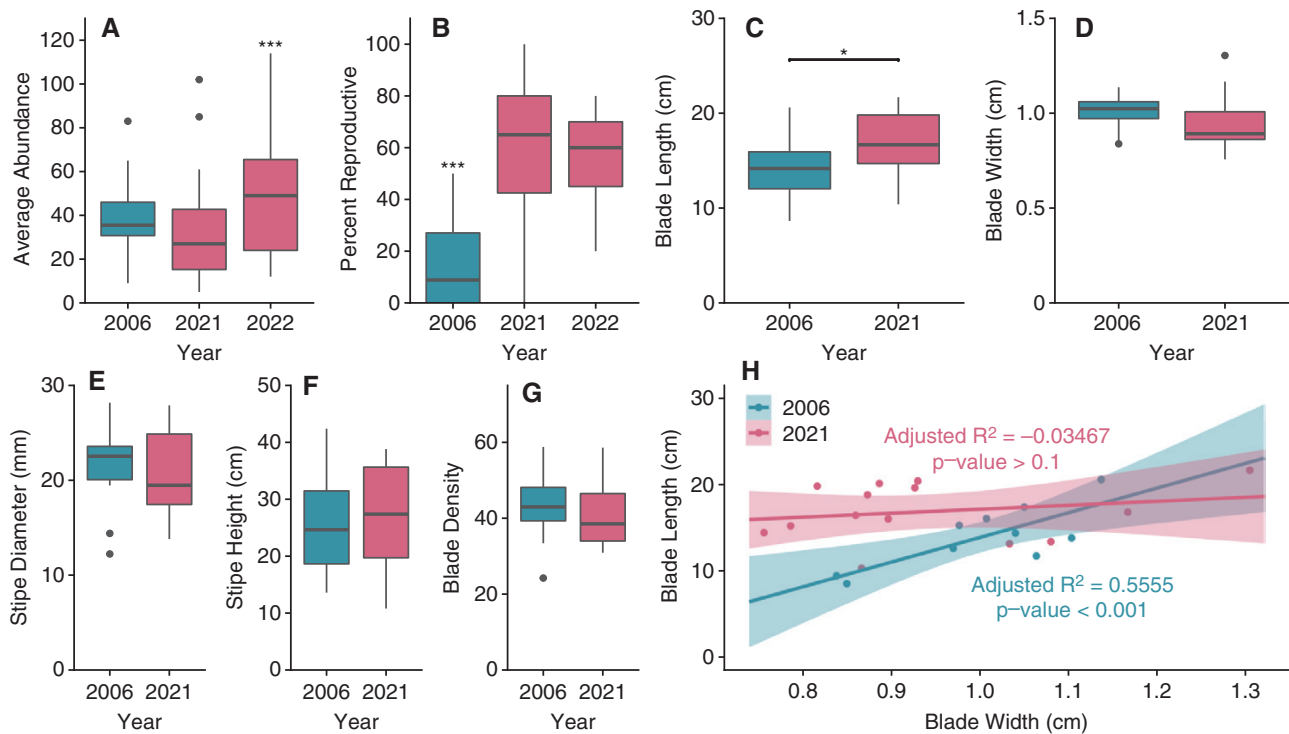


FIG. 5. Patch-level and individual measurements of *Postelsia* at Cape Beale for surveys completed in 2006, 2021 and 2022. Box plot comparisons between (A) density, (B) the percentage of reproductive individuals, (C) blade length, (D) blade width, (E) stipe diameter, (F) stipe height, and (G) blade density are plotted, with significant differences marked using asterisks (\*\*\* $P < 0.001$ , \* $P < 0.05$ ). 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.

1996), but little is known about how long this propagule bank can persist or whether it is more thermally tolerant than macroscopic *Postelsia* sporophytes. Even if microscopic gametophytes and sporophytes were able to survive heatwaves (when adult sporophytes could not) and promote recovery, this would still be considered distributional stability over our study time span of 15 years.

Thus, overall our results are consistent with our first hypothesis, suggesting that marine species such as *Postelsia* have 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 stability of the species was driven by a local mediating factor (i.e. wave exposure), our methods, if 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 might be explained by the specific habitat requirements of *Postelsia* or by its limited dispersal capabilities (Dayton, 1973; Paine, 1988; Nielsen et al., 2006). Although wave exposed (Supplementary Data Fig. S5), rocky shores in this region might not all receive a disturbance regime suitable for *Postelsia* establishment (Paine, 1979; Blanchette, 1996), and differences in bathymetry and aspect could 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 might 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, although 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; Western Society of Naturalists 101st Meeting, unpublished research), this lack of significant distributional expansion in the northern 12 % of the range of *Postelsia* 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 time points. We suspect that the significant increase in density in 2022 reflects the interannual variability to which *Postelsia* is prone 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 quantification of 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 2-week period (11–26 July). This might hint at a phenological shift in reproductive timing, a phenomenon that is common owing 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 (Fig. 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 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 2014–16 heatwave and limited recovery thereafter (Lohse et al., 2020; Western Society of Naturalists 101st Meeting, unpublished research). Our findings highlight the importance of multiscale 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 the response of a species to climate change. Future monitoring of this understudied species should be conducted at its true leading range edge and in other parts of its range with contrasting environmental characteristics to advance our understanding of the overall status of the species and its responses to rapidly advancing climate change.

#### SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online 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 photograph, 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 time point. 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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