Hesketh, A.V., Harley, C.D.G. 2023. Extreme heatwave drives topography-dependent patterns of mortality in a bed-forming intertidal barnacle, with implications for associated community structure. Global Change Biology. 29: 165–178.

Running title: Effects of an acute heatwave on barnacle beds

Extreme heatwave drives topography-dependent patterns of mortality in a bed-forming intertidal barnacle, with implications for associated community structure

Amelia V. Hesketh[1*] and Christopher D.G. Harley[1,2]

1. Department of Zoology, University of British Columbia, 4200-6270 University Blvd., Vancouver, BC, V6T 1Z4

2. Institute for the Oceans and Fisheries, University of British Columbia, 2202 Main Mall, Vancouver, BC, V6T 1Z4

* Corresponding author: ahesketh@sfu.ca

Data availability statement: The data that support the findings of this study are openly available at Borealis under a CC-BY 4.0 License at https://doi.org/10.5683/SP3/MUZIUP. Novel code that pertains to this manuscript is available on Github at https://doi.org/10.5281/zenodo.6471537.

Abstract

Heatwave frequency and intensity will increase as climate change progresses. Intertidal sessile invertebrates, which often form thermally benign microhabitats for associated species, are vulnerable to thermal stress because they have minimal ability to behaviourally thermoregulate. Understanding what factors influence the mortality of biogenic species and how heatwaves might impact their ability to provide habitat is critical. Here, we characterize the community associated with the thatched barnacle, *Semibalanus cariosus* (Pallass 1788), in British Columbia, Canada. Then, we investigate what site-level and plot-level environmental factors explained variations in barnacle mortality resulting from an unprecedented regional heatwave in British Columbia, Canada. Further, we used a manipulative shading experiment deployed prior to the heat dome to examine the effect of thermal stress on barnacle survival and recruitment and the barnacle-associated community. We identified 50 taxa inhabiting *S. cariosus* beds, with variations in community composition between sites. Site-scale variables and algal canopy cover did not predict *S. cariosus* mortality, but patch-scale variation in substratum orientation did, with more direct solar irradiance corresponding with higher barnacle mortality. The shading experiment demonstrated that *S. cariosus* survival, barnacle recruitment, and invertebrate community diversity were higher under shades where substratum temperatures were lower. Associated community composition also differed between shaded and non-shaded plots, suggesting *S. cariosus* was not able to fully buffer acute thermal stress for its associated community. While habitat provisioning by intertidal foundation species is an important source of biodiversity, these species alone may not be enough to prevent substantial community shifts following extreme heatwaves. As heatwaves become more frequent and severe, they may further reduce diversity via the loss of biogenic habitat, and spatial variation in these impacts may be substantial.

Keywords: diversity, facilitation, foundation species, heatwaves, intertidal zone, mortality, *Semibalanus cariosus*, temperature

Introduction

Anthropogenic climate change is marked not only by increasing mean temperatures globally but also by increasing thermal variability (Hoegh-Guldberg et al., 2018; Perkins-Kirkpatrick & Lewis, 2020). These shifting patterns in the thermal environment have far-reaching physiological and ecological consequences, as temperature is inextricably linked to organism performance through biochemistry and metabolism (Brown et al., 2004). This dependence is particularly important for ectotherms, which lack the physiological mechanisms to regulate their internal body temperature (Dillon et al., 2010; Riemer et al., 2018). Thermal extremes that exceed the physiological tolerance of organisms can lead to negative sublethal effects and mortality, making increases in thermal variability a potentially greater threat to organisms than increases in mean temperature (Vasseur et al., 2014).

Heatwaves, which are predicted to become longer, more frequent, and more severe over time (Perkins-Kirkpatrick & Lewis, 2020), can have immense impacts on organisms and ecological communities. Heatwaves are considered to occur when the 90th percentile of temperature, derived from historical baseline data, is exceeded for three or more days in the case of atmospheric heatwaves (Perkins & Alexander, 2013) or five or more days in the case of marine heatwaves (Hobday et al., 2016). These events have been implicated both directly and indirectly in the mortality of many marine ectotherms, among them habitat-forming corals (Babcock et al., 2020), macroalgae (Román et al., 2020; Wernberg et al., 2013), mussels (Harley, 2008), oysters (Scanes et al., 2020), and seagrasses (Arias-Ortiz et al., 2018), motile fish (Genin et al., 2020) and, when concomitant with drought stress, plants in terrestrial systems (De Boeck et al., 2018; Bussotti et al., 2021). The impacts of heatwaves on organisms can affect higher levels of biological organization by altering community structure (De Boeck et al., 2018; Pansch et al., 2018; Sorte et al., 2010), increasing heterogeneity, as measured by beta diversity (Robinson et al., 2019), and driving stochastic patterns in succession and community reassembly (Kreyling et al., 2011; Seifert et al., 2015). While the negative effects of heatwaves are evident, questions remain about what environmental factors and species traits shape mortality risk for populations exposed to heatwaves (Harvey et al., 2022) and how biological interactions may be affected.

The intertidal zone, at the intersection of marine and terrestrial realms, represents a thermally challenging landscape. Within the intertidal zone, where many organisms live near their thermal limits (Tomanek & Helmuth, 2002), there are often steeper thermal gradients found over metres of shore than on a broader latitudinal scale (Helmuth et al., 2006; Jurgens & Gaylord, 2018). While motile species can mitigate temperature stress by relocating to thermal refugia (e.g., Hayford et al., 2015; Reid & Harley, 2021), sessile foundation species that have no such recourse may be especially susceptible to heatwave impacts. For example, temperature can set the upper extent of distribution for certain intertidal sessile invertebrates (Connell, 1961; Connell, 1972; Harley, 2011). At a given shore level, small-scale topographic variation — such as the orientation and angle of the substratum and shading by nearby physical features — can affect solar irradiance and thus organism body temperature (Miller et al., 2009; Seabra et al., 2011). These differences in temperature can in turn drive topography-patterns of organism mortality in response to thermal stress (Harley, 2008).

Many sessile invertebrate species facilitate epifaunal and infaunal communities by creating biogenic habitat (Barnes, 2000; Bracken, 2018; McAfee & Bishop, 2019; van der Ouderaa et al., 2021). In the intertidal zone, this habitat is often more thermally benign than the surrounding shore, and thus the importance of facilitation in promoting the survival of associated species may become more important as thermal stress increases (Bulleri et al., 2016; Jurgens et al., 2021). For instance, the interstices created by *Mytilus californianus* mussel beds, which host some 300 species (Suchanek, 1992), are both cooler and more thermally stable than nearby rock clearings during summer (Jurgens & Gaylord, 2018). This dampening of thermal extremes, along with the moisture retention provided by *M. californianus* beds, results in greater survival of associated fauna within mussel beds compared to adjacent bare plots (Jurgens et al., 2021).

Similar thermally mediated facilitations have been measured for other invertebrate foundation species including barnacles, a cosmopolitan intertidal functional group. In a subtropical high intertidal system, all limpets associating with barnacles survived a six-hour exposure to a 40 ºC simulated heatwave, while 100% mortality was observed when barnacles were absent (Cartwright & Williams, 2014). In addition to affecting temperature, heatwaves also increase desiccation stress (Straub et al., 2019), which barnacles may mitigate by retaining moisture. For example, in the desiccating environment of Argentinian Patagonia, areas with moisture-retaining barnacles host a greater abundance of pulmonate limpets than areas without barnacles (Hesketh et al., 2021). However, we do not fully know if there is an upper threshold of abiotic stress above which such positive interactions weaken or cease entirely. Thus, to understand how the facilitatory role of a given foundation species will be altered by heatwaves, we must first ask: Can the foundation species in question survive heat stress? Survival may depend on microclimatic conditions generated by habitat features or other foundation species in the system. Second, where foundation species survive, can they maintain their facilitatory role in the face of thermally challenging conditions, thereby reducing the impacts of heatwaves on their associated community?

The 2021 Western North American Heat Dome of 2021 (hereafter, ‘heat dome’ for brevity), which occurred in an area stretching from Oregon, USA, to northern British Columbia (BC), Canada, represented an enormous thermal challenge for both human and non-human communities throughout the region (Raymond et al., 2022; Thompson et al., 2022). In BC, the heat dome occurred between 25–29 June 2021 and exceeded historical mean maximum daily temperatures by over 18 ºC and 5 ºC in the Strait of Georgia and along the outer coast, respectively (Climate Canada, 2022; see Fig. S1). These high temperatures coincided with some of the lowest mid-day tides and longest days of the year, generating lethal conditions for many sessile intertidal organisms.

One such organism within this region is the thatched barnacle, *Semibalanus cariosus* (Pallass, 1788), a long-lived mid-intertidal species (Connell, 1972) that forms dense, biodiverse beds where it occurs in high abundance (Dayton, 1971). *Semibalanus cariosus* commonly co-occurs with mussels (*Mytilus* spp.), smaller acorn barnacles (*Balanus glandula* and *Chthamalus dalli*), clonal anemones (*Anthopleura elegantissima*), and algae (mostly notably *Fucus distichus, Endocladia muricata*, and *Mastocarpus* spp.) throughout its range (Dayton 1971). While not as speciose or diverse as co-occurring mussel beds, beds of *S. cariosus* are known to facilitate numerous species such as limpets, littorine snails, whelks, isopods, amphipods, chitons, and polychaete and nemertean worms (Gosselin & Chia, 1995; Harley, unpublished data). Despite its importance as a facilitator, the ecological role of *S. cariosus* remains understudied relative to other dominant spaceholders in this system.

In this study, we sought to characterize the importance of *S. cariosus* as a facilitator across part of its distribution in coastal BC and determine how the heat dome affected the survival of *S. cariosus* and the composition of its associated community. While barnacle abundance is known to be affected by changes in mean sea temperatures (Southward ,1991; Southward et al., 1995) and by aerial exposure to extreme cold (Crisp, 1964; Wethey et al., 2011), the effects of atmospheric heatwaves are not well understood. Here, we investigate what factors, both among and within sites, might have contributed to heat dome-induced mortality patterns in this species. Mortality data were collected through field surveys along a well-characterized thermal gradient from cooler conditions on the temperate outer coast of BC to thermally stressful conditions in the eastern portion of the Salish Sea (Harley, 2011). We expected that *S. cariosus* mortality would increase with air temperature, the timing (hour of day) of the low tide, and at smaller angles of solar incidence — that is, on gently sloping shores facing towards the solar azimuth where solar irradiance was most direct during the heat dome. We also expected that mortality would decrease with decreasing algal cover, which mitigates thermal extremes. Because these variables interact to affect substratum temperature, we hypothesized two-way interactions between them. We then used a factorial experiment with crossed shading and barnacle removal treatments deployed prior to the heat dome to measure how the community associated with *S. cariosus*, along with barnacle mortality and recruitment, varied according to differences in substratum temperature. During our shading experiment, we expected that shades and the presence of barnacles would reduce substratum temperature, thereby increasing *S. cariosus* survival, barnacle recruitment, and the diversity of the associated algal and invertebrate communities. We also expected that associated fauna within *S. cariosus* beds would differ in composition between shaded and unshaded barnacle beds due to species-specific differences in thermal tolerance, and that communities inhabiting shaded barnacle beds would be more diverse.

Materials and Methods

Sampling locations

We performed surveys and collections of *S. cariosus* beds over a part of their distribution in coastal British Columbia, Canada (Fig. 1; Table S1) between 13 April 2021 and 11 September 2021. Most study sites were concentrated in the Salish Sea along the southern tip of Vancouver Island, with additional sites on Calvert Island along the central coast of BC. Shores were predominately granitic bedrock aside from two sites in the Gulf Islands (TE and TK in Fig. 1), which were sandstone bedrock, two sites on Vancouver Island (BO and KE in Fig. 1) that were a mix of bedrock and pilings and bedrock and boulders, respectively, and a site near Vancouver, BC (TS in Fig. 1) that was a granitic boulder shore. Sites ranged in wave exposure, with the outer coast being more wave-exposed and waters toward the Strait of Georgia being more sheltered. Note that Indigenous place names, where known, are used to refer to sites (Table S1).

Summary of data collected

This study occurred in three parts. First, we characterized the community associated with *S. cariosus* by destructively sampling barnacle beds at nine sites and counting the species therein (see Fig. 1 and Table S1), with the goal of better understanding the importance of this little-studied barnacle as biogenic habitat. Second, we capitalized on the extreme thermal challenge presented by the heat dome to determine what environmental factors shaped patterns of heat-induced *S. cariosus* mortality using field surveys. Third, we used a shading experiment deployed in advance of the heat dome at a single site (Sahsima; SA in Fig. 1) to examine the effect of ambient versus artificially reduced temperatures during the heat dome on *S. cariosus* and its associated community in both bare experimental plots and those containing intact barnacle beds.

Characterizing the barnacle-associated community

To characterize the diversity of fauna associated with *S. cariosus*, we collected 15×15 cm areas of *S. cariosus* beds from nine sites. Five replicate samples were collected at the majority of sites after the heat dome had occurred, between 5 August 2021 and 11 September 2021, while eight replicate samples were collected at Prasiola Point (PP in Fig. 1). For sampling purposes, we chose areas of shore where live *S. cariosus* was the dominant spaceholder (>50% cover) and scraped these areas clean of all species using a chisel and putty knife. We preserved samples after collection until processing, either by storing in 70% ethanol at room temperature or freezing. Associated species were identified and counted under a dissecting microscope, in most cases identifying taxa down to genus or species, though polychaete worms were only identified to family, amphipods and insects to order, one unknown bivalve species to class, and platyhelminths and nematodes to phylum (see Table S2 for taxonomic details).

Barnacle mortality surveys

We performed transect-based mortality surveys at a total of 36 transects over 13 sites to measure patterns in mortality across sites. For all sites, we calculated the mean maximum daily temperature during the heatwave period (25–29 June 2021) using data from the most proximate weather station (Climate Canada, 2022) and the mean time of the low tide from the most proximate tidal data station (Fisheries and Oceans Canada, 2022; WWW Tide and Current Predictor, 2021). We also noted the dominant seaward orientation of each transect from satellite images, and from this computed the shore aspect in terms of degrees from the solar azimuth at the peak of the heat dome (see Supplement 1 for estimation details). At each site, we documented mortality along three 10 m transects placed parallel to the shoreline at haphazardly chosen locations within the middle of *S. cariosus* beds. Along each transect, we randomly surveyed ten 12.7×12.7 cm square quadrats, one quadrat in each one-meter interval of the transect. In each quadrat, we recorded the number of live and dead *S. cariosus* individuals and the percent cover of algae overlying barnacles. Overlying algae was predominately *F. distichus*, with some subcanopy *Ulva* spp., *Mastocarpus* spp., and *E. muricata*, but the cover of individual species was not quantified. We surveyed only two transects at ke:ʔioadl (Fishboat Bay; KE in Fig. 1, Table S1) and one at ĆELḰINES (Moses Point; CE in Fig. 1, Table S1), and in some cases fell short of measuring mortality for all ten quadrats due to time constraints. In total, 347 quadrats were surveyed within the 36 transects using these methods.

We performed additional mortality surveys at six sites to better capture the dependence of mortality on substratum angle and orientation. For these surveys, we haphazardly placed 12.7×12.7 cm quadrats on shore, selecting for surfaces that varied in both the compass orientation they faced and their angle relative to the horizontal. We recorded the compass direction and angle of the substratum using the Commander Compass application (version 3.10.9 for iOS) and recorded the number of live and dead *S. cariosus* within the quadrat as described above to determine the proportion mortality of the barnacles therein. Note that the rarity of *S. cariosus* at Thousand-and-one Steps (site TS in Fig. 1) meant that we recorded the mortality of single barnacles in each quadrat area, resulting in mortality being either 0 (barnacle alive) or 1 (barnacle dead). The number of quadrats used varied between sites, ranging between 21 at Thousand-and-one Steps and 29 at Sahsima, but we recorded mortality in 152 total quadrats. To determine the angle of solar incidence (ASI) for each quadrat, we used the solar elevation and azimuth (National Oceanic and Atmospheric Administration, 2022) for what we estimated to be the hottest hour on 28 June 2021, the peak of the heat dome in coastal BC (Fig. S1; see Supplement 1 for estimation details).

All mortality surveys were performed between 19 July and 25 August 2021 (Table S1).

Shading experiment

To determine how *S. cariosus* and its associated community were affected by heat stress, we installed a shading experiment at Sahsima in Victoria, British Columbia, which lies in the traditional territory of the Songhees nation (latitude: 48.40578º, longitude: -123.32331º). We used a randomized block design for this experiment, in which a shading manipulation (unshaded or shaded), which acted as a passive thermal manipulation, was fully crossed with a barnacle removal manipulation (barnacle bed intact or removed). There were 12 blocks, and in each block, all four treatment combinations were present: UI (unshaded, barnacles intact); SI (shaded, barnacles intact); UR (unshaded, barnacles removed); SR (shaded, barnacles removed). The blocks were installed on gently sloping areas of southwest-facing shore where *S. cariosus* was dominant at a shore level of 1.22 ± 0.19 m (mean ± SE).

Within blocks, 15×15 cm experimental plots were established. For the shading manipulation, we fabricated 25 cm ×25 cm x 5 cm shading cages from PVC-coated steel fencing (2.54 cm mesh size; McMaster-Carr, IL, USA) covered in Vexar mesh (6.4 mm mesh size;

NorPlex Inc., WA, USA). Shading limited the solar irradiance reaching, and thus the temperature of, the substratum (Fig. S4). We attached shades to the substratum by zip-tying the cages to eyebolts drilled into the bedrock. To ensure motile invertebrates could access experimental plots, shade structures were constructed with two open sides. We also ensured that closed sides were installed with an orientation that maximized shading of the plot during the hottest part of the afternoon. We marked the area of unshaded plots with stainless steel lag bolts to assist in relocation. For the barnacle removal treatment, we chiselled away adult barnacles and any attached species within the central 15x15 cm area of the plot and scraped biota away with a putty knife.

To measure temperature differences between treatments, we installed iButton temperature loggers (DS1921G-F5# Thermochron, Maxim Integrated, CA, USA) on the substratum surface within five randomly chosen experimental blocks. Temperature loggers, which recorded substratum temperature at hourly intervals, were wrapped in Parafilm (Bemis, WI, USA) and embedded in a small amount of A-788 Splash Zone epoxy (Pettit Paints, NJ, USA) with fewer than 5 mm of epoxy overlying the surfaces of the logger. Some iButtons were installed at the edges of shaded plots and received full solar irradiance at some points during the heat dome. These data were removed from later analysis of temperature differences between treatments because they did not properly capture treatment effects.

The shading experiment was installed on 16 April 2021. We performed visual surveys of experimental plots at the time of installation (for intact treatments only), in early July 2021, and in late August 2021. During each survey, we identified and quantified the invertebrates and algae present and documented barnacle mortality and recruitment. At the end of the experimental period, we destructively sampled and preserved remaining experimental plots containing intact barnacle beds as described previously to characterize differences in the composition and beta diversity of the associated invertebrate community, meiofauna included, in response to shading treatments.

Statistical analyses

We completed all analyses within R version 4.1.2 (R Core Development Team, 2021). Unless otherwise noted, we constructed all linear models as random-intercept models using the *glmmTMB* package (version 1.1.2.3, Brooks et al., 2017), inspected models using the *DHARMa* package (version 0.4.4; Hartig, 2021), and tested models with either a Type III or Type II ANOVA through the *car* package (version 3.0–12; Fox & Weisberg, 2019) depending on whether an interaction term was or was not hypothesized, respectively. We generated maps with Stamen Map tiles using *ggmap* (version 3.0.0.903; Kahle & Wickham, 2019). Further statistical details including model structures, coefficients, and statistical outputs are in Supplement 2.

We modeled the transect-level mortality of *S. cariosus* resulting from the heat dome using multiple regression. We included quadrat-level algal cover, the prevailing orientation of each transect relative to the solar azimuth, and the mean hour of the low tide and the mean maximum daily air temperature at each site during the heat dome (25–29 June 2021). We scaled these variables and allowed two-way interactions between them. We utilized a Tweedie error distribution after logistic and beta error distributions failed due to substantial zero inflation of the data, and we included a random intercept of transect nested within site. We modeled mortality as a function of the quadrat-level ASI separately using a weighted logistic regression, with observations weighted by the total number of barnacles in each quadrat. Within this model, we included a random-slope effect of survey site.

For the shading experiment, we analyzed treatment differences in the mean daily maximum temperature, barnacle mortality and recruitment, algal cover, species richness, Shannon diversity of algal and invertebrate communities, and community composition. Shading and barnacle removal manipulations were fully crossed with blocks as a random effect. Mean daily maximum temperature was analyzed using a Gaussian error distribution. We modeled differences in barnacle mortality using a weighted logistic regression with the total number of barnacles in each quadrat used to weight observations. Algal cover was modeled using a beta distribution after first transforming cover to ensure values were between zero and one (Smithson & Verkuilen 2006). For barnacle recruitment, we used a negative binomial error distribution for analysis. We modeled species richness using a Poisson distribution with a log link. We chose to analyze the Shannon diversity of the algal and invertebrate communities using a Tweedie and Gaussian error distribution, respectively.

We analyzed community diversity using the *vegan* package (version 2.5–7; Okansen et al., 2020). Prior to PERMANOVA and PERMDISP analyses, we first used constrained ordination to visualize the data using the *capscale* function with default settings and 999 random starts. We ran PERMANOVA analyses using the *adonis2* function with constrained permutations within blocks. For PERMDISP analysis, we used the *betadisper* function and allowed bias adjustment to account for small sample sizes.

We also examined the effect of *S. cariosus* mortality on the abundance, species richness, and Shannon diversity of invertebrates in unshaded plots that were destructively sampled. Abundance, species richness, and Shannon diversity were analyzed using a negative binomial error distribution (through the *MASS* package, version 7.3–54; Venables & Ripley 2002), Poisson error distribution, and Gaussian error distribution, respectively.

Results

Barnacle mortality surveys

Following the heat dome, we sought to determine what factors, both across and within sites, affected the mortality of *S. cariosus* in response to extreme thermal stress. The mortality of *S. cariosus* was not significantly explained by air temperature, the timing of the low tide, transect-level shoreline orientation relative to the solar azimuth, algal cover, or the interaction of these variables (Table S8). Although the coarse-scale orientation of shorelines was not related to patterns of mortality, finer-scale orientation was. At the plot-scale, the angle of solar incidence (ASI) had an inverse relationship with mortality following a logistic pattern. That is, a smaller ASI (more direct sunlight) tended to correspond with higher barnacle mortality, while a larger ASI (less direct sunlight) was associated with lower mortality (Fig. 3; Type II ANCOVA: χ^2 = 5.899, df = 1, P = 0.01515).

Shading experiment

Using a shading experiment, we characterized how thermal stress and community successional stage (the presence or absence of barnacle beds) affected *S. cariosus* survival, barnacle recruitment, and the diversity of the community associated with *S. cariosus*. Temperature differences between treatments were most pronounced during fortnightly spring tides, and the heat dome coincided with some of the lowest daytime tides of the summer (Fig. 4a). During the heat dome at low tide, the mean substratum temperature in shaded plots was 6.1 ± 0.7 ºC (mean ± SE) lower than in unshaded plots. Even so, during this period, shaded plots (mean temperature = 23.3 ± 0.5 ºC) were still warmer during the heat dome than were unshaded plots during the rest of the summer (mean temperature = 19.9 ± 0.1 ºC). The mean maximum daily substratum temperature recorded during low tide over the entire experimental period was 5.0 ± 0.9 ºC lower on average in shaded versus unshaded plots, a significant difference (Fig. 4a–b, Fig. S5; Type II ANOVA: $\chi^2 = 207.4$, df = 1, $P < 0.001$). Conditions were warmer in plots where barnacles were removed ($\chi^2 = 6.766$, df = 1, $P = 0.00929$).

Semibalanus cariosus mortality was substantially higher in unshaded plots than shaded plots (Fig. 4c; Type II ANOVA: $\chi^2 = 65.53$, df = 1, $P < 0.001$). Barnacle recruitment (summed across all three species present: *S. cariosus*; *Balanus glandula*; and *Chthamalus dalli*) was lower in unshaded plots (Fig. 4d; Type II ANOVA: $\chi^2 = 11.53$, df = 1, $P < 0.001$). Communities in unshaded plots had lower species richness at the end of the summer than those in shaded plots when barnacles were absent, but the presence of barnacles ameliorated the effect of high temperatures (Fig. 4e; Type III ANOVA: shading × removal, $\chi^2 = 4.538$, df = 1, $P = 0.0332$). A similar pattern was found when considering the Shannon diversity of invertebrate communities, which was high when barnacles, shade, or both were present, but low when both were absent (Fig. 4f; Type III ANOVA: shading × removal, $\chi^2 = 12.23$, df = 1, $P < 0.001$). The cover and Shannon diversity of the algal community were generally low. While these measurements tended to be slightly higher where barnacles were present at the end of the summer, no effect of shading or barnacle removal treatments on algal cover or diversity was statistically supported (Fig. S6a; Supplement 2).

Within destructively sampled barnacle bed samples at the end of the shading experiment, the composition of the associated community differed between shaded and unshaded plots (Fig. 5; PERMANOVA: $F_{1,16} = 5.1284$, $R^2 = 0.2427$, $P = 0.0469$). Communities were more heterogeneous (had higher beta diversity) in unshaded than in shaded communities (PERMDISP:

$F_{1,16} = 9.3662$, $P = 0.00747$). Results were similar when we removed rare species from the analysis (see Fig. S7 for details). In unshaded plots, the abundance, richness, and diversity of taxa present within *S. cariosus* beds tended to be negatively related to barnacle mortality (Fig. S8), but only the relationship between invertebrate abundance and barnacle mortality was statistically significant (Type I ANOVA: residual deviance = 7.9952, df = 7, $P = 0.00873$; Supplement 2).

Discussion

Through our study, we addressed the following questions: What diversity of species does *S. cariosus* facilitate? What environmental factors affected the mortality of *S. cariosus* during the heat dome? Was the facilitatory role of *S. cariosus* strengthened or weakened under substantial thermal stress? We found that *S. cariosus* facilitates a speciose and diverse community across a regional gradient of temperature and wave exposure, though the exact composition of the community varied among sites. *Semibalanus cariosus* mortality caused by the heat dome was extremely variable, ranging from 0–100% at the quadrat level. Contrary to our expectations, we found that mortality was not explained well by any of the site- or transect-level factors considered, algal cover, or the interaction of these factors. However, at the quadrat level, *Semibalanus cariosus* beds on gently sloping substrata facing the sun during the hottest portion of the low tide had greater mortality than those on surfaces angled more obliquely to incoming solar radiation (e.g., steeply sloping and/or northeast facing surfaces). Experimental shading, which lowered the substratum temperature, was associated with higher *S. cariosus* survival and barnacle recruitment but had no apparent effect on algal communities. The presence of both barnacles and shade had an interactive effect on species richness and invertebrate Shannon diversity, indicating that facilitation by barnacles is stronger under stressful conditions. Unshaded barnacle beds hosted a significantly different invertebrate assemblage at the end of the summer than did shaded plots, which we expected, though beta diversity in unshaded beds was greater, not less, than in shaded plots.

The diversity of species we observed within *S. cariosus* beds across the distribution surveyed is consistent with the limited data available for this species. *Semibalanus cariosus* beds in Barkley Sound, BC (location of site PP in Fig. 1) are known to facilitate minute clams (*Lasaea rubra*) and juvenile mussels (*Mytilus californianus*) in the same abundance as do *M. californianus* beds, providing prey as well as protection for juvenile *Nucella ostrina* whelks (Gosselin & Chia, 1995). We found these same three species within *S. cariosus* beds during our study, with *M. californianus* and *L. rubra* present in high abundances at West Beach (Calvert Island) and Prasiola Point (Barkley Sound), the most wave-exposed sites. Across all sites, we documented 50 unique taxa, some of which most likely included multiple species (e.g., Nereidae, Amphipoda). *Semibalanus cariosus* beds collected at Calvert Island in 2017 contained 52 identified species (Harley, unpublished data), comparable to our findings here. Notably, the assemblages sampled in our study differed in their composition between sites. Previous studies of mussel beds have found that meiofauna community composition varies regionally, probably driven by differences in the richness of the local species pool or in the substratum underlying the biogenic habitat (Buschbaum et al., 2009). Interestingly, peak Shannon diversity coincided with an intermediate level of wave exposure, consistent with the intermediate disturbance hypothesis (Connell, 1978). As wave stress was not formally quantified and sample sizes were small for these surveys, we cannot definitively ascribe this qualitative pattern to wave exposure alone. In any case, certain species may have been abundant in some locations and not others depending on their species-specific tolerances to abiotic stressors, since complex environmental and ecological gradients are present over the geographic gradient sampled (Harley, 2011; Ianson et al., 2016; Widdowson, 1965).

For intertidal species that are in close contact with the substratum, body temperature is tightly coupled to substratum temperature (Helmuth, 1998; LaScala-Gruenewald & Denny, 2020). Thus, we would expect the body temperature of *S. cariosus*, and thus its survival, to be affected by air temperature, prevailing shore orientation, and the timing of the low tide. For example, even if aerial temperatures are high, low daily maximum substratum temperatures are measured if low tides occur during evening or morning, while the highest maximum substratum temperatures are observed only if low tides occur during the afternoon (Hayford et al., 2015). East-facing shores are often warmer than equatorward-facing shores if low tides occur during the morning, but if the low tide occurs during the afternoon, the reverse is true (Gilman et al., 2015). However, none of these factors — nor their interactions — explained *S. cariosus* mortality well in this study. The lack of significant effects may have occurred due to the lack of resolution for these variables. Air temperatures were collected from the most proximate weather station to each site, but more inland weather stations may not accurately reflect coastal temperatures. Here, too, shore orientation was measured at the level of each transect, but this technique did not capture small-scale topographic differences between quadrats in a transect.

While we expected algal cover to increase the survival of underlying barnacles via shading and evaporative cooling, cover had no significant effect on mortality. *Fucus distichus* — the dominant canopy-forming alga in this study — can decrease mid-intertidal invertebrate body temperatures by 2.3 ºC on average and reduce the incidence at which lethal temperatures are recorded relative to adjacent sun-exposed areas (Gilman et al., 2015). The reduction in temperature and desiccation stress provided by both subcanopy and canopy-forming algal species has been implicated in increased barnacle survival (Dayton, 1971; Hawkins, 1983; Leonard, 2000) and increased invertebrate abundance (Umanzor et al., 2017) and alpha diversity (Lilley & Schiel, 2006) in the underlying community. Algal cover may have been too low in our study to provide adequate thermal and desiccation protection (e.g., Hay, 1981). Perhaps what thermal protection algae did provide could not be sustained during the acute, prolonged thermal stress of the heat dome as has been found for other algal facilitations under high levels of environmental stress (Navarro-Barranco et al., 2022; Scrosati, 2017). Further, the exact composition of algal species differed between sites and was not quantified; different species, by virtue of their morphology, may vary in the extent to which they retain moisture and provide thermal protection to underlying organisms. Canopy algae can also reduce the survival of small barnacles through algal whiplash (Hancock & Petraitis, 2001; Hawkins, 1983; Jenkins et al., 1999), though the large size of the *S. cariosus* studied likely minimized this negative effect.

While across-site factors did not explain *S. cariosus* mortality, small-scale topographic differences did. Previous studies have found that substratum temperature, which closely tracks the body temperature of barnacles (Harley & Lopez, 2003), is highly correlated with the ASI at the substratum surface (Harley, 2008). At temperate latitudes, equatorward-facing shores experience both higher mean temperatures and more frequent extreme high temperatures than poleward-facing shores (Amstutz et al., 2021). Similarly, in the northeast Pacific, the body temperature of whelk biomimetics on sun-exposed south-facing shores were 2.8 ºC hotter than those on similarly sun-exposed east-facing shores (Gilman et al., 2015). These temperature differences may translate to patterns in organismal mortality and distribution. Smaller values of ASI have been linked to higher rates of mussel mortality and localized decreases in limpet abundance, with both trends following a roughly logistic pattern (Harley, 2008). Similarly, the upper limit of limpet distribution on shore was highest on poleward-facing shores (high ASI) and lowest on shores facing towards the solar azimuth (low ASI; Miller et al., 2009). Despite an overall significant relationship between ASI and mortality, the exact shape of this relationship differed between sites, which may be due to site-level differences in the timing of low tides during the heat dome, wave exposure, or other factors not captured by the underlying model.

In our shading experiment, which we conducted on a predominantly southwest-facing shore with a low ASI, shades reduced substratum temperature by several degrees, which generally benefited the underlying barnacle-associated community. Shading treatments, while they reduce thermal stress, cannot be disentangled from a concurrent reduction in desiccation stress and incoming light (Harley & Lopez, 2003; Morelissen & Harley, 2007). Thus, the effects of shading cannot be wholly assigned to temperature differences for species that are strongly influenced by desiccation and light availability (e.g., seaweeds). For heterotrophs that can resist desiccation, including many shelled invertebrates such as barnacles, temperature would likely be the most important environmental difference between shaded and unshaded areas. Barnacles within shaded beds had lower mortality after exposure to hot summer temperatures than those in unshaded control plots in our study, a pattern that has been documented by others (Levine et al., 1999; Wethey, 1984). This mortality difference was likely driven by differences in the level of physiological stress encountered in unshaded versus shaded plots. The upper limit of the congener *Semibalanus balanoides* within the intertidal zone is known to be set by intolerance of thermal and desiccation stress (Connell, 1961; Wethey, 1984). Mussels in sun-exposed areas, even though they are better acclimated to withstand thermal stress, are still more likely to experience lethal temperatures that exceed their critical upper limit of cardiac function than those in shaded areas, resulting in higher mortality in sun versus shade (Li et al., 2021). Barnacle recruitment was more successful in shaded plots, consistent with previous studies (Pardal-Souza et al., 2017). Here, we found that the presence of barnacles had a small but significant effect in reducing the maximum substratum temperature. Barnacles are known to reduce heat and desiccation stress where present by providing shade (Cartwright & Williams, 2014) and increasing moisture retention (Harley & O'Riley, 2011), enhancing community diversity in the face of thermal stress (e.g., Kordas et al., 2018). Where shades were absent during the heat dome and substratum temperatures were high, barnacles beds hosted similar species richness and invertebrate Shannon diversity to shaded plots. The facilitatory role of barnacles was thus stronger in the face of thermal stress, reducing the effect of heat on the barnacle-associated community. However, we detected no effects of shading or barnacle presence on algal cover or diversity, consistent with prior observations of macroalgal cover in response to shading (Morelissen & Harley, 2007). Even if thermal stress is lower beneath shades, low light may have limited algal growth (Pardal-Souza et al., 2017), preventing the benefit of reduced temperatures from becoming apparent. High intertidal acorn barnacles tend to facilitate a greater abundance of fleshy macroalgae in the northeast Pacific (Hesketh et al., 2021), so an effect of barnacle removal on algae may also have been observed with a longer experiment. Further, the generally low prevalence of algae in terms of both cover (0–20 % cover) and diversity (six species present) at this site may have prevented the detection of any treatment effects.

Within destructively sampled barnacle beds, shading treatments altered the invertebrate communities associated with *S. cariosus*, which may have been driven by differences in abiotic tolerance between taxa, changes in the microhabitats available, or both. Shifts in community composition in response to heatwaves have been documented in various systems and appear to be mediated by species-specific responses to thermal stress (De Boeck et al., 2018; Pansch et al., 2018; Sorte et al., 2010; Tituskin et al., 2021). We observed that taxa dominating unshaded plots at the end of summer were typically motile, small, and more thermally tolerant (e.g., littorine snails, limpets, amphipods, isopods), while taxa in shaded plots were typically less motile, larger, and/or less thermally tolerant (e.g., sea cucumbers, anemones, chitons, whelks). Highly motile species, such as those dominating unshaded barnacle beds here, can more easily escape to thermal refugia during stressful periods and/or recolonize following a disturbance, and thus may be expected to re-establish in perturbed systems more quickly than less motile species following a heatwave (Harvey et al., 2022). Larger organisms are less tolerant of short-term thermal stress than smaller organisms (Peralta-Maraver et al., 2021), and calcified structures such as the shells of high intertidal gastropods (e.g., family Littorinidae) confer protection against thermal and desiccation stress (Vermeij, 1978). Thus, we might expect small, calcified invertebrates to be more tolerant of heatwaves, which may explain the divergence in taxonomic assemblages between shaded and unshaded barnacle beds following the heat dome. As *S. cariosus* mortality increased in unshaded plots, the abundance of invertebrate taxa within destructively sampled beds declined significantly. Similar effects were observed on invertebrate species richness and Shannon diversity, but these lacked statistically significance, possibly due to the low sample size, and thus low power, of this experiment. Other intertidal biogenic species have been found to maintain their facilitative ability beyond the point of death, though sometimes the identity of species associated with the biogenic habitat changes (Liversage et al., 2020; McAfee & Bishop, 2019; Uyà et al., 2020). Empty barnacle tests form important microhabitats for intertidal organisms (Barnes, 2000) and may thus continue to facilitate communities of organisms adapted to empty tests after barnacle death. While unshaded *S. cariosus* beds had higher beta diversity than shaded beds, likely reflecting the stochastic nature of community assembly following heatwave disturbances (Kreyling et al., 2011), empty barnacle tests are ultimately an ephemeral habitat at higher risk of dislodgement than live barnacles (Reimer, 1976). As dead barnacles are removed from shore, the effects of subsequent heatwaves may be greater due to the absence of moisture-retaining foundation species.

Overall, our results suggest that heatwave-induced mortality of foundation species may be somewhat predictable at certain scales. The patchy mortality of *S. cariosus* was largely explained by small-scale differences in intertidal topography. Barnacle beds on substrata that are shaded or receive only oblique solar irradiance will likely be able to persist through future heatwaves and continue to facilitate a diverse community, while populations on shores where irradiance is high will be increasingly impacted, along with the species they facilitate. *Semibalanus cariosus* that survived the heat dome were clearly able to acclimate to extreme temperatures through physiological means (e.g., Muir et al., 2016), but the energetic costs associated with this acclimation may have had sublethal effects on fitness (e.g., reduced fecundity; Curd et al., 2022) not measured here. The ability of *S. cariosus* to adapt to increased thermal stress is unknown, but given that aquatic invertebrates at mid-latitudes generally demonstrate acclimation capacity to warm conditions (Morley et al., 2019) and that the generation time of barnacles is relatively short, limited adaptation may be possible. Prediction of mortality risk from heatwaves remains difficult given that this risk is affected not only by the constitutive thermal tolerance of organisms, but also their degree of induced defense (e.g., through production of heat shock proteins; Denny, 2018) and the duration (Peralta-Maraver et al., 2021) and frequency (Siegle et al., 2018) of heatwaves. The Salish Sea region of BC is a known “hot spot” (Helmuth et al., 2002), and thus *S. cariosus* in the study region may already be close to the limits of their adaptive capacity. Further, *S. cariosus*, while its generation time may be short, is at high risk of predation by whelks (*Nucella* spp.) until the age of two (Connell, 1972), and grows slowly thereafter (Sebens & Lewis, 1985); thus, it is unclear whether mature *S. cariosus* beds can re-establish if repeated heatwaves occur in close succession.

While habitat provision by biogenic species remains an important mechanism by which the environmental stress experienced by associated species can be mitigated (Jurgens et al., 2021; Jurgens & Gaylord, 2018), there may be an upper limit to the stress under which such facilitations can occur (Navarro-Barranco et al., 2022; Scrosati, 2017). Extreme heatwaves like the 2021 Western North American Heat Dome will only occur more frequently through time (Perkins-Kirkpatrick & Lewis, 2020), and events of this magnitude may prove lethal for foundation species or disrupt their ability to facilitate associated organisms. In order to assess the potential benefit that facilitative interactions will provide to ecological communities in the future, we must characterize not only the thermal tolerances of important foundation species under single and repeated heatwaves of varying magnitudes, but also determine the thresholds beyond which facilitative interactions collapse. Our results highlight the importance of consistently monitoring populations of foundation species to capture the full effects of extreme events and conserving foundation species, which may be critical to conserving biodiversity in the face of climate change.

Acknowledgements

We thank the First Nations on whose traditional and (in most cases) unceded territories this work was conducted for their historic and current care for our lands and water, namely the Wuikiuxv, Huu-ay-aht, Pacheedaht, T'Souke, Esquimalt, Songhees, W̱SÁNEĆ, and Semiahmoo peoples. In addition, we thank J. Li, C. Burtlake, A. Garg, C. Steell, and G. Brownlee for field assistance, S. Emry and C. Konecny for support during early barnacle excursions, and L. & C. Hesketh and G. Jesse for accommodation and sustenance during field work. We thank C. Brauner, S. Dudas, R. Germain, S. Hawkins, P. Petraitis, and an anonymous reviewer for comments on this manuscript. We acknowledge Bamfield Marine Sciences Centre for their generous support of this work and the Hakai Institute for field support and supplying hourly air temperature data for Calvert Island. Funding was provided by a Natural Sciences and Engineering Research Council of Canada Discovery Grant to CDGH.

Literature cited

Amstutz, A., Firth, L.B., Spicer, J.I., & Hanley, M.E. (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

Arias-Ortiz, A., Serrano, O., Masqué, P., Lavery, P. S., Mueller, U., Kendrick, G. A., Rozaimi, M., Esteban, A., Fourqurean, J.W., Marbà, N., Mateo, M.A., Murray, K., Rule, M.J., & Duarte, C.M. (2018). A marine heatwave drives massive losses from the world’s largest seagrass carbon stocks. Nature Climate Change, 8, 338–344. doi: 10.1038/s41558-018-0096-y

Babcock, R.C., Thomson, D.P., Haywood, M.D.E., Vanderklift, M.A., Pillans, R., Rochester, W.A., Miller, M., Speed, C.W., Shedrawi, G., Field, S., Evans, R., Stoddart, J., Hurley, T. J., Thompson, A., Gilmour, J., Depczynski, M., Babcock, R. C., Thomson, D. P., Haywood, M.D.E., … Depczynski, M. (2020). Recurrent coral bleaching in north-western Australia and associated declines in coral cover. Marine and Freshwater Research, 72, 620–632. doi: 10.1071/MF19378

Barnes, M. (2000). The use of intertidal barnacle shells. In: Oceanography and Marine Biology: An Annual Review (Vol. 38, pp. 157–187). Taylor & Francis.

Bracken, M.E.S. (2018). When one foundation species supports another: Tubeworms facilitate an extensive kelp bed in a soft-sediment habitat. Ecosphere, 9, e02429. doi: 10.1002/ecs2.2429

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A.,Skaug, H.J., Maechler, M. & Bolker, B.M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal, 9(2), 378-400.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., & West, G.B. (2004). Toward a Metabolic Theory of Ecology. Ecology, 85, 1771–1789. doi: 10.1890/03-9000

Bulleri, F., Bruno, J.F., Silliman, B.R., & Stachowicz, J.J. (2016). Facilitation and the niche: Implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology*, 30, 70–78. doi: 10.1111/1365-2435.12528

Buschbaum, C., Dittmann, S., Hong, J.-S., Hwang, I.-S., Strasser, M., Thiel, M., Valdivia, N., Yoon, S.-P., & Reise, K. (2009). Mytilid mussels: Global habitat engineers in coastal sediments. Helgoland Marine Research, 63, 47–58. doi: 10.1007/s10152-008-0139-2

Bussotti, F., Papitto, G., Di Martino, D., Cocciufa, C., Cindolo, C., Cenni, E., Bettini, D., Iacopetti, G., & Pollastrini, M. (2021). Defoliation, recovery and increasing mortality in Italian forests: levels, patterns and possible consequences for forest multifunctionality. Forests, 12, 1476. doi: 10.3390/f12111476

Cartwright, S.R., & Williams, G.A. (2014). How hot for how long? The potential role of heat intensity and duration in moderating the beneficial effects of an ecosystem engineer on rocky shores. Marine Biology, 161, 2097–2105. doi: 10.1007/s00227-014-2489-4

Climate Canada. (2022, January 26). Historical Data. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html.

Connell, J.H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology, 42, 710–723.

Connell, J.H. (1972). Community interactions on marine rocky intertidal shores. Annual Review of Ecology and Systematics, 3, 169–192.

Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. Science, 199, 1302–1310.

Crisp, D.J. (1964). The effects of the severe winter of 1962–63 on marine life in Britain. Journal of Animal Ecology, 33, 165–210.

Curd, A., Boyé, A., Cordier, C., Pernet, F., Firth, L.B., Bush, L.E., Davies, A.J, Lima, F.P., Meneghesso, C., Quéré, C., Seabra, R., Vasquez, M., & Dubois, S.F. (2021). Environmental optima for an ecosystem engineer: a multidisciplinary trait-based approach. Scientific Reports, 11, 22986.

Dayton, P.K. (1971). Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs, 41, 351–389.

De Boeck, H.J., Hiltbrunner, E., Verlinden, M., Bassin, S., & Zeiter, M. (2018). Legacy effects of climate extremes in alpine grassland. Frontiers in Plant Science, 9, 1586. doi: 10.3389/fpls.2018.01586

Denny, M.W. (2018). Survival in spatially variable thermal environments: Consequences of induced thermal defense. Integrative Zoology, 13, 392–410. doi: 10.1111/1749-4877.12308

Dillon, M.E., Wang, G., & Huey, R.B. (2010). Global metabolic impacts of recent climate warming. Nature, 467, 704–706. doi: 10.1038/nature09407

Fisheries and Oceans Canada. (2022, February 9). Tides, currents, and water levels. https://tides.gc.ca/en.

Fox, J. & Weisberg, S. (2019). An {R} companion to applied regression, third edition. Thousand Oaks CA: Sage.

Genin, A., Levy, L., Sharon, G., Raitsos, D.E., & Diamant, A. (2020). Rapid onsets of warming events trigger mass mortality of coral reef fish. Proceedings of the National Academy of Sciences of the United States of America, 117, 25378–25385. doi: 10.1073/pnas.2009748117

Gilman, S., Hayford, H., Craig, C., & Carrington, E. (2015). Body temperatures of an intertidal barnacle and two whelk predators in relation to shore height, solar aspect, and microhabitat. Marine Ecology Progress Series, 536, 77–88. doi: 10.3354/meps11418

Gosselin, L., & Chia, F. (1995). Distribution and dispersal of early juvenile snails: effectiveness of intertidal microhabitats as refuges and food sources. Marine Ecology Progress Series, 128, 213–223. doi: 10.3354/meps128213

Hancock, K.M., & Petraitis, P.S. (2001). Effects of herbivorous snails and macroalgal canopy on recruitment and early survivorship of the barnacle *Semibalanus balanoides* (L.). Journal of Experimental Marine Biology and Ecology, 257, 205–218. doi: 10.1016/S0022-0981(00)00337-3

Harley, C.D.G. (2008). Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. Marine Ecology Progress Series, 371, 37–46. doi: 10.3354/meps07711

Harley, C.D.G. (2011). Climate change, keystone predation, and biodiversity loss. Science, 334, 1124–1127.

Harley, C.D.G., & Lopez, J.P. (2003). The natural history, thermal physiology, and ecological impacts of intertidal mesopredators, *Oedoparena spp.* (Diptera: Dryomyzidae). Invertebrate Biology, 122, 61–73. doi: 10.1111/j.1744-7410.2003.tb00073.x

Harley, C.D.G., & O'Riley, J.L. (2011). Non-linear density-dependent effects of an intertidal ecosystem engineer. Oecologia, 166, 531–541. doi: 10.1007/s00442-010-1864-1

Hartig, F. (2021). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.4.

Harvey, B.P., Marshall, K.E., Harley, C.D.G., & Russell, B.D. (2022). Predicting responses to marine heatwaves using functional traits. Trends in Ecology & Evolution, 37(1), 20–29. doi: 10.1016/j.tree.2021.09.003

Hawkins, S. (1983). Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.) Journal of Experimental Marine Biology and Ecology, 71, 55–72.

Hay, M.E. (1981). The functional morphology of turf-forming seaweeds: Persistence in stressful marine habitats. Ecology, 62, 739–750.

Hayford, H., Gilman, S., & Carrington, E. (2015). Foraging behavior minimizes heat exposure in a complex thermal landscape. Marine Ecology Progress Series, 518, 165–175. doi: 10.3354/meps11053

Helmuth, B., Broitman, B.R., Blanchette, C. A., Gilman, S., Halpin, P., Harley, C.D.G., O'Donnell, M.J., Hofmann, G.E., Menge, B., & Strickland, D. (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

Helmuth, B., Harley, C.D.G., Halpin, P.M., O'Donnell, M., Hofmann, G.E., & Blanchette, C.A. (2002). Climate change and latitudinal patterns of intertidal thermal stress. Science, 298,1015–1017. doi: 10.1126/science.1076814

Helmuth, B. S. T. (1998). Intertidal mussel microclimates: Predicting the body temperature of a sessile invertebrate. Ecological Monographs, 68, 51–74. doi: 10.1890/0012-9615(1998)068[0051:IMMPTB]2.0.CO;2

Hesketh, A.V., Schwindt, E., & Harley, C.D.G. (2021). Ecological and environmental context shape the differential effects of a facilitator in its native and invaded ranges. Ecology, 102, e03478. doi: 10.1002/ecy.3478

Hobday, A.J., Alexander, L.V., Perkins, S.E., Smale, D.A., Straub, S.C., Oliver, E.C.J., Benthuysen, J.A., Burrows, M.T., Donat, M.G., Feng, M., Holbrook, N.J., Moore, P.J., Scannell, H.A., Sen Gupta, A., & Wernberg, T. (2016). A hierarchical approach to defining marine heatwaves. Progress in Oceanography, 141, 227–238. doi: 10.1016/j.pocean.2015.12.014

Hoegh-Guldberg, O., Jacob, D., Taylor, M., Bindi, M., Brown, S., Camilloni, I., Diedhiou, A., Djalante, R., Ebi, K. L., Engelbrecht, F., Hijioka, Y., Mehrotra, S., Payne, A., Seneviratne, S. I., Thomas, A., Warren, R., Zhou, G., Halim, S. A., Achlatis, M., … Sherstyukov, B. (2018). Impacts of 1.5°C of Global Warming on Natural and Human Systems. In: Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R.

Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (Eds.), Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty.

Ianson, D., Allen, S.E., Moore-Maley, B.L., Johannessen, S.C., & Macdonald, and Robie W. (2016). Vulnerability of a semienclosed estuarine sea to ocean acidification in contrast with hypoxia. Geophysical Research Letters, 43, 5793–5801. doi: 10.1002/2016GL068996

Jenkins, S.R., Norton, T.A., & Hawkins, S.J. (1999). Settlement and post-settlement interactions between *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) and three species of fucoid canopy algae. Journal of Experimental Marine Biology and Ecology, 236, 49–67.

Jurgens, L.J., Ashlock, L.W., & Gaylord, B. (2021). Facilitation alters climate change risk on rocky shores. Ecology, e03596. doi: 10.1002/ecy.3596

Jurgens, L.J., & Gaylord, B. (2018). Physical effects of habitat-forming species override latitudinal trends in temperature. Ecology Letters, 21, 190–196. doi: 10.1111/ele.12881

Kahle, D. & Wickham, H. (2013). ggmap: Spatial Visualization with ggplot2. The R Journal, 5(1), 144-161.

Kordas, R. L., Donohue, I., & Harley, C.D.G. (2018). Herbivory enables marine communities to resist warming. Scientific Advances, 3, e1701349. doi: 10.1126/sciadv.1701349

Kreyling, J., Jentsch, A., & Beierkuhnlein, C. (2011). Stochastic trajectories of succession initiated by extreme climatic events. Ecology Letters, 14, 758–764. doi: 10.1111/j.1461-0248.2011.01637.x

LaScala-Gruenewald, D.E., & Denny, M.W. (2020). Long-term mechanistic hindcasts predict the structure of experimentally-warmed intertidal communities. Oikos, 129, 1645–1656. doi: 10.1111/oik.07468

Leonard, G.H. (2000). Latitudinal variation in species interactions: A test in the New England rocky intertidal zone. Ecology, 81, 1015–1030. doi: 10.2307/177175

Levine, J.M., Bruno, J.F., Leonard, G.H., & Bertness, M.D. (1999). Climate-driven interactions among rocky intertidal organisms caught between a rock and a hot place. Oecologia, 120, 446–450. doi: 10.1007/s004420050877

Li, X., Tan, Y., Sun, Y., Wang, J., & Dong, Y. (2021). Microhabitat temperature variation combines with physiological variation to enhance thermal resilience of the intertidal mussel *Mytilisepta virgata*. Functional Ecology, 35, 2497–2507. doi: 10.1111/1365-2435.13885

Lilley, S.A., & Schiel, D.R. (2006). Community effects following the deletion of a habitat-forming alga from rocky marine shores. Oecologia, 148, 672–681. doi: 10.1007/s00442-006-0411-6

Liversage, K., Kotta, J., Fraser, C.M.L., Figueira, W.F., & Coleman, R.A. (2020). The overlooked role of taphonomy in ecology: Post-mortem processes can outweigh recruitment effects on community functions. Oikos, 129, 420–432. doi: 10.1111/oik.06780

McAfee, D., & Bishop, M.J. (2019). The mechanisms by which oysters facilitate invertebrates vary across environmental gradients. Oecologia, 189, 1095–1106. doi: 10.1007/s00442-019-04359-3

Miller, L.P., Harley, C.D.G., & Denny, M.W. (2009). The role of temperature and desiccation stress in limiting the local-scale distribution of the owl limpet, *Lottia gigantea*. Functional Ecology, 23, 756–767. doi: 10.1111/j.1365-2435.2009.01567.x

Morelissen, B., & Harley, C.D.G. (2007). The effects of temperature on producers, consumers, and plant–herbivore interactions in an intertidal community. Journal of Experimental Marine Biology and Ecology, 348, 162–173. doi: 10.1016/j.jembe.2007.04.006

Morley, S.A., Peck, L.S., Sunday, J.M., Heiser, S., & Bates, A.E. (2019). Physiological acclimation and persistence of ectothermic species under extreme heat events. Global Ecology and Biogeography, 28, 1018–1037. doi: 10.1111/geb.12911

Muir, A.P., Nunes, F.L.D, Dubois, S.F., & Pernet, F. (2016). Lipid remodelling in the reef-building honeycomb worm, *Sabellaria alveolata*, reflects acclimation and local adaptation to temperature. Scientific Reports, 6, 25669.

Navarro-Barranco, C., Gribben, P.E., Ledet J.J., & Poore, A.G.B. (2022). Habitat-complexity regulates the intensity of facilitation along an environmental stress gradient. Oikos, e08818. doi: 10.1111/oik.08818

National Oceanic and Atmospheric Administration. NOAA Solar Calculator. (2022, February 9). https://gml.noaa.gov/grad/solcalc/.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R. B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H.

(2020). vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Pansch, C., Scotti, M., Barboza, F.R., Al-Janabi, B., Brakel, J., Briski, E., Bucholz, B., Franz, M., Ito, M., Paiva, F., Saha, M., Sawall, Y., Weinberger, F., & Wahl, M. (2018). Heat waves and their significance for a temperate benthic community: A near-natural experimental approach. Global Change Biology, 24, 4357–4367. doi: 10.1111/gcb.14282

Pardal-Souza, A.L., Dias, G.M., Jenkins, S.R., Ciotti, Á. M., & Christofoletti, R.A. (2017). Shading impacts by coastal infrastructure on biological communities from subtropical rocky shores. Journal of Applied Ecology, 54, 826–835. doi: 10.1111/1365-2664.12811

Pedersen, T.L. (2020). patchwork: The Composer of Plots. R packages version 1.1.1. https://CRAN.R-project.org/package=patchwork

Peralta-Maraver, I. & Rezende, E.L. (2021). Heat tolerance in ectotherms scales predictably with body size. Nature Climate Change, 11, 58–63. doi: 10.1038/s41558-020-00938-y

Perkins, S.E., & Alexander, L.V. (2013). On the measurement of heat waves. Journal of Climate, 26, 4500–4517. doi: 10.1175/JCLI-D-12-00383.1

Perkins-Kirkpatrick, S.E., & Lewis, S.C. (2020). Increasing trends in regional heatwaves. Nature Communications, 11, 3357. doi: 10.1038/s41467-020-16970-7

Raymond, W.W., Barber, J.S., Dethier, M.N., Hayford, H.A., Harley, C.D.G., King, T.L., Blair, P., Speck, C.A., Tobin, E.D., Raymond, A.E.T., & McDonald, P.S. (2022). Assessment of the impacts of an unprecedented heatwave on intertidal shellfish of the Salish Sea. The Scientific Naturalist. doi: 10.1002/ecy.3798

Reid, H., & Harley, C. (2021). Low temperature exposure determines performance and thermal microhabitat use in an intertidal gastropod (*Littorina scutulata*) during the winter. Marine Ecology Progress Series, 660, 105–118. doi: 10.3354/meps13588

Reimer, A.A. (1976). Succession of invertebrates in vacant tests of *Tetracfita stalactifera panamensis*. Marine Biology, 13, 239-251.

Riemer, K., Anderson-Teixeira, K.J., Smith, F.A., Harris, D.J., & Ernest, S.K.M. (2018). Body size shifts influence effects of increasing temperatures on ectotherm metabolism. Global Ecology and Biogeography, 27, 958–967. doi: 10.1111/geb.12757

Robinson, J.P.W., Wilson, S.K., Jennings, S., Graham, N.A.J. (2019). Thermal stress induces persistently altered coral reef fish assemblages. Global Change Biology, 25: 2739–2750

Román, M., Román, S., Vázquez, E., Troncoso, J., & Olabarria, C. (2020). Heatwaves during low tide are critical for the physiological performance of intertidal macroalgae under global warming scenarios. Scientific Reports, 10, 21408. doi: 10.1038/s41598-020-78526-5

Scanes, E., Parker, L.M., O'Connor, W.A., Dove, M.C., & Ross, P.M. (2020). Heatwaves alter survival of the Sydney rock oyster, *Saccostrea glomerata*. Marine Pollution Bulletin, 158, 111389. doi: 10.1016/j.marpolbul.2020.111389

Scrosati, R.A. (2017). Community-level facilitation by macroalgal foundation species peaks at an intermediate level of environmental stress. Algae, 32, 41–46. doi: 10.4490/algae.2017.32.2.20

Seabra, R., Wethey, D.S., Santos, A.M., & Lima, F.P. (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

Sewbens, K.P. & Lewis, J.R. (1985). Rare events and population structure of the barnacle *Semibalanus cariosus* (Pallass, 1788). Journal of Experimental Marine Biology and Ecology, 87, 55–65.

Seifert, L.I., Weithoff, G., & Vos, M. (2015). Extreme heat changes post-heat wave community reassembly. Ecology and Evolution, 5, 2140–2148. doi: 10.1002/ece3.1490

Siegle, M.R., Taylor, E.B., & O'Connor, M.I. (2018). Prior heat accumulation reduces survival during subsequent experimental heat waves. Journal of Experimental Marine Biology and Ecology, 501, 109–117. doi: 10.1016/j.jembe.2018.01.012

Sorte, C.J.B., Fuller, A., & Bracken, M.E.S. (2010). Impacts of a simulated heat wave on composition of a marine community. Oikos, 119, 1909–1918. doi: 10.1111/j.1600-0706.2010.18663.x

Southward, A.J. (1991). Forty years of changes in species composition and population density of barnacles on a rocky shore near Plymouth. Journal of the Marine Biological Association of the United Kingdom, 71, 495–513.

Southward, A.J., Hawkins, S., & Burrows, M.T. (1995). Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. Journal of Thermal Biology, 20, 127–155.

Straub, S.C., Wernberg, T., Thomsen, M.S., Moore, P.J., Burrows, M.T., Harvey, B.P., & Smale, D.A. (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

Suchanek, T. (1992). Extreme biodiversity in the marine environment: Mussel bed communities of *Mytilus californianus*. The Northwest Environmental Journal, 8, 150–152.

Thompson, V., Kennedy-Asser, A.T., Vosper, E., Lo, Y.T.E., Huntingford, C., Andrews, O., Collins, M., Hegerl, G.C., & Mitchell, D. (2022). The 2021 western North America heat wave among the most extreme events ever recorded globally. Science Advances, 8, eabm6860. doi: 10.1126/sciaadv.abm6860.

Tituskin, J.R., Waddell, S.M., & Mabry, K.E. (2021). Species-specific responses to warming alter community composition. Ecological Entomology. doi: 10.1111/een.13112

Tomanek, L., & Helmuth, B. (2002). Physiological ecology of rocky intertidal organisms: A synergy of concepts. Integrative and Comparative Biology, 42, 771–775. doi: 10.1093/icb/42.4.771

Umanzor, S., Ladah, L., Calderon-Aguilera, L., & Zertuche-González, J. (2017). Intertidal macroalgae influence macroinvertebrate distribution across stress scenarios. Marine Ecology Progress Series, 584, 67–77. doi: 10.3354/meps12355

Uyà, M., Bulleri, F., Wright, J.T., & Gribben, P.E. (2020). Facilitation of an invader by a native habitat-former increases along interacting gradients of environmental stress. Ecology, 101, e02961. doi: 10.1002/ecy.2961

van der Ouderaa, I.B.C, Claassen, J.R., van de Koppel, J., Bishop, M.J. & Eriksson, B.K. (2021). Bioengineering promotes habitat heterogeneity and biodiversity on mussel reefs. Journal of Experimental Marine Biology and Ecology, 540, 151561. doi: 10.1016/j.jembe.2021.151561

Vasseur, D.A., DeLong, J.P., Gilbert, B., Greig, H.S., Harley, C.D.G., McCann, K.S., Savage, V., Tunney, T.D., & O'Connor, M.I. (2014). Increased temperature variation poses a greater risk to species than climate warming. Proceedings of the Royal Society B: Biological Sciences, 281, 20132612. doi: 10.1098/rspb.2013.2612

Venables, W. N. & Ripley, B. D. (2002). Modern Applied Statistics with S. Fourth Edition. Springer, New York.

Vermeij, G. J. (1978). Biogeography and Adaptation: Patterns of Marine Life. Harvard University Press.

Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett, S., & Rousseaux, C.S. (2013). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nature Climate Change, 3, 78–82. doi: 10.1038/nclimate1627

Wethey, D.S. (1984). Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus*: A field experiment. Biological Bulletin, 167, 176–185. doi: 10.2307/1541346

Wethey, D.S., Woodin, S.A, Hilbish, T.J., Jones, S.J., Lima, F.P., & Brannock, P.M. (1991). Response of intertidal populations to climate: Effects of extreme events versus long term change. Journal of Experimental Marine Biology and Ecology, 400, 132–144. doi: 10.1016/j.jembe.2011.02.008

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takhashi, K., … & Yutani,

H. (2019). Welcome to the tidyverse. Journal of Open Source Software, 4, 1686, doi: 10.21105/joss.01686

Widdowson, T. B. (1965). A survey of the distribution of intertidal algae along a coast transitional in respect to salinity and tidal factors. Journal of the Fisheries Research Board of Canada, 22, 1425–1454.

WWW Tide and Current Predictor. (27 October 2021). http://tbone.biol.sc.edu/tide/

Figure 1. Map of sites surveyed along the coast of British Columbia, Canada. Symbols associated with each site indicate which data were collected at that site (A = substratum angle/orientation, C = community, M = mortality), and symbol color is used to visually distinguish between sites. Note that not all data were collected at all sites. **(a)** Inset map of sites along the Strait of Juan de Fuca. **(b)** Inset map of sites on Calvert Island. **(c)** Inset map of sites on the south coast of Vancouver Island and in the Strait of Georgia region; note that site SA is the location at which the shading experiment was conducted. See Table S1 for site details.

Figure 2. (a) Taxonomic richness of invertebrate assemblages removed from 15×15 cm samples of *S. cariosus* beds collected at sites along the west coast of British Columbia (see Table S1 for site codes and locations; n=5 for all sites except WBS, where n=8). Note that collection sites are arranged along the x-axis from the outer coast of BC (WBS; most exposed) to the Strait of Georgia (TK; least exposed) going from left to right. **(b)** Shannon diversity of invertebrates from the same samples. **(c)** Mean abundance of invertebrates counted within the same samples, with colours corresponding to coarse taxonomic groupings. **(d)** Visual example of community removed from one *S. cariosus* sample.

Figure 3. The effect of the angle of solar incidence (ASI; direct sun = 0º) on the proportional mortality of *S. cariosus* within 12.7×12.7 cm quadrats (N =152). Thin coloured lines represent site-specific relationships, while the central black trendline represents values predicted by the generalized linear model when the site-level random effect is removed. The shaded ribbon about the best-fit line represents standard error.

Figure 4. **(a)** Mean daily maximum substratum temperature over time for each treatment recorded by iButton temperature loggers. The grey box indicates the period of the heat dome (25–29 June 2021). **(b)** Hourly temperature during the heat dome for each treatment. **(c)** The effect of shading treatment on the mortality of adult *S. cariosus* in intact barnacle beds as recorded on 21 August 2021 (n=12 for UI, n=10 for SI). **(d)** The effect of shading treatment on the recruitment of barnacles (*S. cariosus*, *B. glandula*, and *C. dalli*) to barnacle removal plots when recruits were most abundant (8 July 2021; n=12). **(e)** Differences in the overall species richness of communities for each treatment group including both invertebrate and algal taxa at the end of the experiment (21 August 2021; n=12). **(f)** Differences in the Shannon diversity of invertebrate taxa between treatment groups at the end of the experiment (21 August 2021; n=12). For treatment codes, U=unshaded plot, S=shaded plot, I=intact barnacle bed, R=removed barnacle bed.

Figure 5. Two-dimensional capscale plot showing differences in associated community composition between shaded and unshaded *S. cariosus* barnacle beds at Sahsima, Victoria, British Columbia at the end of summer shading experiment (n=8). We collected all samples on 21 August 2021. Overlaid photos demonstrate stark visual differences in survival between an unshaded (left) and shaded barnacle bed (right).