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The effect of single versus successive warm summers on an intertidal community

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ABSTRACT

To accurately predict how organisms and ecological communities will respond to future conditions caused by climate change, we must consider the temporal dynamics of environmental stressors, including the effects of repeated exposures to stress. We performed a two-year passive thermal manipulation in coastal British Columbia, Canada to determine how intertidal communities responded to single and successive warm summers. Warm temperatures had both negative contemporaneous effects within years and persistent negative effects across years. Warming reduced organism densities, altered population dynamics, and affected community structure and diversity, patterns which were likely mediated by differences in foundation species (barnacle) abundance between treatments. Unexpectedly, the effects of thermal stress in the second year were rarely dependent on whether temperatures were warm during the first year. Our study suggests that, while this intertidal community can recover from single warm summers, recurring thermal stress has additive negative effects, resulting in a more depauperate, less diverse community over time, particularly if foundation species are negatively affected.

INTRODUCTION

Just as global mean surface temperatures are expected to increase over the coming decades (IPCC 2023), so, too, are the frequency, severity, and duration of extreme temperature events such as heatwaves (Oliver et al. 2018, Perkins-Kirkpatrick and Lewis 2020). Extreme temperatures have biological consequences. Heatwaves increase the probability of environmental temperatures surpassing the thermal optima and maxima of organisms (Vasseur et al. 2014). Thus, heatwaves can impair fitness (Siegle et al. 2022) and, ultimately, cause mortality for thermally sensitive species (Harley 2008, Hesketh and Harley 2023), with ramifications for populations, communities, and ecosystems (Harris et al. 2018; Montie and Thomsen 2023).

The effects of heatwaves on organisms are increasingly well-studied; however, the consequences of repeated exposures to thermal stress have received less attention. Thermal stress events that are prolonged or occur in rapid succession can exert stronger negative effects on organism survival and fitness (Ma et al. 2018; Siegle et al. 2022). However, responses vary among species — for species with acclimatory capacity, prior exposure to thermal stress may engender resilience to subsequent heatwaves, while for those without, the negative effects of repeated heatwaves may instead accumulate (Pansch et al. 2018). At the community level, for which controlled warming manipulations can be experimentally challenging and studies are correspondingly limited, repeated heatwaves have resulted in communities that are more depauperate (Dal Bello et al. 2019) and homogenous (Hammill and Dart 2022). However, community-level resilience to thermal stress may increase with repeated exposures as thermally sensitive species are eliminated and thermally tolerant species survive (Hughes et al. 2019). Manipulating the timing of thermal stress events is an important additional step towards understanding their ecological effects.

While environmental extremes affect organisms, the reverse is also true. Foundation species, abundant species that physically structure ecological communities, often create environmentally benign microhabitats for associated organisms (e.g., through moisture retention and shading; Hesketh et al. 2021, Lee et al. 2021, Jurgens et al. 2022, Gutiérrez et al. 2023). The loss of foundation species can thus profoundly impact communities by disrupting interspecific facilitative relationships (Hesketh and Harley 2023; Montie and Thomsen 2023). The importance of such facultative facilitations for bolstering organism survival and performance often increases with environmental stress, though there may be an upper limit beyond which stress cannot be effectively buffered (Bulleri et al. 2016).

Intertidal organisms are regularly exposed to stressors including hydrodynamic forces, desiccation, and seasonally hot and cold air temperatures. In this highly variable, physiologically taxing environment, foundation species may play an outsized role in attenuating stress and supporting biodiversity. While many intertidal species act as foundation species (e.g., bed-forming bivalves, tunicates, macroalgae, and vascular plants), here, we focus on acorn barnacles. Acorn barnacles are cosmopolitan organisms that facilitate a relatively diverse intertidal community (Harley 2006, Hesketh et al. 2021). Barnacles can retain moisture (Vermeij 1978, Harley and O'Riley 2011), thereby reducing desiccation stress for closely associated species when present at high densities. However, thermal stress can increase barnacle mortality and reduce barnacle abundance (Little et al. 2021; Hesketh and Harley 2023). While empty barnacle tests provide humid, thermally benign microhabitats for other species (Barnes 2000), such habitats are ultimately ephemeral. Barnacle mortality events and recruitment failures, by reducing available habitat, significantly impact the abundance, identity, and diversity of associated organisms (Kordas et al. 2015, Hesketh and Harley 2023).

Here, we tested the effect of single and successive warm summers on high intertidal barnacle bed communities (Fig. 1a) through a two-year passive thermal manipulation using black (warm) and white (cool) settlement tiles (Fig. 1b; Kordas et al. 2015). To manipulate the temporal dimension of thermal stress, the treatments (color) of half of the tiles were swapped after one year. We hypothesized that: H1) because elevated temperatures can reduce organism performance and increase mortality, communities within the warm treatments would have lower invertebrate abundance, algal cover, and alpha diversity than those within cool treatments; H2) warming during the first year, because of its negative contemporaneous effects on foundation species cover, would exert persistent indirect negative effects during the second year; and H3) the effects of warming in the second year of study would be stronger in communities that were previously exposed to warming due to pre-existing reductions in foundation species cover, and thus reduced availability of thermal refugia (i.e., a positive interaction of warming across years; Fig 1b).

MATERIALS AND METHODS

Site description

This study was completed near ŦESNO¸EN̲ (Beaver Point), a site that lies within the traditional, unceded territory of the W̱SÁNEĆ peoples in what is now known as Ruckle Provincial Park on Salt Spring Island, British Columbia, Canada (48.77324, -123.36637). The substratum at this site is dominated by a southeast-facing semi-exposed sandstone bench, and tides are mixed semi-diurnal. Relative to the rest of British Columbia's Southern Gulf Islands, this area is exposed to cooler, more saline water and larger waves due to its proximity to Haro Strait and the Strait of Juan de Fuca. However, like these and the neighboring San Juan Islands (USA), the intertidal zone at this site is considered a thermal "hot spot" due to its summertime midday low tides coupled with relatively clear, sunny weather (Helmuth et al. 2006).

Here, the upper intertidal zone is dominated by the acorn barnacles *Balanus glandula* and *Chthamalus dalli*, with sporadic beds of the perennial brown alga *Fucus distichus*. Filamentous ephemeral algae (predominantly the green algae *Ulothrix* sp. and *Urospora* sp.) occur as early colonizers of bare space and foliose ephemeral algae (predominantly *Ulva* spp., *Pyropia* sp., and *Petalonia fascia*) occur in winter, often attached to underlying barnacles. Dominant herbivores include the littorine snails *Littorina scutulata* and *Littorina sitkana* and the limpets *Lottia* *paradigitalis* and *Lottia digitalis*, which tend to migrate down shore with the onset of daytime low tides in spring and return to higher tidal elevations in August (Kordas et al. 2015).

Study design

Individual settlement tiles were built based on previous methods (Kordas et al., 2015; see Appendix S1). In brief, each 15x15 cm tile consisted of a central epoxy settlement surface (6.9x6.9 cm, < 5 mm high Sea Goin' Poxy Putty; Permalite Plastics, USA) bordered by either white (cool treatment) or black (warm treatment) high-density polyethylene (6.4 mm thick; Redwood Plastics, Canada). Temperature differences were driven by the differential absorption of incoming solar radiation during daytime summer low tides. These settlement tiles were affixed to a bottom tile unit composed of thicker white high-density polyethylene (9.5 mm thick; Redwood Plastics, Canada) that was used to anchor the assembly to the underlying bedrock.

This study followed a randomized block design, with six blocks consisting of eight black and eight white tiles (n = 48). Tiles were initially installed on 12 April 2019. Some were relocated in June 2019 to avoid disturbance from wave-cast logs, resulting in a final shore level of 2.34 ± 0.07 m (mean ± SE) above Canadian chart datum. In May 2019, we enclosed tiles with copper "fences" to manipulate grazer diversity and densities (see Appendix S1). We ceased manipulations in August 2019 because wave action, moreso than we, controlled littorine snail densities and high summer temperatures caused mortality for limpets, which were prevented from accessing thermal refugia by copper fences. On 3 April 2020, we randomly selected and switched the colour of half of each treatment within each block using white and black heavy-duty tape (Gorilla Tape; Gorilla Glue, Inc., USA; adhesion enhanced with LePage Ultra Gel super glue). This change created four thermal history treatments during the second year (cool summer–cool summer, CC; cool–warm, CW; warm–cool, WC; and warm–warm, WW; n = 24). Sample sizes varied over time due to tile damage and dislodgement (Appendix S1: Fig. S3).

Temperature measurements

For small ectotherms with a large area of attachment to the substratum (e.g., barnacles), substratum temperature is a reasonably good proxy for body temperature (Kordas et al. 2015). Thus, the substratum temperature of both settlement tiles and adjacent bedrock were collected using pre-programmed iButton temperature loggers (model DS1921G-F5# Thermochron, Dallas Semiconductor, USA). To record tile temperature, loggers were sealed in nitrile pouches and sandwiched between the two plates of experimental tile units. To record bedrock temperature, loggers were wrapped in Parafilm and affixed to shore with a 2–3 mm layer of A–788 Splash Zone epoxy (Pettit Paints, USA) separating the logger from both the underlying shore and surrounding air. The number of loggers recording within each treatment varied through time due to changes in the number of treatment groups between years and instrument failure. Temperatures were recorded hourly except over the second winter of the study, when temperatures were instead recorded every two hours.

Community surveys

We characterized organism abundance and community diversity through regular visual surveys of tiles and destructive sampling at the end of the study. Visual surveys occurred approximately monthly during summer and every two months during winter from 8 May 2019 to 24 February 2021. During surveys, each invertebrate species was counted and the percent cover of each algal species was recorded. Organisms were identified to species except for amphipods and isopods, which were identified to order, and diatom mats, which were lumped into one taxon. Sessile species were only recorded within the central 6.4 × 6.4 cm area of the epoxy settlement surface using a wire mesh quadrat (mesh size = 6.4 mm × 6.4 mm) to avoid edge effects. Any sessile species growing on the colored tile borders were removed during surveys. Motile invertebrates were counted on the entire tile surface, including on colored tile borders where their influence on the experimental community could not be ruled out. We destructively sampled half of the tiles within each treatment and block on 14 September 2020 (permanently removing these from the study) and sampled remaining tiles on 24 February 2021, scraping all biota from the settlement surface into containers of 70% ethanol (v/v in water). Epifauna were identified and counted under a dissecting microscope. Intertidal organisms were collected under Fisheries and Oceans Canada scientific collection permits (XR 61 2019 and XR 196 2020).

Statistical analyses

We used linear mixed effects models, constructed with *glmmTMB* (Brooks et al. 2017), to test for differences in mean daily maximum (MDM) temperature between treatments. Because of frequent logger failures, temperature records for individual tiles were often incomplete, potentially biasing data. Thus, we imputed missing hourly temperatures with the *mice* package (van Buuren and Groothuis-Oudshoorn 2011) for all bedrock temperature records and the two most complete tile records per year two treatment in each block (i.e, for bedrock, N=6 and for tiles N=12 in year two, N=24 in year one). Data from each year were imputed separately using five iterations with the classification and regression trees method, with hourly ERA5 satellite-derived 2m surface temperature (Hersbach et al. 2023) used as an auxiliary variable. The resulting set of imputations was averaged. Because differences were driven by solar irradiance, temperature data were retained only if they were collected during daytime summer low tides (1 May – 31 August; see Appendix S1 for details), when treatment differences were likely strongest. Calculated MDM temperatures were modeled as a function of treatment. Random intercept effects of individual tile and date were included, the latter with an AR(1) process to account for autocorrelation.

We tested how temperature treatments affected barnacle recruitment and abundance, grazer abundance, and alpha diversity using generalized linear models with *glmmTMB* (Brooks et al. 2017). Differences in barnacle recruitment between treatments were evaluated during peak recruitment (May or June), while differences in adult abundance were evaluated in winter when spring recruits had reached maturity. Grazer abundance and community diversity were evaluated at the end of summer to characterize the immediate effects of heat stress and again in late winter to allow an opportunity for community recovery. During the first year, responses were modeled as a function of the treatment (cool or warm), while during the second year, they were modeled as a function of the factorial combination of year one treatment and year two treatment. Experimental block was included as a random effect. A fixed effect for original grazer treatments (see details in Appendix S1) was initially included in models of data collected from 8 May 2019 until September 2020, one year after manipulations ceased. If this term was significant, data were not analyzed (true for algal Shannon diversity and cover in year one); if this term was not significant, then it was dropped from the model. Grazer abundance data collected prior to September 2020 were not modeled due to initial grazer community manipulations. Model assumptions were checked using the *DHARMa* package (Hartig 2022). Species richness was log-transformed in for the post-summer timepoint in year two to ensure the model met assumptions. *P*-values were calculated using the Anova function within the *car* package (Fox and Weisberg

2019) with a significance threshold of $P = 0.05$. We also chose to use multiple comparisons tests (Tukey-Kramer *post hoc* tests) to detect differences between treatment combinations because we expected the consistently warm treatment to have substantially different structure than other treatments (Hypothesis 3). For these tests, we used the *emmeans* package (Lenth 2022).

Given the complex and, at times, opposite effects of temperature on algal cover over time, we used generalized additive modeling with the *mgcv* package (Wood 2011) to analyze how temperature affected algal cover dynamics during each year. Within these autoregressive AR(1) models, we included linear terms — for year one, treatment alone, and for year two, an factorial combination of treatments in year one and year two — smooth terms of time (days since the experiment start) for each treatment, and a random effect of block. Pairwise differences in algal cover over time between control treatments (C or CC) and other treatments were calculated and visualized using the methods of Rose et al. (2012). Early grazer manipulations exerted a significant effect on algal cover during the first year, and thus survey data collected during the first year were excluded from analysis.

Treatment-driven differences in epifaunal community structure and beta diversity were modeled with the *vegan* package (Oksanen et al. 2020) for communities immediately following summer heat stress and after winter recovery in the second year of study. Data were ordinated using distance-based redundancy analysis with Bray-Curtis distances. Community structure was modeled as a function of the interaction of treatment in year one and year two using PERMANOVA analyses with 9999 permutations constrained within experimental blocks. Multiple pairwise comparisons were made with *multiconstrained* in the *BiodiversityR* package (Kindt and Coe 2005). Beta diversity was modeled as a function of treatment using PERMDISP analyses with bias adjustment for small sample sizes.

To reflect our underlying analyses, results are subsequently reported by response variable. We relate patterns in each biological response to our initial hypotheses (H1–H3) in Appendix S1: Table S3 and report all the statistical outputs of our models in Appendix S2.

RESULTS

Differences in substratum temperature

Substratum temperatures differed significantly among the cool treatment (white tiles), warm treatment (black tiles), and adjacent bedrock during daytime low tides from May through August. Mean daily maximum (MDM) summer temperatures were consistently ~2 ºC higher in warm versus cool treatments (Appendix S1: Table S2), with a grand mean of 29.2 ± 7.0 ºC across all warm treatments and 27.1 ± 6.4 ºC across all cool treatments. Meanwhile, bedrock was 28.5 ± 7.0 ºC during the first summer and 28.1 ± 6.4 ºC during the second summer. During the first summer, both the warm treatment and bedrock had significantly higher MDM temperatures than the cool treatment (Figure 2; ANOVA: $\chi^2_2 = 40.53$, $P < 0.001$; Appendix S2: Tables S1–2). During the second summer, warm treatments had significantly higher MDM temperatures than cool treatments, with bedrock temperatures intermediate and statistically similar to all other treatments (ANOVA: $\chi^2_4 = 52.34$, $P < 0.001$; Appendix S2: Tables S3–4). During the second year, taped tile surfaces effectively mimicked the treatment effect of bare tile surfaces (i.e., WC and CW had analogous MDM temperatures to CC and WW, respectively; Appendix S2: Table S7). Mean substratum temperatures displayed analogous patterns to MDM temperatures (Appendix S1: Table S3; Fig. S5; Appendix S2: Tables S5–8).

Effects on barnacle recruitment and abundance

Warm summer temperatures tended to reduce the abundance of barnacle recruits. When peak recruitment was observed during the first year (May and June, respectively, for *B. glandula* and *C. dalli*), temperature treatment did not significantly affect *B. glandula* recruitment (Fig. 3a; Appendix S2: Table S9), but *C. dalli* recruitment was lower within the warm treatment (Fig. 3b; Type II ANOVA, $\chi^2_1 = 4.13$, $P = 0.0422$; Appendix S2: Table S10). Warming had both contemporaneous and carry-over effects on barnacle recruitment during the peak recruitment window of the second year (June for both species). Fewer *Balanus glandula* were present in warm treatments, whether warming occurred during the second summer (Type III ANOVA, treatment_{y2}; $\chi^2_1=38.34$, $P < 0.001$; Appendix S2: Tables S11–12) or during the first summer (treatment_{y1}; $\chi^2_1=6.07$, $P = 0.0138$). The recruitment of *C. dalli* in year two was similarly negatively affected by warming in both years (Fig. 3b; Type III ANOVA; treatment_{y2}: $\chi^2_1=19.16$, $P < 0.001$; treatment_{y1}: $\chi^2_1=5.56$, $P = 0.0184$; Appendix S2: Tables S13–14).

Warming reduced the abundance of adult *B. glandula*, but not adult *C. dalli*. At the end of the first winter, there were substantially fewer adult *B. glandula* in the warm treatment (Fig. 3c; Type II ANOVA; $\chi^2_1=106.20$, $P < 0.001$; Appendix S2: Table S15). At the end of the study, *B. glandula* abundance appeared to be lower where warming was applied in both summers, but this trend lacked significant statistical support (Type III ANOVA; $P \sim 0.1$ for treatment_{y1} and treatment_{y2}; Appendix S2: Table S16). However, *post hoc* testing suggested that *B. glandula* was more abundant in the consistently cool treatment compared to the consistently warm treatment (Tukey-Kramer; z ratio = 3.08, $P = 0.0111$; Appendix S2: Table S17). During summer in both years, the mortality of *B. glandula* was higher and surviving barnacles were smaller within warm treatments (Appendix S1: Fig. S7–8; Appendix S2: Tables S18–21). The abundance of adult *C. dalli* was similar between treatments in both years (Fig, 3d; Appendix S2: Tables S22–24).

Effects on grazer abundance

During the second year of study, grazer abundance was negatively correlated with warming. Warming had a contemporaneous effect on limpet abundance (Fig. 4a), both immediately following summer (September 2020; Type III ANOVA; $\chi^2_1 = 11.07$, $P < 0.001$; Appendix S2: Tables S25–26) and at the end of winter (February 2021; Type III ANOVA; $\chi^2_1 = 3.87$, $P = 0.0491$; Appendix S2: Tables S26–27). Post-summer littorine snail abundance was lower in warm treatments, whether warming was applied during the first or second summer (Fig. 4b; Type III ANOVA; treatment_{y1}: $\chi^2_1 = 17.56$, $P < 0.001$; treatment_{y2}: $\chi^2_1 = 13.38$, $P < 0.001$; Appendix S2: Tables S28–29). Similar trends in littorine snail abundance were observed at the end of winter, though with reduced statistical support (Type III ANOVA; treatment_{y1}: $\chi^2_1 = 3.29$, $P = 0.0698$; treatment_{y2}: $\chi^2_1 = 3.87$, $P = 0.0491$; Appendix S2: Tables S30–31).

Effects on algal cover

Algal cover and the timing of algal blooms differed between treatments, particularly in the first year of study (Fig. 5a-b). Algal cover reached a similar maximum between treatments, driven by a bloom of the green ephemeral alga *Ulothrix* sp. near the end of the first summer. However, the temporal dynamics of algal cover differed between treatments; cover peaked earlier and declined more rapidly within the cool treatment relative to the warm treatment. After ineffectual grazer manipulations were abandoned during the first year, algal cover in the warm treatment remained significantly higher than in the cool treatment until winter (Fig. 5b; *gamm*; t = 3.30, $P = 0.00109$; Appendix S2: Table S32). During the second year, algal cover remained relatively low, but was higher in treatments that alternated thermal conditions relative to those that were consistently cool or warm (*gamm*; t = -2.57, $P = 0.0104$; Appendix S2: Table S33).

Effects on diversity

Warming tended to reduce alpha diversity and alter community structure, particularly in communities that experienced successive warm summers. During the first year, species richness was lower in the warm treatment, whether richness was assessed immediately after summer (Fig. 6a; Type II ANOVA; $\chi^2_1=16.33$, $P < 0.001$; Appendix S2: Table S34) or at the end of winter (Type II ANOVA; $\chi^2_1=74.85$, $P < 0.001$; Appendix S2: Table S35). During the second year, post-summer species richness was lower in treatments that experienced contemporaneous warming (Fig. 6b; Type III ANOVA; $\chi^2_1=4.73$, $P = 0.0297$; Appendix S2: Tables S36–37), but were unaffected by warming applied in the first year. After winter recovery, no overall effect of temperature treatment in either summer was discernible (Appendix S2: Table S38), but *post hoc* pairwise comparisons suggested that the treatment that was successively warmed had lower diversity than treatments that were cool during the second summer (Appendix S2: Table S39; Tukey-Kramer; CC–WW: z ratio = 3.87, $P < 0.0001$; WC–WW: z ratio = 3.27, $P = 0.00590$). Warming also exerted a negative effect on the Shannon diversity of the invertebrate community; during winter of the first year, diversity was significantly lower within the warm treatment, and during the second year, diversity was lower in treatments where warming was applied during the first year (Appendix S1: Fig. S11a–b, Appendix S2: Tables S40–45). The Shannon diversity of the algal community, meanwhile, was reduced by warm temperatures during the first year, but not affected during the second year (Appendix S1: Fig. S11c, Appendix S2: Tables S46–48).

Epifaunal communities characterized on destructively sampled tiles demonstrated that community structure, but not beta diversity, differed between treatments. At the end of the second summer (September 2020; Fig. 6c), there were no significant differences in community structure between treatments based on PERMANOVA (Appendix S2: Table S49), though *post hoc* pairwise comparisons indicated the CC and WW treatments differed in composition (Appendix S2: Table S50; *multiconstrained*; $F_1 = 2.68$, $P = 0.018$). At the end of the experiment (February 2021; Fig. 6d), however, warm temperatures in year one and year two interacted to drive differences in community structure (PERMANOVA; $F_{1,37} = 2.22$, $P = 0.0125$; Appendix S2: Table S51). *Post hoc* comparisons showed that this was primarily driven by differences between the structure of the consistently cool treatment and all others (Appendix S2: Table S52). Beta diversity was similar among treatments (Appendix S2: Tables S53–54). The alpha diversity of these epifaunal communities was generally lowest in the consistently warm treatment, particularly compared with samples where temperatures were cool during the second summer (Appendix S1: Figure S12; Appendix S2: Tables S55–62).

DISCUSSION

In this study, we passively manipulated the substratum temperature of intertidal settlement tiles over two consecutive summers to determine the effects of present and past warming and whether prior thermal stress influences the impact of subsequent thermal stress. We expected that warming would have contemporaneous direct negative effects on organism abundance and diversity (H1) and persistent indirect negative effects mediated by lower foundation species cover (H2). We expected that warming during the second year would have greater negative effects where conditions were previously warm, since foundation species cover and thus thermal refugia would be constrained, thereby increasing stress for associated biota (H3). As anticipated, we found that warming often had both contemporaneous and persistent negative effects on organism abundance and community alpha diversity, though its effects on algae were more complex. Contrary to our prediction, the magnitude of the effects of warming in the second summer were usually independent of whether warming had been previously applied.

The methodology employed in this study was effective in manipulating substratum temperatures. In both years, the surfaces of white tiles were cooler than those of black tiles, as in previous studies (Kordas et al. 2015, 2017). Interestingly, bedrock temperatures were more analogous to those of black tiles during the first year. This unexpected pattern could be an artefact of shading from copper fences that encircled tiles for most of the first summer, but not the second, which may have artificially cooled tile surfaces relative to adjacent bedrock. The intermediate temperatures of bedrock recorded in the second year of study may reflect its grey color, which absorbs more solar insolation than a purely white surface, but reflects more solar insolation than a purely black surface. Regardless of trends in bedrock temperature, the temperatures of white (cool) and black (warm) tiles and the degree of difference between them were consistent across years, which drove corresponding biological differences.

The recruitment and abundance of acorn barnacle foundation species (*B. glandula* and *C. dalli*) was typically lower within warm treatments, consistent with past studies (Kordas et al. 2015, 2017, Kordas and Harley 2016). For *B. glandula*, the dominant barnacle in this system, the highest recorded LT_{50} in air is 43 ºC (Hamilton and Gosselin 2020), though mortality has been observed at 40 ºC (Ober et al. 2019). Substratum temperatures within all treatments exceeded these lethal thresholds during daytime summer low tides, with warm treatments reaching 45 ºC during both years. While barnacles tend to remain slightly cooler than surrounding bedrock (Harley and Lopez 2003), the higher mortality we observed for *B. glandula* within warm treatments suggest that barnacle body temperatures, particularly on black tiles, exceeded critical thermal limits. Even exposure to sublethal temperatures can incur metabolic costs; high temperatures can impair *B. glandula* respiration for many hours after exposure (Ober et al. 2019), and sustained warm temperatures can slow barnacle growth (Kordas and Harley 2016). Here, *B. glandula* tended to be smaller within warm treatments, indicating that surviving barnacles experienced sublethal thermal stress that impaired growth. The tendency of barnacles to settle gregariously may magnify direct negative effects on abundance and recruitment if warming is sustained. Barnacles preferentially recruit to areas containing conspecifics, a strategy that increases the likelihood of successful sexual reproduction via internal fertilization (Wu 1981). Thus, recruitment to previously warm tiles during the second year may have been lower because these tiles hosted fewer adult barnacles. The other acorn barnacle present, *C. dalli*, was not prevalent during the first year, possibly due to interannual variation in recruitment dynamics common in barnacles (Scrosati and Ellrich 2016). Recruitment in the second year was lower within warm treatments, but adult abundance was unaffected by treatment, possibly because adult *C. dalli* are more robust to thermal stress than *B. glandula*, with an LT_{50} near 44.5 ºC (Hamilton and Gosselin 2020). Grazer manipulations during the first summer may have reduced barnacle recruitment and hampered the detection of a treatment effect, since limpets, which were purposefully included or excluded from both white and black tiles, are known to remove barnacle recruits during grazing (Dayton 1971).

During the second year, reduced grazer abundance in the warm treatments may have been due to the direct effects of temperature and/or indirect effects mediated by differences in barnacle abundance. One common limpet in this system, *Lottia digitalis*, has an upper thermal limit of 38 ºC in air (Bjelde and Todgham 2013). High intertidal littorine snails have a slightly greater tolerance to elevated temperatures (41.01 ºC for *L. sitkana* and 41.47 ºC for *L. scutulata* during five-hour emersions; Stickle et al. 2017). While these dominant grazers are thermally robust, recorded summer substratum temperatures frequently exceeded these thresholds for short periods. Temperatures likely regularly fluctuated above grazer thermal optima (e.g., 30 ºC for *L. digitalis*; Bjelde and Todgham 2013), which could have suppressed grazer activity, and thus foraging effectiveness (Rickards and Boulding 2015). Motile organisms can behaviourally thermoregulate by moving to avoid thermal stress. Grazers were not commonly observed on tiles during the summer, though surveys occurred exclusively at low tide, when some grazers avoid feeding (Little 1989), and we may have thus underestimated abundance. However, these temporal dynamics suggest that, while warm temperatures may have directly reduced grazer abundance, indirect effects are more likely. Limpets and littorine snails were generally more abundant within cool treatments where barnacle cover was higher, a pattern consistent with other studies (Silva et al. 2015, Hesketh et al. 2021). Barnacles can reduce desiccation stress for associated species by creating moist, humid microhabitats during low tides (Vermeij 1978; Harley and O'Riley 2011); thus, the abundant, larger barnacles present on cool tiles may have generated a higher density of favorable microhabitats, begetting a higher abundance of grazers.

Barnacles, in addition to providing microhabitats, may have influenced grazer abundance through their effects on algal food supply. The green filamentous *Ulothrix* sp. initially dominated bare tiles, but eventually declined and was replaced by other foliose algal species — usually growing on barnacle tests — a pattern observed in past studies (Kordas et al. 2017). While maximum algal cover was similar between temperature treatments during the first year, its temporal dynamics differed; algal cover peaked later and declined more slowly within the warm treatment. High temperatures can have highly variable interspecific effects on algae (Kordas et al., 2017). *Ulothrix* sp. may have thrived under warm summer conditions due to higher growth rates, because grazer activity was suppressed by high temperatures, or because barnacles, which can compete with algae for space or harbor populations of voracious grazers (Hesketh et al. 2021), were less abundant and smaller. On adjacent bedrock, *Ulothrix* sp. was most commonly observed in bare, log-damaged patches within barnacle beds, supporting an indirect negative effect of barnacles on this species (as has been documented with the ephemeral green alga *Urospora* spp.; Harley 2006). Meanwhile, other algae (here, *Pyropia* sp. and *Ulva* sp.) may preferentially attach to rugose barnacle tests, and barnacles can provide refuge from desiccation and grazing (particularly by limpets) for algal spores and germlings (Farrell 1991; Geller 1991). Thus, algal cover may have been highest in the warm-cool and cool–warm treatments during the second year because shifting thermal conditions created a heterogenous mixture of bare space and sparse barnacles, allowing for the growth of both desiccation-tolerant, barnacle-phobic and desiccation-intolerant, barnacle-philic algae.

Thermal stress, by shaping barnacle, grazer, and algal populations, had higher-level impacts on diversity and community structure. Alpha diversity generally increased over the course of succession but remained lower in warm treatments, as has been found previously (Kordas et al. 2015, Kordas et al. 2017). Barnacle recruits, followed by opportunistic ephemeral algae, appeared shortly after tiles were installed, consistent with studies involving intertidal disturbance and succession in the northeast Pacific (Farrell 1991, Geller 1991). Because barnacles act as both facilitators (Farrell 1991) and food sources (Harley and O'Riley 2011) within the high intertidal zone, their presence allowed grazers (e.g., amphipods, limpets), secondary successional species (e.g., perennial algae), and predators (e.g., ribbon worms) to enter the nascent community. Of all treatments, the consistently cool and consistently warm treatments were most different in their composition, indicating that persistent thermal stress shapes not only the diversity of, but also the identity of, species within communities. Thus, the higher alpha diversity and differing community structure of cool compared to warm treatments may have been driven by the facilitatory ability of larger, more abundant barnacles, by more and/or different species surviving under thermally benign versus thermally taxing conditions, or — more likely — by a mixture of these two mechanisms. Disentangling these indirect and direct effects is challenging given the experimental design employed.

Because foundation species (barnacle) cover was lower within the warm treatment compared to the cool treatment after the first year, we anticipated that the effects of warm temperatures would be magnified during the second year. However, the negative effect of warming in the second summer was independent of warming in the first year. While intertidal foundation species can improve the survival, growth, and diversity of associated species in the face of thermal stress (Jurgens et al. 2022; Hesketh and Harley 2023), the size and density of foundation species can affect their facilitative ability (Irving and Bertness 2009). Here, though *B. glandula* had generally surpassed the size threshold for sexual maturity (~5 mm; Hines 1976), they may still have been too small or sparse to effectively buffer thermal and desiccation stress (Rickards and Boulding 2015) at the start of the second summer.

While intertidal systems are resilient up to a point, repeated atmospheric warming threatens to disrupt even these historically stalwart communities (Menge et al. 2022). Our results suggest that even for high-turnover barnacle bed communities (Farrell 1991), thermal stress exerts lasting effects on community structure by reducing barnacle density. Increasing mean temperatures and intensifying heatwaves may cause substantial mortality (Hesketh and Harley 2023) and accelerate shifts in ecological communities (Harris et al. 2018). Climate change also encompasses multiple stressors beyond temperature that may co-occur and interact with warming

(MacLennan and Vinebrooke 2021). To understand the full risk of climate change to ecological communities, we must embrace complexity by integrating stochasticity, considering the temporal dimensions of stress, and seeking to emulate natural processes within our experimental designs.

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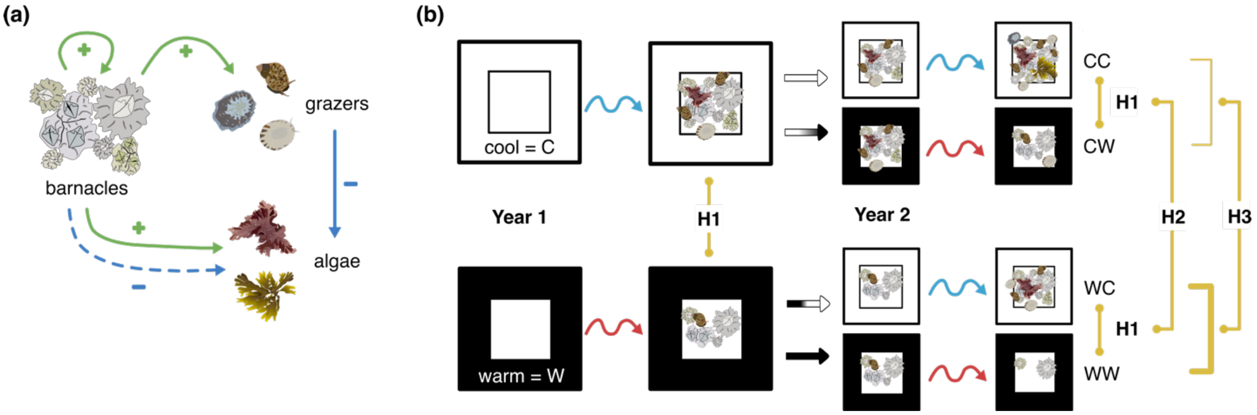

(a)
barnacles
grazers
algae
+
+
+
−
−
(b)
cool = C
warm = W
Year 1
Year 2
H1
H1
H1
H2
H3
CC
CW
WC
WW

Figure 1

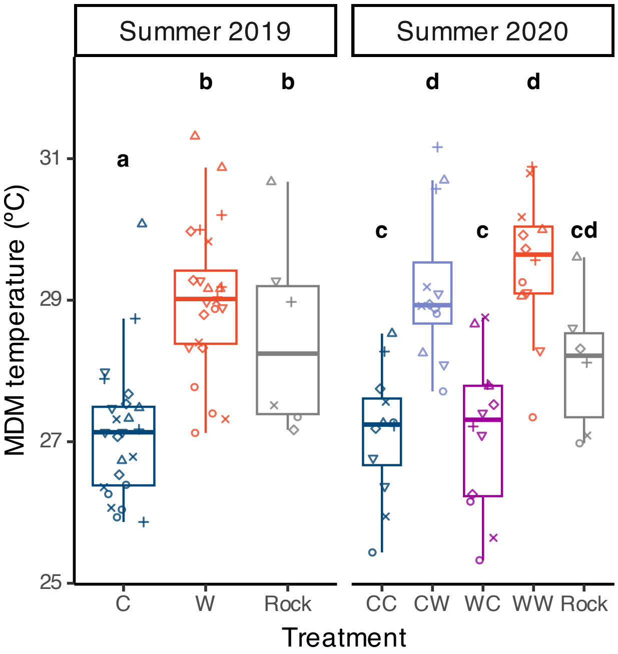

Summer 2019
Summer 2020
MDM temperature (°C)
25
27
29
31
a
b
b
c
d
c
d
cd
C
W
Rock
CC
CW
WC
WW
Rock
Treatment

Figure 2

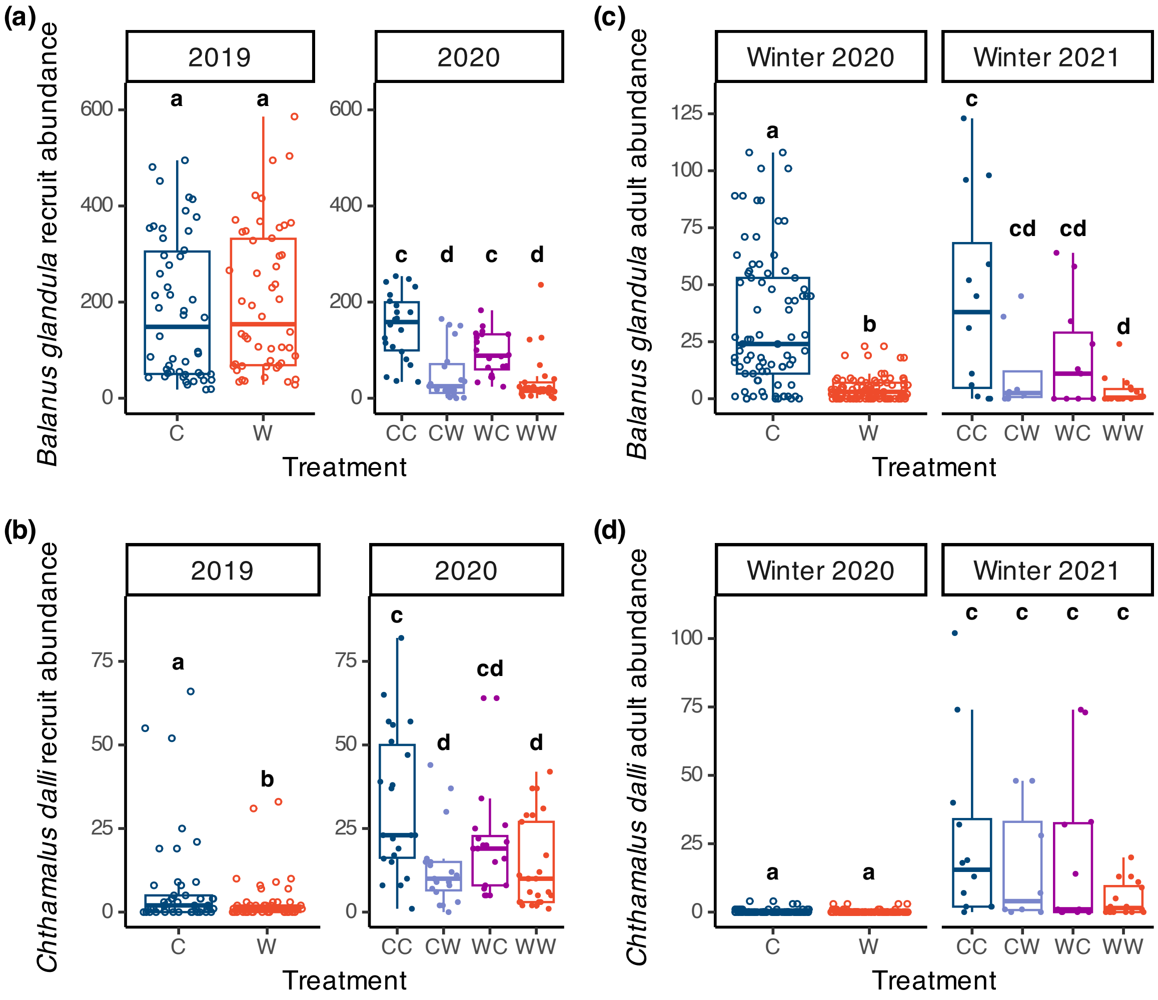
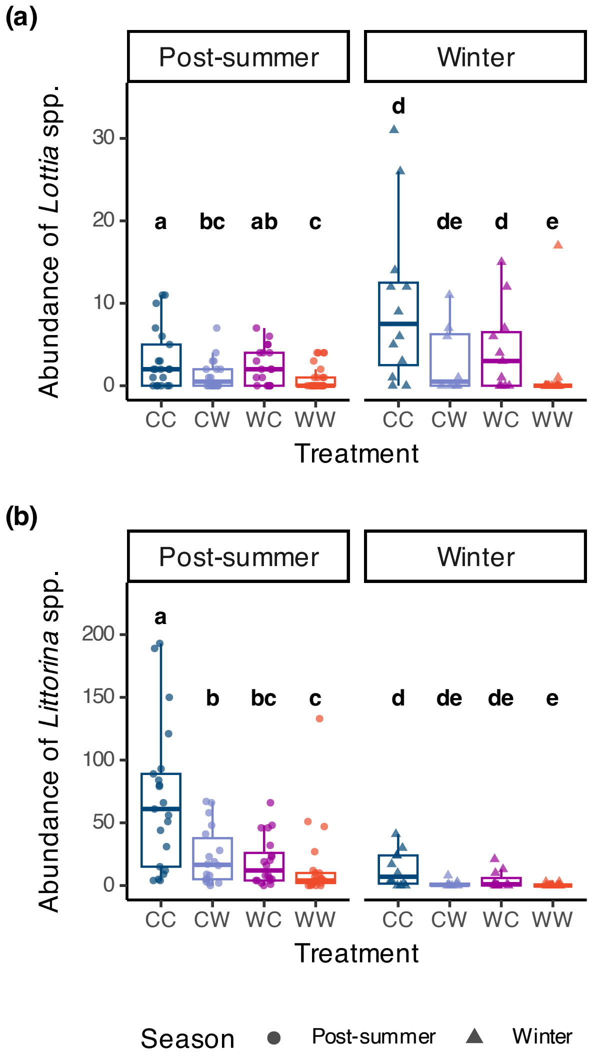
(a)
Balanus glandula recruit abundance
2019
2020
0
200
400
600
a
a
c
d
c
d
C
W
CC
CW
WC
WW
Treatment
(b)
Chthamalus dalli recruit abundance
2019
2020
0
25
50
75
a
b
c
d
cd
d
C
W
CC
CW
WC
WW
Treatment
(c)
Balanus glandula adult abundance
Winter 2020
Winter 2021
0
25
50
75
100
125
a
b
c
cd
cd
d
C
W
CC
CW
WC
WW
Treatment
(d)
Chthamalus dalli adult abundance
Winter 2020
Winter 2021
0
25
50
75
100
a
a
c
c
c
c
C
W
CC
CW
WC
WW
Treatment

Figure 3



(a)
Post-summer
Winter
Abundance of *Lottia* spp.
0
10
20
30
a
bc
ab
c
d
de
d
e
CC
CW
WC
WW
CC
CW
WC
WW
Treatment
(b)
Post-summer
Winter
Abundance of *Littorina* spp.
0
50
100
150
200
a
b
bc
c
d
de
de
e
CC
CW
WC
WW
CC
CW
WC
WW
Treatment
Season
● Post-summer
▲ Winter

Figure 4

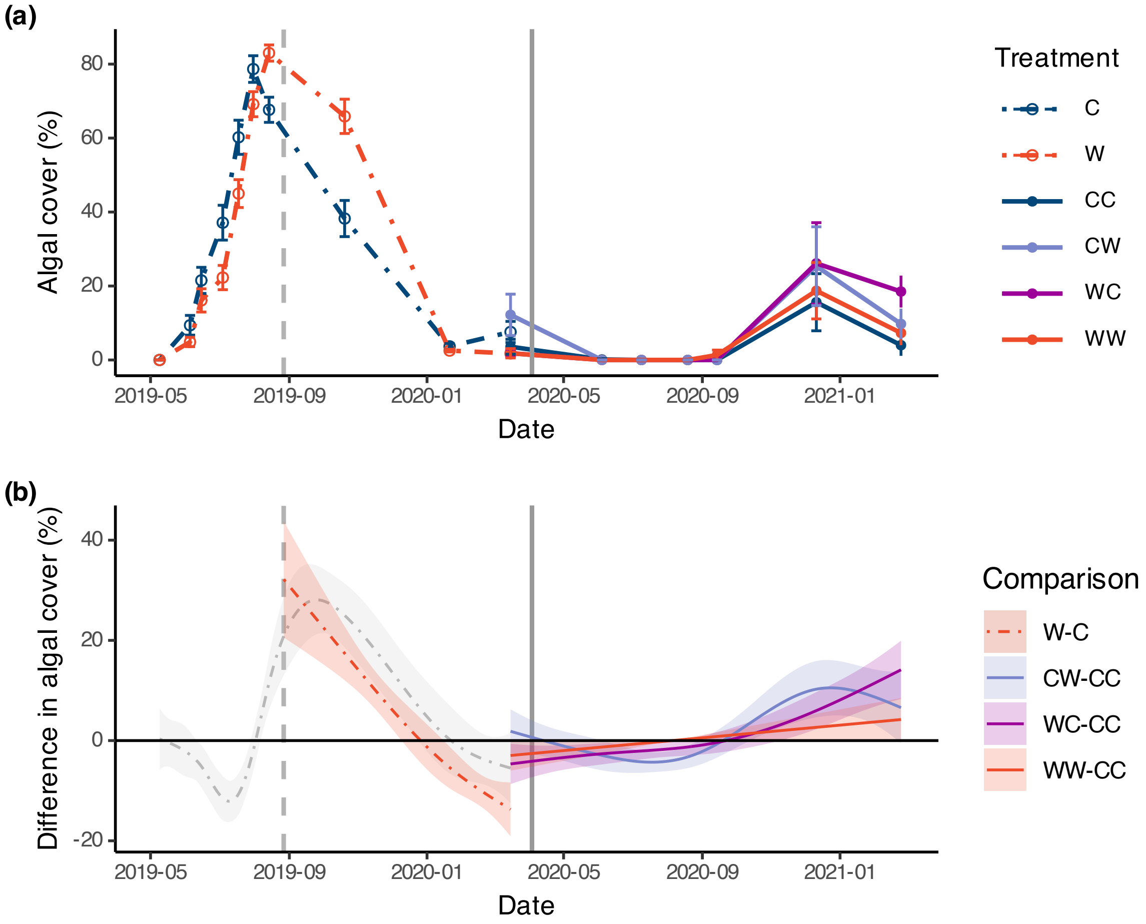

(a)
Algal cover (%)
0
20
40
60
80
2019-05
2019-09
2020-01
2020-05
2020-09
2021-01
Date
Treatment
C
W
CC
CW
WC
WW
(b)
Difference in algal cover (%)
-20
0
20
40
2019-05
2019-09
2020-01
2020-05
2020-09
2021-01
Date
Comparison
W-C
CW-CC
WC-CC
WW-CC

Figure 5

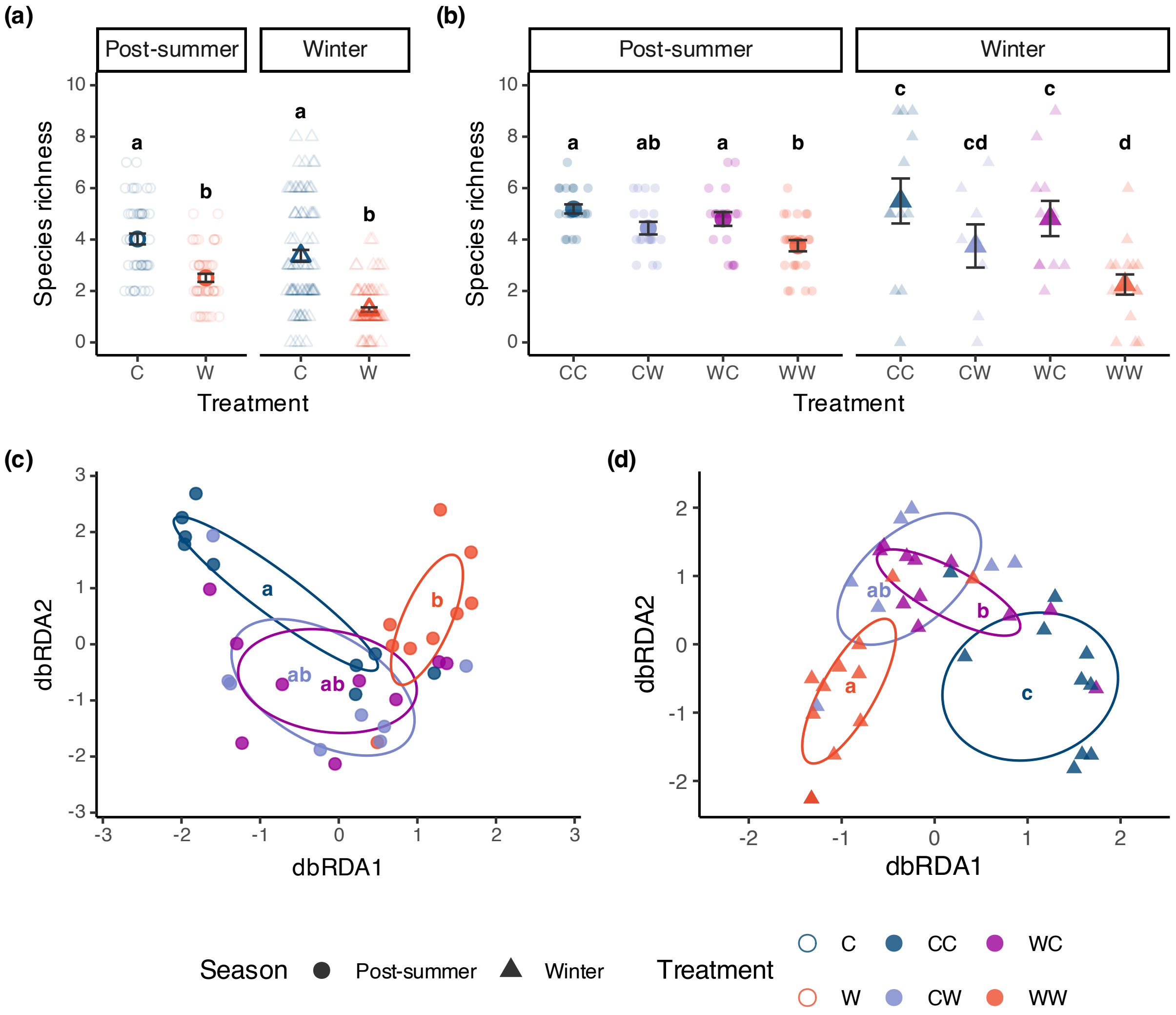

(a)
Post-summer
Winter
Species richness
10
8
6
4
2
0
a
b
a
b
C
W
C
W
Treatment
(b)
Post-summer
Winter
Species richness
a
ab
a
b
c
cd
c
d
CC
CW
WC
WW
CC
CW
WC
WW
Treatment
(c)
dbRDA2
dbRDA1
a
b
ab
ab
(d)
dbRDA2
dbRDA1
ab
b
a
c
Season
Post-summer
Winter
Treatment
C
CC
WC
W
CW
WW

Figure 6

Figure 1. **(a)** Simplified interaction diagram for a *Balanus glandula*-dominated intertidal community in the northeast Pacific. Barnacles facilitate gregarious barnacle recruitment and the presence of grazers and algae through habitat provision and moisture retention, while grazers consume algae. **(b)** Experimental design for this multi-year warming study and treatment comparisons to address hypotheses (H1–H3). White (cool = C) tiles and black (warm = W) settlement tiles were installed in the intertidal zone before the onset of summer. Tiles were then exposed to summertime low tides, wherein warming was expected to drive temperature-linked differences in community composition. At the start of the second year, the colour of half of each treatment was swapped using heavy-duty tape, generating four treatments (CC, CW, WC, and WW) that were monitored until the end of Year 2. Digital art by Amelia V. Hesketh.

Figure 2. Differences in residual mean daily maximum substratum temperatures of experimental tiles and adjacent bedrock recorded by temperature loggers at ȾESNO¸EN̲. Points represent the mean value for each experimental tile for which temperature was measured, with different shapes used to represent each experimental block (n=4 per treatment per block in year one, n=2 per treatment per block in year two, n=1 per block for rock temperature in both years). Only temperature data collected during daytime summer low tides between 1 June – 31 August were used. Bold lowercase letters represent statistically different groups, as determined by Tukey-Kramer *post hoc* tests on temperature models. C = cool summer, W = warm summer, CC = cool–cool, CW = cool–warm, WC = warm–cool, WW = warm–warm.

Figure 3. Temperature-driven differences in acorn barnacle abundance on experimental tiles at ȾESNO¸EN̲, in terms of **(a)** abundance of *B. glandula* and **(b)** *C. dalli* recruits during peak

observed recruitment (*B. glandula* May 2019: n = 50; *C. dalli* June 2019: n = 46 and 50 for C and W, respectively; 4 June 2020: n = 22, 19, 20, and 25 for CC, CW, WC, and WW) and **(c)** abundance of *B. glandula* and **(d)** *C. dalli* adults at the end of the first and second winters (March 2020: n=82 for C, n=91 for W; February 2021: n = 12, 8, 11, and 16 for CC, CW, WC, and WW). Letters indicate significant differences between treatment groups determined by Type II ANOVA (year one) and Tukey-Kramer *post hoc* tests (year two). Treatment codes as in Fig. 1.

Figure 4. Temperature-driven differences in **(a)** *Lottia* spp. (limpet) and **(b)** *Littorina* spp. (littorine snail) abundance on experimental tiles at ȾESNO¸EṈ immediately following summer (September 2020; n = 21, 18, 20, and 25 for CC, CW, WC, and WW) and during winter (February 2021; n = 12, 8, 11, and 16 for CC, CW, WC, and WW). Grazers were counted on the entire 15 x 15 cm upper surface of the tiles. Bold lowercase letters indicate significant differences between treatment groups determined by Tukey-Kramer *post hoc* tests. See Fig. 1 for treatment codes.

Figure 5. (a) Temperature-driven differences in algal cover on experimental tiles at ȾESNO¸EṈ. **(b)** Pairwise differences in fitted *gamm* smoothers for algal cover in the control (C or CC) treatment and all other treatments. Shaded areas represent an approximate 95% pointwise confidence interval; when this area does not overlap zero, a significant difference can be inferred. The vertical dashed line indicates when early herbivore manipulations stopped, while the vertical solid line indicates when treatments were swapped at the beginning of year two. During year one, the grey smoother represents *gamm* smoother differences (W-C comparison) when all data are modeled; the red smoother represents *gamm* smoother differences with data

removed for the period that grazer manipulations were active.

Figure 6. Temperature-driven differences in intertidal community diversity on experimental tiles at ȾESNO¸EN̲. **(a)** Species richness in year one and **(b)** in year two, determined from visual surveys post-summer and during late winter. Error bars represent standard error about the mean. Symbols/letters denote differences between treatment groups determined by Type II ANOVA (year one) and Tukey-Kramer *post hoc* tests (year two). **(c)** Community structure of destructively sampled epifauna in September 2020 and **(d)** February 2021, plotted in multidimensional space using distance-based redundancy analysis with Bray-Curtis distances. Each point represents a single experimental tile. In year one, n = 47 and 49 for C and W, respectively post-summer and n = 41 and 46 for C and W, respectively, in winter. For year two, n = 21, 18, 20, and 25 for CC, CW, WC, and WW post-summer and n = 12, 8, 11, and 16 for CC, CW, WC, and WW during winter. Letters denote differences between treatment groups determined using post-hoc testing through *multiconstrained*.