

# Demographic responses of coexisting species to *in situ* warming

Rebecca L. Kordas<sup>1,2,\*</sup>, Christopher D. G. Harley<sup>1</sup>

<sup>1</sup>University of British Columbia, 6270 University Blvd, Vancouver, BC V6T 1Z4 Canada

<sup>2</sup>Present address: Imperial College London, Silwood Park Campus, Buckhurst Rd, Ascot, SL5 7PY, UK

**ABSTRACT:** Climate warming may drive organismal body temperatures beyond important physiological thresholds, ultimately leading to detrimental effects on populations and communities. Much of what we currently know about species responses to warming has come from correlations with weather patterns or laboratory experiments, which can lack mechanism and realism, respectively. We incorporated both of these properties into warming experiments by manipulating substratum temperature *in situ*, using passively warmed black and white settlement plates. We monitored vital rates of coexisting barnacles over 1 yr at mid- and high shore levels of the rocky intertidal on Salt Spring Island (British Columbia, Canada), a 'hot spot' for intertidal thermal stress. Warming by ~2°C negatively affected the vital rates and population sizes of both barnacle species; however, survival of the competitive dominant, *Balanus glandula*, was more severely affected than that of *Chthamalus dalli*, leading to a temperature-induced change in relative space occupancy in the mid intertidal. Survival of *B. glandula* was reduced by 38–97%, leading to a 94–95% reduction in space occupancy, depending on shore level. *C. dalli* survival was also reduced by warming (10–44%), leading to a 63–73% reduction in space occupancy. Further, growth rates of both species were lower (16–50%) in warm treatments than in cool treatments, resulting in smaller adult body sizes, which can cause delays in reproductive maturity. Experiments like this one, which manipulate warming in the field on multiple species across ontogeny, will further enhance our understanding of the ecological effects of climate change.

**KEY WORDS:** Climate change · Temperature · barnacles · Growth rate · Survival · Population · Ontogeny

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## INTRODUCTION

As anthropogenic carbon emissions continue in the coming decades, the global mean temperature will continue to increase, as will the frequency and magnitude of high-temperature events (IPCC 2013). For organisms living in habitats where temperatures are near their thermal optimum, rising environmental temperatures will likely be detrimental (Deutsch et al. 2008, Sunday et al. 2011). Many tropical and marine intertidal organisms currently live near their thermal limits (Davenport & Davenport 2005, Deutsch et al. 2008, Tomanek 2010), and slight increases in temper-

ature have resulted in mass mortality events (Hoegh-Guldberg 1999, Harley 2008). However, thermotolerance varies within individuals (across ontogeny), among individuals, and among species (Angilletta et al. 2002, Denny et al. 2011, Dell et al. 2011, Kingsolver et al. 2011, Byrne 2012). Therefore, rising temperatures may affect physiological processes (e.g. growth vs. reproduction) in different ways, cause demographic bottlenecks, or alter interspecific interactions (Visser & Both 2005, Byrne 2012). Understanding how and why different species respond to temperature in unique ways will improve our ability to predict species' population responses to climate change.

\*Corresponding author: r.kordas@imperial.ac.uk

Barnacles are excellent model organisms for determining how variability in temperature-dependent vital rates can affect populations in a changing climate. The relatively large contact area between a barnacle's body and the substratum, combined with its small size, constrains barnacle body temperature to within a few degrees of substratum temperature (Harley & Lopez 2003). The lack of mobility and dearth of effective behavioral thermoregulatory options coupled with the high variability in intertidal rock temperatures (e.g. Harley & Helmuth 2003) mean that barnacle body temperatures can fluctuate considerably, more than 20°C over a single low tide (Wong et al. 2014). Barnacles may be sensitive to increasing temperature because they already experience temperatures near, at, or above their thermal optima (Bertness 1989, Berger & Emlet 2007). For example, hot low-tide conditions can decrease barnacle growth and survival (Foster 1969, Bertness 1989, Berger & Emlet 2007) and set upper distributional limits (Harley & Helmuth 2003, Chan et al. 2006, Gedan et al. 2011). However, thermal sensitivity varies among barnacle life stages and between co-occurring barnacle species. As barnacles age and increase in size, lethal thermal limits increase by several degrees (Crisp & Ritz 1967, Foster 1969, Chan et al. 2006). Interspecific differences in thermal tolerance have been associated with vertical differences in intertidal zonation and latitudinal differences in geographic ranges; species that experience warmer conditions (e.g. those that live higher on shore or have more equatorial ranges) have higher thermal tolerances than those that experience milder conditions (Foster 1971, Wong et al. 2014). Further, in areas where such species' habitats overlap, warmer environmental conditions favor the heat-tolerant species (Southward 1958, Wethey 1984a, Poloczanska et al. 2008).

Although the thermal biology of barnacles has received a fair amount of attention, most of our knowledge about barnacle thermal sensitivity comes from correlations with sea surface temperature, laboratory experiments with warmed water, or field experiments with cooled (i.e. shaded) treatments. Comparatively little is known about how barnacles (or any other intertidal invertebrates) respond *in situ* to warming during low tide (but see Lathlean et al. 2013), particularly in the presence of interspecific competitors. In this study, we measured the responses of barnacles to conductive heating in the field using passively warmed settlement plates in the mid and high intertidal. We focused on *Balanus glandula* and *Chthamalus dalli*, which are co-occurring barnacles in the northeast Pacific that

play an important ecological role in intertidal habitats. *B. glandula* is faster-growing and reaches a larger adult size than *C. dalli* and is the competitive dominant of the pair (Dayton 1971, Menge 2000, Harley & O'Riley 2011). Following a half century of warming air temperatures in the northeast Pacific, the upper limits of *B. glandula* and *C. dalli* have moved down-shore (Harley 2011), implying that aerial thermal stress may have profound consequences for their distribution and abundance. However, warming may affect these co-occurring species differently. Both species inhabit the high intertidal and have ranges from Alaska to Mexico (Barnes & Barnes 1956, Southward & Southward 1967); however, the upper limit of *C. dalli* extends approximately 5 cm higher than that of *B. glandula* (in British Columbia; C.D.G.H. unpubl. data). Because the 2 species are morphologically similar, the relationship between body temperature and microhabitat temperature may be similar. Therefore, *C. dalli* may be able to withstand higher environmental temperatures because the upper lethal temperature of *C. dalli* is slightly higher than that of *B. glandula* (W. Liao & C. D. G. Harley unpubl. data), consistent with longer emersion times experienced by the former.

We investigated how *in situ* warming affected an annual cohort of *B. glandula* and *C. dalli*, using black- and white-bordered settlement plates. Vital rates (growth and survival) were monitored over 1 yr to determine species-specific sensitivities across the ontogeny of barnacle benthic stages. We hypothesized that rates would be negatively affected by warming because these barnacles live near their thermal limits in the intertidal. We also expected that the detrimental effects of warming would vary depending on when barnacles settled during the summer and/or the age of barnacles. As has been found previously in laboratory experiments, we hypothesized that younger barnacles would be more sensitive to warming than older barnacles. Because temperatures in the region peak in July and August, we expected that barnacles settling in spring would fare better than those settling in summer because the latter would have been small when exposed to hotter low-tide conditions. Finally, we predicted that the 2 barnacle species would differ in thermal sensitivity, with growth and survival being more sensitive to heating in *B. glandula* than in *C. dalli*. This sensitivity could reduce the population density and/or space occupancy of the former and thereby weaken the competitive dominance of *B. glandula*.

## MATERIALS AND METHODS

### Study system

This experiment was conducted on the southeastern shore of Salt Spring Island, one of the southern Gulf Islands in British Columbia, Canada (48.753° N, 123.388° W). Tides around the Gulf Islands are mixed semidiurnal and had a maximum tidal range of 3.9 m during 2009 and 2010. Lower low tides in spring and summer months (March to August) coincide with the hottest portion of the day (10:00 to 15:00 h). Like nearby San Juan Island, which is climatically similar, Salt Spring Island can be considered a 'hot spot' (Helmuth et al. 2002) for stressful intertidal temperatures relative to the outer west coast. These conditions make Salt Spring Island an ideal location for the study of thermal stress on intertidal invertebrates.

### Experimental warming treatment

We used black- and white-bordered settlement plates to assess the effect of warming on barnacles. Substrate temperatures are highly correlated with *Balanus glandula* body temperatures, although adult barnacles tend to remain ~2°C cooler than the substrate on hot days (Harley & Lopez 2003). Settlement plates were installed at each of 2 tidal heights (1.6 and 2.6 m above the lowest astronomical tide estimated by the Canadian Hydrographic Service chart datum) in the rocky intertidal in 2009 to 2010. Seven plates of each color were installed at each tidal height.

Settlement plates were made of black or white high-density polyethylene (HDPE). Each HDPE plate was 15.25 × 15.25 cm with a centered 6.9 × 6.9 cm area of white epoxy (Sea Goin' Poxy Putty HD; Permalite Plastics), 3 mm thick on top of the HDPE. To avoid plate color affecting the organisms settling on plates (i.e. through increased reflectance), we used the same material on all plates for the central settlement area (Fig. 1). Settlement surface temperature was monitored using iButton temperature loggers (Maxim/Dallas Semiconductor), placed in a central recessed hole located under the epoxy surface. Rock temperature was monitored using 3 iButtons embedded in Z-Spar (A-788 Splash Zone Compound) per height, interspersed among plates. All plates were installed on a gently sloping (0 to 15°) southeast facing bench and were adhered in an alternating black-white sequence, spaced 15 to 30 cm apart (see Kordas et al. 2015 for additional details



Fig. 1. Representative photographs of warm (black) and cool (white) plates and the nearby rocky bench 1 yr after the start of the experiment. Plots on the rocky bench were adjacent to plates and were cleared of organisms on the same day as plate deployment. Dark brown-grey barnacles are *Chthamalus dalli*; white-to-tan barnacles are *Balanus glandula*. In the bottom photograph, the wire quadrat is the same size as the epoxy surface of the plates

about the rationale for substratum warming and experimental design).

Because stressfully cold temperatures for barnacles were not reached during this experiment (*Chthamalus dalli* are active at water temperatures below zero; Southward & Southward 1967), we focused our analyses on the potentially stressful warm temperatures. Daily maximum (DM) temperatures were calculated for each logger in a plate. Due to logger failure, few individual plates had complete temperature records for the duration of the experiment. This limitation could potentially bias thermal comparisons among plates due to differences in the time periods over which temperatures were recorded. Thus, we calculated residual temperature for each plate that had a functioning logger (as in Kordas et al. 2015). To do so, we first calculated a 'daily grand mean' by averaging DM temperatures across all plates (in all treatments) for each day. We then calculated the residual for each of those plates on each day (as the difference between the daily grand mean and the DM recorded by the logger). Finally, we calculated the average of these residuals across the summer, for each plate (i.e. average residual DM temperature). We also calculated the variability in residual DM temperatures across dates for each plate.

Daily maximum temperature is a useful metric of thermal stress, but it ignores the potential effects of the duration of hot temperatures. As complementary measures of thermal stress, we calculated the number of degree hours and number of days when plate and rock temperatures exceeded a thermal threshold for barnacles. *B. glandula* produces maximal levels of heat shock proteins when exposed to aerial incubation temperatures of 33°C (Berger & Emlet 2007). Barnacle body temperatures in our experiments may have differed from plate temperature by 0 to 2°C, depending on barnacle size. Therefore, we chose 33 and 35°C as the relevant thresholds for defining degree hours. Similar thermal thresholds have not been examined for *C. dalli*, so we also explored thresholds of 31°C and 37°C. Analyses revealed similar results for all 4 tested thresholds; for brevity, we only report the results for thresholds of 33°C and 35°C. We calculated degree hours as the sum difference between each threshold and all substratum temperature measurements (for the entire summer) higher than the threshold, divided by 2 to convert the 30 min sampling interval of the loggers into hours. To avoid pseudoreplication, we calculated the average of each metric (daily max, variance, or degree hours) over the summer for each plate. For the 'number of days' analysis, we used counts of the days when plate

and rock temperatures reached or exceeded threshold temperatures over the summer. For all temperature analyses, we used 2-way ANOVAs to determine if temperature varied among plate colors or shore levels.

### Demography measurements and analyses

Plates were installed between 12 and 30 April 2009 and monitored at 2 wk intervals during spring and summer months (May to September) and every 3 mo during fall and winter (September to March). Starting on 22 May, and for each census thereafter, live barnacle densities were randomly subsampled (31 % of epoxy area counted). A 3 mm area at the edge of the epoxy was excluded from counts to avoid edge effects because barnacles were observed to prefer the topographic heterogeneity provided by the raised epoxy edge.

To determine how the temperature treatment and intertidal height affected the abundance of barnacles, we used repeated measures RM ANOVA to take time correlations across sampling dates into consideration. Loss of replicates became prevalent starting in September, so only data through 15 August 2009 were used (n = 24 plates). To check the sensitivity of excluding winter data in RM-ANOVA, we repeated the analysis with all sampling dates (n = 15), and the pattern of significance was the same. In the winter, we expected no temperature difference between plate colors (because low tides were at night). However, it was possible that biological differences existed in the (mostly) adult cohort after 1 yr as a result of carry-over effects from the summer. Therefore, we conducted an ANOVA on the last sampling date (24 March 2010) to test the main effects of temperature treatment and intertidal height (n = 15 plates).

Digital photographs were taken of all plates at all sampling dates and were later used to determine percent cover, survival, and growth rates of barnacles. To detect whether warming affected competition between *B. glandula* and *C. dalli*, we quantified the percent cover of barnacles. Asymmetric competition can be inferred by a decrease in a competitively inferior species in response to an increase in the cover (via growth) of the competitive dominant (Dayton 1971, Menge 2000). We estimated percent cover of each species on each plate at each sampling date by overlaying the photograph of the settlement area with a digital grid of 100 intersecting points. The species found under each point was noted and percent

cover estimated. We tested whether percent cover was affected by temperature treatment, tidal height, or species over the summer using RM-ANOVA and after 1 yr using ANOVA on the last date.

We also tracked the fate of 25 to 40 barnacles on each plate over the summer, using the photographs described above. We haphazardly chose barnacles from the 5 June photographs because 5 June was the first date when metamorphosed barnacles were visible on all plates. Using photographs from each subsequent sampling date (taken at 2 wk intervals), we recorded whether each of these juvenile barnacles ( $n = 3$  to 38 per plate) was still present, concluding on 15 August (because replicate loss began in September). Barnacle survival on some plates, on some dates (particularly mid-intertidal plates in July) could not be assessed because a transient pulse of green filamentous algae covered 100% of the plate, preventing identification of barnacles. Total barnacle survival of each species relative to the initial time point (5 June) was calculated for each plate and for each date. We tested whether survival varied with intertidal height or temperature treatment in a RM-ANOVA, using the 5 periods between 5 June and 15 August 2009.

To determine species-specific growth rates, the basal area of barnacles was measured from photographs taken at each sampling date, using Image J 1.44v (National Institutes of Health, USA). We located 9 barnacles of each species from the last photograph taken of each plate (March 2010 or earlier if the replicate was lost). To reduce the influence of crowding on our results, we selected the most solitary barnacles and excluded data if barnacles became noticeably crowded (i.e. shell edges became indented). We also selected the largest barnacles in order to obtain growth rates that spanned more of the experimental period (e.g. a barnacle measuring 18 mm<sup>2</sup> on 15 September settled just prior to 22 May, while a barnacle measuring 7.5 mm<sup>2</sup> on 15 September settled just prior to 4 August). The complete dataset included barnacles that settled during different periods and, therefore, experienced different environmental conditions and were different ages. In addition, recruitment was very low for *B. glandula* on black plates high in the intertidal and for *C. dalli* on all plates in the mid intertidal, so growth rate data were limited for these groups. We dealt with these complications in 2 ways: (1) to determine how warming affected barnacles settling at different times and of different ages, we isolated several cohorts of *C. dalli* from high intertidal plates (see below), and (2) to compare growth rates of both species, we extracted

the first 2 mo of barnacle growth following settlement (regardless of when barnacles settled). These latter data were separated into summer and winter settlers to account for seasonal effects on growth rates. Barnacle growth rates were averaged to generate a single value for each species for each plate to avoid pseudoreplication. An analysis of covariance, using average initial size as a covariate, was used to test the effects of temperature treatment and tidal height on growth rate. The effect of initial size was not significant ( $p > 0.25$ ; likely due to the similarity in initial barnacle sizes), so the term was dropped for ease of interpretation; the results for both analyses showed the same pattern of significance among terms, but we present the results of the 2-way ANOVA.

To determine how warming affected the daily growth rate and body size of barnacles that settled at different times of the year or varied in age, we conducted several complementary analyses on the *C. dalli* high intertidal data set, described above (the only data set complete enough for this level of scrutiny). We isolated 3 cohorts that had at least 3 *C. dalli* per plate: those that settled just prior to 22 May ('May'), 24 June ('June'), and 9 July 2009 ('July'). First, we hypothesized that barnacles settling in July, when we expected that low tide conditions would be more stressful, would have slower growth rates than barnacles settling in spring, when low tide conditions were milder. We tested for this effect by analyzing growth rates from the first ca. 14 wk following settlement (which were standardized for barnacle age), corresponding to 22 May–19 July for May settlers, 24 June–15 August for June settlers, and 9 July–15 September for July settlers. Second, we hypothesized that younger barnacles would be more sensitive to warming than older barnacles. We tested for this effect by analyzing data during the same period (19 July–15 September), when May settlers were ca. 116 d old, June settlers were ca. 83 d old, and July settlers were ca. 68 d old. For both analyses, the average daily growth rate per plate was used to test for the effects of temperature treatment and settlement period, using RM-ANOVA. Analogous analyses were performed on *C. dalli* body size data. Finally, we conducted a 2-way ANOVA on the last date (March 2010) to determine if the body size of *C. dalli* adults was affected by summer warming or settlement period.

Barnacle density, percent cover, and growth rate data were log transformed in all analyses to meet assumptions of normality and homoscedasticity. Survival data were converted to proportions and transformed using arcsine square root prior to analyses. If the sphericity of the variance-covariance matrix was

violated for any RM-ANOVA, the degrees of freedom were altered according to the Mauchly test using the Huynh-Feldt Epsilon correction. Bonferroni corrections were applied to the analyses of recruit density, summer density, and summer growth rates to account for multiple comparisons. Statistical analyses were performed in JMP Pro 9.0.3 (SAS Institute).

## RESULTS

### Temperature

The daily maximum temperature, averaged across plates (average daily maximum [ADM]), varied with the fortnightly tidal cycle in the mid intertidal and, to a lesser degree, in the high intertidal (Kordas et al. 2015). At low tide, mid-intertidal plates reached higher temperatures (ADM 25–38°C) during spring low tides that coincided with the hottest portion of the day (10:00–15:00 h), and lower temperatures (ADM 10–20°C) during neap low tides when plates were emersed for  $<4 \text{ h d}^{-1}$ . High intertidal plates were significantly warmer than mid-intertidal plates (4.7–5.6°C difference in mean ADM) through most of spring and summer (Tables S1 and S2 in the Supplement at [www.int-res.com/articles/suppl/m546p147\\_supp.pdf](http://www.int-res.com/articles/suppl/m546p147_supp.pdf)) because they were only submerged during the highest of the bimonthly spring tides, which were at night. Consequently, high intertidal plates were emersed during most daylight hours. Because temperature differences were created by solar radiation, all plates were approximately the same temperature at high tide and at night (Kordas 2014), when they remained cool (5–9°C; Fig. 2, Table S1). The average ocean temperature was 12°C (range: 6.4–23°C over the experimental period; Fig. S1 in the Supplement), but air temperatures as low as 4.5°C were reached in the intertidal during low tide at night in the spring.

Once exposed to the sun at low tide, all plates warmed by  $>20^\circ\text{C}$ , and the temperature on black and white plates diverged. Mean ADM temperatures were 2 to 3°C higher on black (hereafter, warm) plates than on white (hereafter, cool) plates during spring and summer months (Fig. 2A, Table S2A). The mean ADM temperature of cool plates was statistically similar to that of the surrounding bedrock (Fig. 2A, Table S1). Temperature variability was significantly higher on warm plates than on cool plates (Tables S1 & S2B).

The cumulative amount of heating was greater on warm plates and high on shore over the experimental period (Fig. 2B, Tables S1 & S2). Temperatures were  $\geq 33^\circ\text{C}$  and  $\geq 35^\circ\text{C}$  for significantly more degree hours

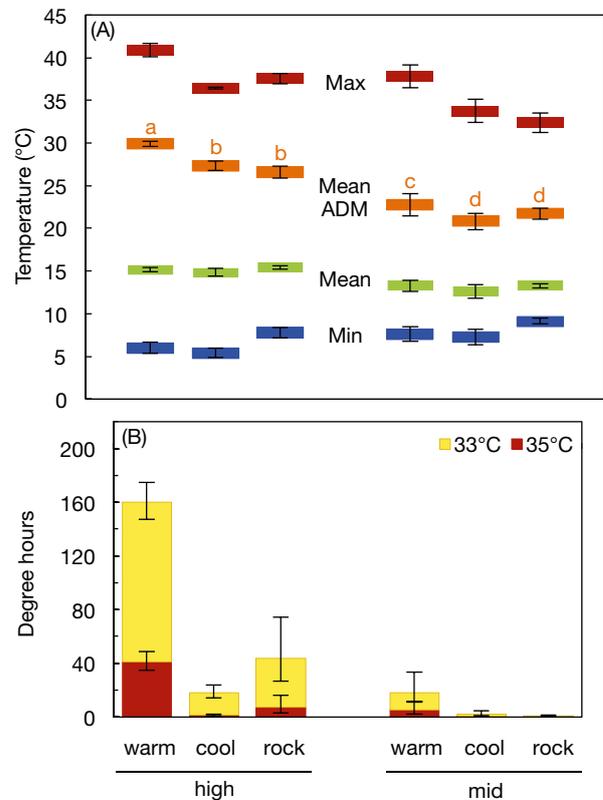


Fig. 2. (A) Mean ( $\pm$ SE) of temperature metrics measured on black (warm) and white (cool) plates, and the nearby rock in the high and mid intertidal. For mean average daily maximum (ADM), different letters indicate significant differences (temp  $p < 0.001$ ; height  $p < 0.001$ ; temp  $\times$  height  $p = 0.208$ ) according to Tukey post-hoc comparisons. Red: maximum; orange: ADM; green: mean; blue: minimum recorded temperature. (B) Mean number of degree hours ( $\pm 1$  SE) when plate and rock temperature exceeded important thresholds: 33°C and 35°C (see 'Materials and methods'). Loggers were deployed from April to September 2009. Averages and error limits were back-transformed for all graphical presentations

on warm plates compared to cool plates, at both heights (Fig. 2B, Table S2C,D). Prolonged heating was also significantly greater high on the shore than on comparable plates lower down. Finally, there were significantly more days reaching or exceeding daily maximum temperatures of 33°C and 35°C on warm plates compared to cool plates and the surrounding bedrock, and more days reached those thresholds high in the intertidal (Tables S1 & S2E,F).

### Recruitment

Early patterns of barnacle recruitment, assessed on 22 May 2009, revealed that recruitment was higher in the mid intertidal than in the high intertidal (Fig. 3)

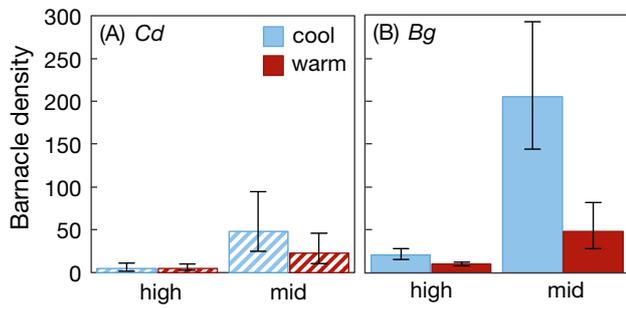


Fig. 3. Recruitment of (A) *Chthamalus dalli* and (B) *Balanus glandula* in cool and warm treatments in the mid and high intertidal. Mean ( $\pm$ SE) density estimated 22 d (22 May 2009) after plate installation.  $n = 6$  to  $7$  for each treatment

and almost twice as high for *Balanus glandula* compared to *Chthamalus dalli* (spp.:  $p = 0.013$ ; Tables 1, S3, S4). Barnacle recruitment on warm plates was half that on cool plates, although the trend was not significant (temperature:  $p = 0.086$ ; Table 1) because densities were variable in the mid intertidal but similar in the high intertidal (Fig. 3).

### Survival

The warming treatment reduced juvenile survival for both species of barnacles, and this effect did not vary over spring and summer (temperature:  $p < 0.001$ ; Fig. 4, Tables 2 & S5). The negative effect of

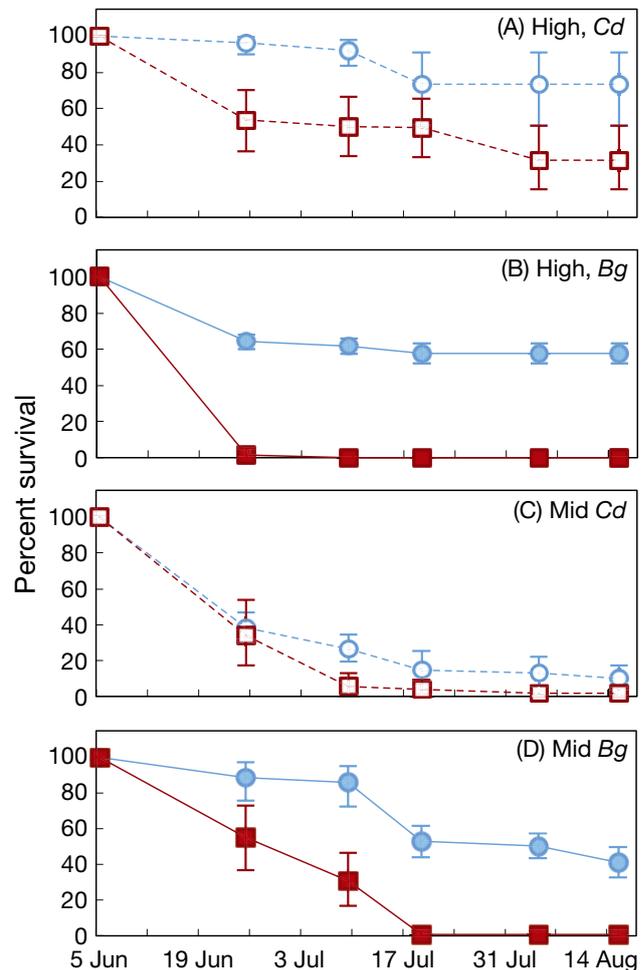


Fig. 4. Mean ( $\pm$ SE) percent survival of juvenile barnacles in the (A,B) high and (C,D) mid intertidal on cool (circles) and warm (squares) plates. Survival of (A,C) *Chthamalus dalli* (Cd; open symbols) and (B,D) *Balanus glandula* (Bg; filled symbols) that recruited to plates between 30 April and 5 June was assessed every 2 wk until 15 August 2009. Initial assessment date (5 June) is included in graphs for visual interpretation but was not included in analyses

Table 1. ANOVA p-values and analysis information for barnacle responses: early recruitment (density after 22 d), growth rates in summer and winter, density after 1 yr, and percent cover after 1 yr. Sample size (N) indicates the number of plates used in analyses. The data used in analyses were either from a single date (density, cover) or a season (growth). Responses were  $\log(x + 1)$  transformed to meet assumptions of parametric tests. Bolded p-values indicate significance (by applying a Bonferroni correction where appropriate) at  $\alpha = 0.025$  for recruitment density,  $\alpha = 0.017$  for summer growth rates, and  $\alpha = 0.05$  for the remaining factors. Dates are mo/yr. Full ANOVA tables can be found in the Supplement

ANOVA	Recruit density	Summer growth	Winter growth	Density after 1yr	Cover after 1yr
Temperature (T)	0.086	<b>0.016</b>	0.888	<b>0.005</b>	<b>&lt;0.001</b>
Tidal height (H)	<b>&lt;0.001</b>	0.282	0.073	0.255	0.730
Species (Spp.)	<b>0.013</b>	<b>&lt;0.001</b>	<b>0.006</b>	0.236	0.700
T $\times$ H	0.305	0.454	0.936	0.447	0.512
T $\times$ Spp.	0.343	0.468	0.899	0.367	0.865
H $\times$ Spp.	0.868	0.895	0.134	0.304	0.915
T $\times$ H $\times$ Spp.	0.936	0.335	0.885	0.426	0.398
Sample size (N)	52	45	24	30	30
Date	5/2009	Summer	Winter	3/2010	3/2010

warming on *B. glandula* survival was more than twice that of *C. dalli* (temperature  $\times$  spp.:  $p = 0.031$ ); after 20 d, warming reduced *B. glandula* survival by 98% and *C. dalli* survival by 44% in the high zone and by 38% and 11%, respectively, in the mid-intertidal zone (Table S3). The survival of each species varied with intertidal height; *C. dalli* survival was greater in the high intertidal compared to the mid intertidal, where survival was very low in both treatments, while *B. glandula* survival was slightly greater in the mid intertidal (height  $\times$  spp.:  $p < 0.001$ ). However, the effect of the temperature treatment was similar at both heights (temperature  $\times$  height:  $p = 0.193$ ; temperature  $\times$  height  $\times$  spp.:  $p = 0.965$ ).

Table 2. Repeated measures ANOVA p-values and analysis information for barnacle responses: survival of juvenile barnacles, density, and percent cover over summer 2009. Sample size (N) indicates the number of plates used in analyses. Log, square root, and arcsine square root transformations were explored for all data sets. The transformation yielding the most normally distributed data and least sphericity is listed. The p-value for Mauchly's sphericity criterion was  $<0.05$  for all responses, so the Huynh-Feldt  $\epsilon$  corrected p-values were reported for within-subjects effects. **Bold** indicates significant effects at  $\alpha = 0.05$  (except for summer density, to which we applied a Bonferroni correction;  $\alpha = 0.025$ ). Full RM-ANOVA tables can be found in the Supplement

RM-ANOVA	Summer survival	Summer density	Summer cover
Time	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Temperature (T)	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
T × time	0.588	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Tidal height (H)	<b>0.045</b>	0.228	<b>&lt;0.001</b>
H × time	<b>0.015</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Species (Spp.)	0.286	0.556	<b>0.013</b>
Spp. × time	0.682	<b>0.013</b>	0.831
T × H	0.193	0.341	<b>0.049</b>
T × H × time	0.368	0.169	0.172
T × Spp.	<b>0.031</b>	0.103	<b>&lt;0.001</b>
T × Spp. × time	0.553	0.642	<b>0.001</b>
H × Spp.	<b>&lt;0.001</b>	<b>0.009</b>	<b>&lt;0.001</b>
H × Spp. × time	0.050	<b>&lt;0.001</b>	<b>&lt;0.001</b>
T × H × Spp.	0.965	0.763	<b>0.025</b>
T × H × Spp. × time	0.906	0.666	0.053
Sample size (N)	36	48	48
Transformation	arcsine	$\log(x + 1)$	$\log(x + 1)$

### Growth rate and size

Warming reduced growth rates of both species during the warm season (temperature:  $p = 0.016$ ; Table 1, Fig. 5). On average, the growth rate of *C. dalli* individuals was 64 % slower than for *B. glandula* in summer, and overall, growth rates were 58 % slower in winter compared to summer (Tables 1 & S6). However, the effect of temperature did not differ between species in either season (summer & winter: temperature × spp.:  $p > 0.4$ ).

Over the course of the experiment, *C. dalli* growth rates increased from May to September, then decreased in winter (Fig. 6A). This change caused body size to increase exponentially during spring and summer, then increase linearly during winter (Fig. 6B). Growth rates were depressed on warm plates, especially in warmer summer months (temperature:  $p < 0.001$ , temperature × time:  $p \leq 0.014$ , Tables 3 & S7). This difference caused average body sizes to diverge

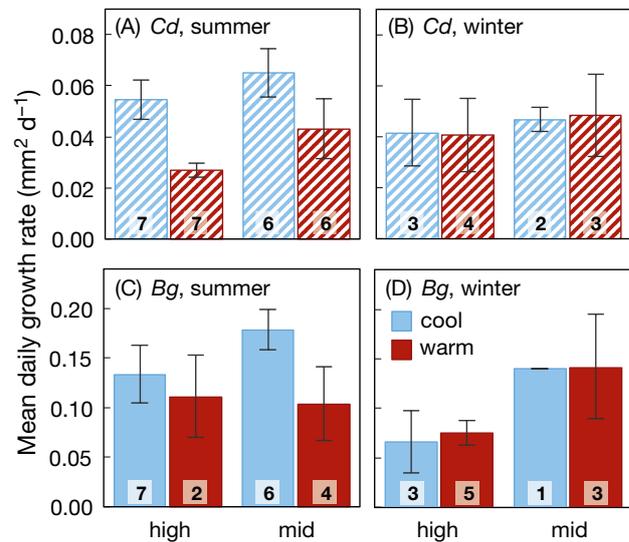


Fig. 5. Mean ( $\pm$ SE) daily growth rates of juvenile (A,B) *Chthamalus dalli* and (C,D) *Balanus glandula* in cool and warm treatments in the mid- and high intertidal (note the differences in y-axis scaling between species). Nine barnacles (of each species, on each plate) that survived the duration of the experiment were measured at each sampling date. Growth rates were calculated from the 2 mo period following initial settlement. Summer (left) rates are from barnacles that settled in May to August. Winter (right) rates are for barnacles settling in September to January. Numbers on bars represent the number of replicate plates per treatment

between treatments in mid-summer (temperature:  $p \leq 0.002$ , temperature × time:  $p < 0.001$ ; Tables 3 & S8).

To determine how warming affected barnacles settling at different times and of different ages, we compared the growth rate and body size of 3 cohorts of *C. dalli* settlers. We conducted 2 complementary analyses to determine whether cohort differences were due to age or seasonal timing. First, we examined the effect of seasonal timing, keeping barnacle age approximately the same (52 to 85 d old; Table 3, Fig. 6, solid grey boxes). Daily growth rate differed between cohorts (settlement period:  $p = 0.006$ ; Table 3). For ca. 14 wk old barnacles, growth rates for May settlers were lower on average (0.045 and 0.016  $\text{mm}^2 \text{d}^{-1}$  in cool and warm treatments, respectively) than for later settlers (June: 0.064 and 0.028  $\text{mm}^2 \text{d}^{-1}$  and July: 0.072 and 0.047  $\text{mm}^2 \text{d}^{-1}$ ), and the differences between cohorts increased over time (settlement period [SP] × time:  $p < 0.001$ ). Nonetheless, on average, barnacle body size was statistically similar among cohorts following Bonferroni correction (sett. per.:  $p = 0.043$ , Table 3), although the trend was similar to that of growth rates, and the differences between cohorts also increased over time (SP × time:  $p < 0.001$ ). Regardless of the timing of settlement, warming reduced

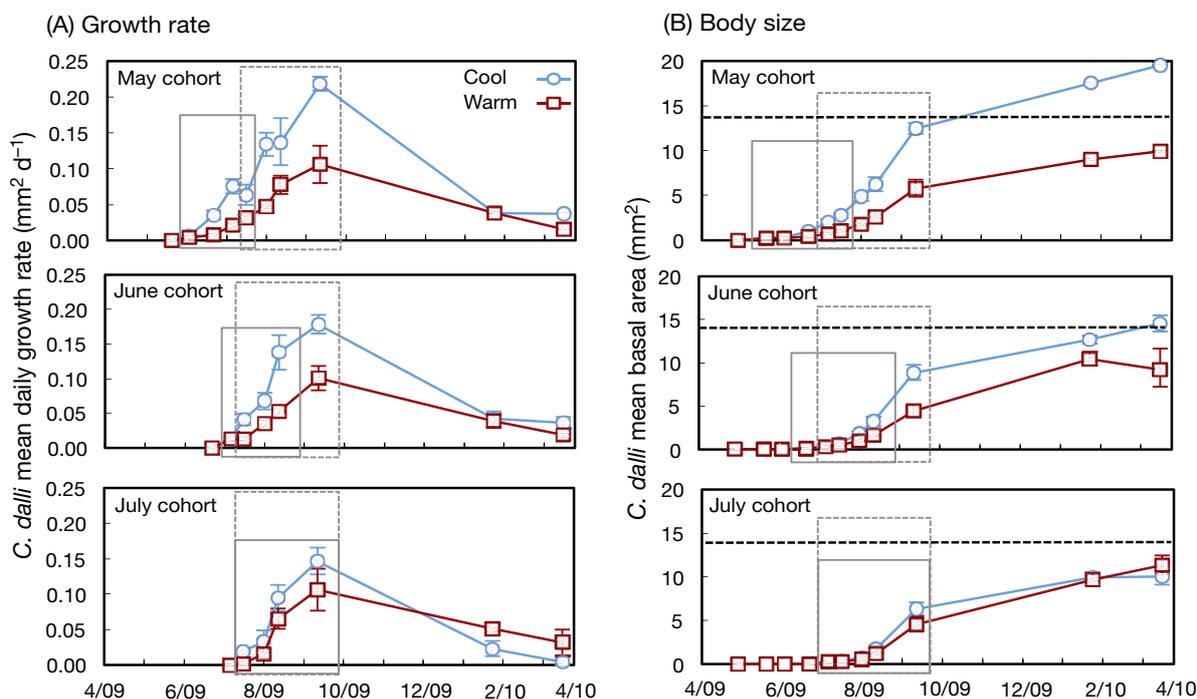


Fig. 6. Juvenile *Chthamalus dalli* (A) mean daily growth rates and (B) mean basal area in cool and warm treatments over time, for barnacles settling in May, June, and July in the high intertidal. Means ( $\pm$ SE) were calculated from plate averages. Solid and dashed grey boxes indicate data included in RM-ANOVAs assessing the effects of season and cohort age, respectively (Table 3). The dashed horizontal black line in (B) indicates the approximate size when *C. dalli* reaches maturity ( $14 \text{ mm}^2$  basal area; Southward & Southward 1967). Dates are mo/yr

Table 3. RM-ANOVA p-values for *Chthamalus dalli* growth rate and body size in the high intertidal during summer. Average body size (basal area) was calculated for barnacle cohorts that settled during May, June, and July 2009 (corresponding age range of barnacles in each cohort is given). Effects were examined for (1) seasonal timing, using data for barnacles of approximately the same age but settling on different dates (solid grey boxes in Fig. 6) and for (2) age, using data from the same period but for different aged barnacles (dashed grey boxes in Fig. 6). Degrees of freedom and p-values were adjusted by Huynh-Feldt  $\epsilon$  for within-subjects effects. **Bold** p-values indicate significance (using a Bonferroni correction; alpha = 0.017 for growth and 0.025 for size). Full results are given in Tables S7 & S8 in the Supplement

Cohort	Timing (ca. same age) Age (d)		Age (same timing) Age (d)	
	May	June	July	Age (d)
May:	58–80		116–138	
June:	52–85		83–115	
July:	68–82		68–82	
Effect	Growth	Size	Growth	Size
Time	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Temperature (T)	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
T $\times$ time	<b>0.007</b>	<b>&lt;0.001</b>	0.062	<b>&lt;0.001</b>
Settlement Period (SP)	<b>0.006</b>	0.043	<b>0.010</b>	<b>&lt;0.001</b>
SP $\times$ time	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.282	<b>&lt;0.001</b>
T $\times$ SP	0.798	0.303	0.231	0.026
T $\times$ SP $\times$ time	0.189	0.335	0.174	0.282

the growth rates and body sizes of all cohorts similarly (temperature  $p < 0.001$ , temperature  $\times$  SP:  $p > 0.3$ , Table 3). On average, warming reduced the growth rates for May, June, and July settlers by 64, 56, and 35% respectively.

In a second analysis, we examined the effect of warming on barnacles of different ages but over the same seasonal period (July to September; Fig. 6, dashed grey boxes). In general, we found that *C. dalli* were larger overall if they were older (i.e. settled earlier; SP:  $p < 0.001$ ; Table 3), due to longer growing times and compounded by faster growth rates associated with larger, older individuals (SP:  $p = 0.010$ ; Table 3). Over this period, warming affected the growth rate and body size of all cohorts similarly (temperature  $\times$  SP:  $p \geq 0.026$ ). Warming reduced growth rates of May, June, and July settlers by 50, 53, and 35% respectively. Finally, although different cohorts of barnacles were similar in size after 1 yr (SP:  $p = 0.48$ , Table S8C), summer differences caused barnacles on warm plates to be 27% smaller than barnacles on cool plates, although the effect was marginally significant, probably due to the loss of replicates (temperature:  $p = 0.063$ ; Table S8C).

## Abundance

Over the summer, *B. glandula* were more abundant low on shore than high on shore and more abundant than *C. dalli* at either height (height  $\times$  spp.:  $p = 0.009$ ; Table 2). Both barnacle species were less numerically abundant on warm plates compared to cool plates (Fig. 7). Warming reduced barnacle density by an average of 85% over the summer (temperature:  $p < 0.001$ , Table 2), and the reduction was similar for both species (temperature  $\times$  spp.:  $p = 0.103$ ) and at both heights (Tables 2 & S9). The difference between treatments varied over the summer; when barnacle density declined, it did so more precipitously in warm treatments (e.g. from 22 May to 5 June, *B. glandula* density on mid-intertidal plates declined by 74% on warm plates and 40% on cool plates). After 1 yr, barnacle density was 90% lower in warm treatments (temperature:  $p = 0.005$ ), which was largely driven by *C. dalli* in the high intertidal (Table 1, last time point in Fig. 7).

The percent cover of barnacles was lower in warm treatments over the summer (temperature:  $p < 0.001$ , Tables 2 & S10, Fig. 8). Cover of all barnacles remained low on warm plates throughout the year (<10%), while cover increased over time on cool plates (temperature  $\times$  time:  $p < 0.001$ ). The severity of warming impacted the species differently and depended on intertidal height (temperature  $\times$  height  $\times$  spp:  $p = 0.025$ ). In the high zone, warming affected both species similarly. In the mid zone, *B. glandula* occupied more space than *C. dalli* on cool plates, and on warm plates, the 2 species occupied the same (minimal) amount of space (Fig. 8). The large apparent late-summer drop in *B. glandula* percent cover on cool plates in the mid zone was due to the loss of one particularly densely settled plate in September; however, this loss did not affect statistical results because only sampling dates through late August were used in RM-ANOVA. On average, warming reduced the percent cover of *B. glandula* by 95% and *C. dalli* by 73% during summer in the mid intertidal. One year later, warming reduced the relative cover of barnacles by 88% (temperature:  $p < 0.001$ ), regardless of species or intertidal height (Table 1).

## DISCUSSION

Many species live in habitats where temperatures are close to their thermal optima (Sunday et al. 2011); consequently, climate warming may drive organismal

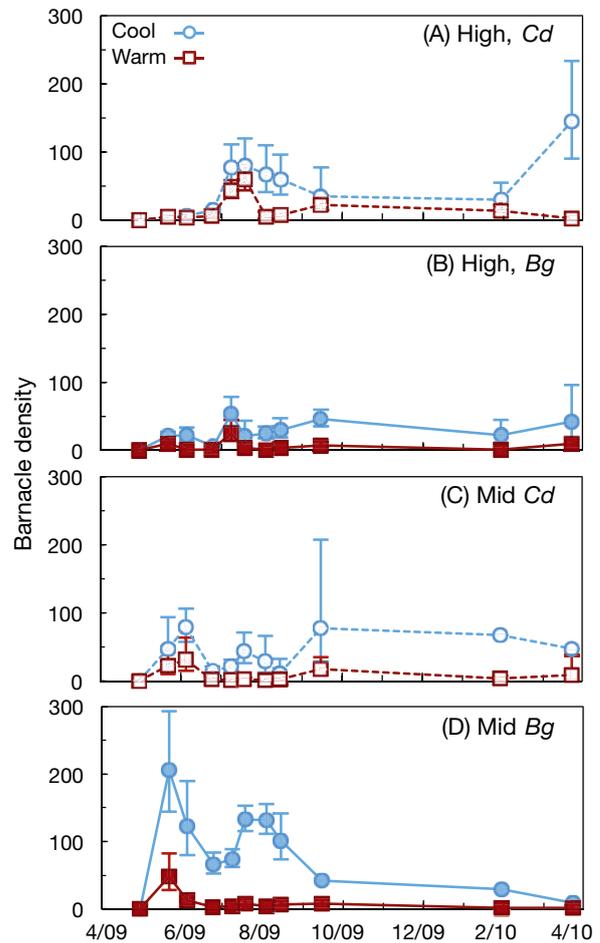


Fig. 7. Mean density (per 43.56 cm<sup>2</sup> plate) of (A,C) *Chthamalus dalli* (*Cd*; open symbols) and (B,D) *Balanus glandula* (*Bg*; filled symbols) on cool (circles) and warm (squares) plates in the (A,B) high and (C,D) mid intertidal. Error bars are standard error and are smaller than symbols in some cases. Dates are mo/yr

body temperatures beyond important physiological thresholds, ultimately leading to detrimental effects on populations (Vasseur et al. 2014). Integrating warming effects across ontogeny in a natural setting can elucidate mechanisms behind warming responses that cannot be perceived by studying a single life stage. This integration has rarely been attempted (but see Radchuk et al. 2013) and has rarely been quantified entirely from field-based manipulations. Doing so may provide better estimates of species' responses to climate change.

### Efficacy of experimental temperature manipulation

The intertidal substratum was successfully heated *in situ* by  $\sim 2^{\circ}\text{C}$  during summer low tides. The pas-

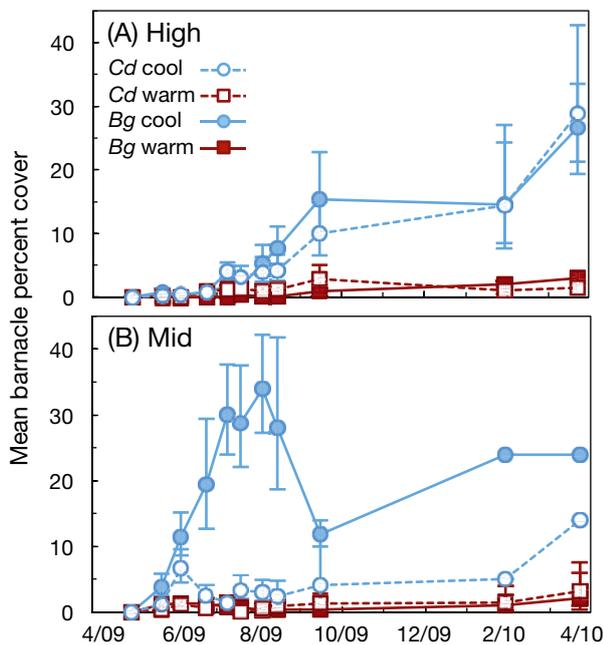


Fig. 8. Mean ( $\pm$ SE) percent cover of *Chthamalus dalli* (Cd; open symbols) and *Balanus glandula* (Bg; filled symbols) on cool (circles) and warm (squares) plates in the (A) high and (B) mid intertidal. Dates are mo/yr

sively heated thermal plates used are imperfect proxies for future thermal conditions because winter, nighttime, and water temperatures could not be manipulated (Kordas et al. 2015). However, these intertidal organisms experience thermal stress during emersion (Hofmann & Somero 1995), so increasing summer air temperatures may be more detrimental than increasing water temperatures. Globally, air temperatures are expected to increase faster than water temperature (Sutton et al. 2007), a trend which has been observed in coastal British Columbia since 1950 (Environment 2006). Experimentally warming the substrate is not the same thing as climatic warming of the air, but the effects of aerial vs. substratum warming on body temperature are extremely similar for small animals with large areas of attachment to the rock. The relationship between substratum, body, and air temperature is strong and approximately 1:1 (for limpets and snails; Denny et al. 2006, Marshall et al. 2010). Therefore, the experimental warming of black vs. white plates (2°C average) should increase body temperatures by approximately the same amount as would the global average change in air temperature expected by 2100 (for further discussion, see Kordas et al. 2015).

The warmed plates reached higher average and maximum temperatures and spent more time above

important thermal thresholds than the cool plates and the surrounding bedrock. Cumulative heating was greater in warm treatments at both intertidal heights; the number of degree hours and the number of days reaching or exceeding thresholds ( $\geq 33^\circ\text{C}$  and  $\geq 35^\circ\text{C}$ ) were higher on black plates compared to white plates. Cumulative warming was also higher in the high intertidal compared to the mid intertidal. Although high temperatures were recorded in all treatments, prolonged high temperatures were more frequent on black plates and high on shore compared to other treatments. The prolonged nature of this heating is important because chronic aerial thermal stress decreases the ability of intertidal organisms to recover between stressful events (Pincebourde et al. 2008). In addition, the high variability characteristic of warm plates is expected to be more important than increasing mean temperature alone, especially for mid-latitude ectotherms (Vasseur et al. 2014). Overall, the thermal characteristics of the warmed plates offer a realistic comparison to future summer thermal regimes, which are expected to feature longer, more frequent, more variable, and more intense high-temperature events (IPCC 2013).

### Demographic responses to warming

Barnacles are thought to be sensitive to increasing temperatures because they may already be living near their thermal maximum. Laboratory studies using heated air and field studies using shades have found that barnacle growth and survival decline in warmer treatments (Foster 1969, Wetthey 1984a, Bertness 1989, Bertness et al. 1999, Lamb et al. 2014). Field studies that manipulated substratum temperature confirm that warming negatively affects barnacles (Gedan et al. 2011, Lathlean & Minchinton 2012, this study). Consistent with our hypothesis, we found that barnacle vital rates (survival and growth, but not recruitment) were negatively affected by warming, which led to smaller population sizes of *Balanus glandula* and *Chthamalus dalli* on warm plates. Recruitment was statistically equivalent between cool and warm treatments, although there was a trend toward reduced recruitment in warm treatments. This trend was likely because our 2 wk estimates of recruit density included settlement, which was unlikely to be affected by plate color because settlement occurs at high tide, and survival, which was reduced by warming. For barnacles that survived, warming depressed growth rates for both species and at both intertidal heights, consistent with results

for Australian barnacles, where similar experimental methods were employed (Lathlean & Minchinton 2012). Barnacle survival was reduced on warmed plates, which resulted in smaller cohort sizes during summer and after 1 yr. The temperatures recorded on plates never reached or exceeded the thermal maxima recorded for adults of these species (W. Liao & C. D. G. Harley unpubl. data) but may have for younger barnacles. Regardless, the thermal conditions on warm plates were lethal to both species. This lethality is likely due to the chronic nature of the heating. For example, previous work that measured barnacle responses to aerial warming found that Hsp70 expression peaked at 33°C, suggesting that this temperature may represent an important thermal threshold (for *B. glandula*; Berger & Emlet 2007). However, Berger and Emlet did not observe any sign of irreversible protein damage when barnacles were exposed to temperatures up to 34°C for 8.5 h (the highest temperature tested), indicating that *B. glandula* are well adapted to their current thermal regime (Berger & Emlet 2007). In the present study, the ADM substratum temperature reached or exceeded 33°C for many more consecutive hours and days on warm plates. Although *B. glandula* may be able to withstand temperatures in excess of this threshold for 8 continuous hours on a few consecutive days (on cool plates), it is likely that the increased periods and frequency of hot (33–34°C) and very hot (35–41°C) temperatures were too thermally stressful for *B. glandula*, causing irreversible protein damage and reductions in survival.

Barnacle mortality can either result directly from environmental stress (Gedan et al. 2011) or indirectly from predators, such as the dogwhelk *Nucella ostrina*, the sea star *Pisaster ochraceus*, or dipterans in the genus *Oedoparena* (Harley & Lopez 2003, Harley et al. 2006, Harley & O'Riley 2011). *N. ostrina* were not observed on the plates during surveys, nor when just submerged (R. L. Kordas pers. obs.). Many mobile consumers feed when submerged rather than while exposed at low tide (Dahlhoff et al. 2002), so it is possible that predation occurred outside of survey periods. In fact, *P. ochraceus* were sometimes seen on plates shortly after submergence in the mid intertidal. However, *P. ochraceus* feed by pulling the entire barnacle off the substratum, leaving only basal plates behind. Since empty tests remained behind following barnacle death, it is unlikely that this predator contributed to our mortality patterns. *Oedoparena* have higher barnacle infestation rates in cooler areas (Harley & Lopez 2003), which would lead to the opposite pattern of mortality from that

observed. In addition, nocturnal predators were not observed on plates during nighttime surveys in winter. Lastly, *N. ostrina* and small *P. ochraceus* were found under plates with equal frequency among heating treatments (Kordas et al. 2015). Therefore, we are confident that the change in barnacle survival and abundance in warm treatments was due to the thermal manipulation rather than predation.

### Seasonal and ontogenetic variation in thermal sensitivity

For surviving *C. dalli*, sublethal effects of warming were evident in slower growth rates that led to smaller body sizes during summer on warm plates compared to cool plates. Contrary to our expectations, the severity of the warming effect was consistent for individuals settling at different times during the summer. However, the cohorts did exhibit different growth rates; barnacles settling earlier in the summer (May) had slower growth rates than later settlers (June and July). This difference may have been due to warmer than usual low tide conditions in May, or warmer water temperatures in late summer, or both. In 2009, the weather in May and early June was unusually hot, so barnacles settling before 22 May experienced 50% more days that exceeded thermal thresholds (33°C) compared to barnacles settling later (in June and July). In addition, ocean temperatures increased steadily from an average of 12°C in late May to 18°C in late August (see Fig. S1 in the Supplement). Because *C. dalli* cirral activity increases linearly over this temperature range (Southward & Southward 1967), it is likely that feeding rates during high tide were greater in later summer. Together, cooler ocean temperatures combined with hot low tide conditions in early summer likely led to reduced growth rates for the May cohort.

We also hypothesized that younger barnacles would be more sensitive to warming than older barnacles because smaller barnacles have a larger surface to volume ratio and thinner shells and therefore are more prone to water loss in warm conditions (Foster 1971, Ware & Hartnoll 1996). However, our results did not align with our initial hypotheses. Although younger barnacles had slower growth rates and were smaller than older barnacles, warming consistently reduced growth rates and body sizes of barnacles of all ages.

Nonetheless, the overarching detrimental effect of warming on the body size of all *C. dalli* cohorts remained pronounced. *C. dalli* reach maturity around

14 mm<sup>2</sup> basal area (Southward & Southward 1967). Smaller barnacles have lower reproductive outputs than larger barnacles (Wetthey 1984b). Because warming slowed growth rates, *C. dalli* of all ages were <14 mm<sup>2</sup> in the warmed treatment by the winter reproductive season and thus were unlikely to reproduce during that year (Fig. 6B, dashed black line). In a future with hotter aerial temperatures, the age of first reproduction may be delayed from Year 1 to Year 2 of a barnacle's life. For an organism with a 4 to 6 yr lifespan (Southward & Southward 1967), warming could significantly decrease lifetime reproductive output if it is not able to adapt in other ways (e.g. increase the frequency of reproduction).

### Interspecific variation in sensitivity to warming

Species living in similar habitats can be affected differently by abiotic conditions. As the climate changes, this may lead to changes in biotic interactions, as species respond to rising temperatures in different ways. In intertidal systems, species living higher on shore tend to be better adapted to high temperatures (Barnes et al. 1963, Foster 1971, Tomanek & Somero 1999, Wong et al. 2014). In British Columbia, the upper limit of *C. dalli* extends approximately 5 cm higher than that of *B. glandula*, and the upper lethal temperature of *C. dalli* is slightly higher than that of *B. glandula* (W. Liao & C. D. G. Harley unpubl. data). Perhaps not surprisingly, then, we found that warming reduced the survival and space occupancy of *B. glandula* more than *C. dalli*. At both heights, the entire June cohort of *B. glandula* died within 5 wk in warm treatments, while 31% of *C. dalli* in the high intertidal warm treatment survived until the end of the summer.

In the mid intertidal, biotic interactions with other species, such as green filamentous algae, likely contributed to interspecific differences in responses. Survival and cover of *C. dalli* were extremely low in both treatments. Algal (*Urospora* sp. and *Ulothrix* sp.) cover reached 50 to 100% and was similar in both mid-height treatments in June to July but was absent in the high intertidal until September (Kordas et al. 2015). When green algal mats were thick, we observed that *B. glandula* were tall enough to rise above the 3 to 4 mm thick mat, but *C. dalli* were not. Algae may have inhibited *C. dalli* respiration at low tide or interfered with their cirral activity during high tide (Barnes 1955).

Although interspecific differences in the relationship between temperature and survival were pro-

nounced, there were no interspecific differences in warming impacts on cohort densities or individual growth rates. Density estimates incorporated settlement and recruitment of new cyprids and their survival. Settlement was unlikely to vary (see 'Demographic responses to warming'), and recruitment did not vary between treatments. Therefore, the continual influx of new cyprids into the cohort probably swamped out potential interspecific differences in density, despite treatment effects on survival. *C. dalli* had slower growth rates and reached a smaller adult size than *B. glandula*, but warming had a similarly negative effect on the growth of both species. This may have been because the sample size was too low to detect a difference ( $n = 2$  warm plates in the high intertidal for *B. glandula*) or because only particularly robust barnacles survived thermal stress.

There was an apparent temperature-induced change in relative space occupancy during the hottest portion of the year in the mid intertidal. The relative percent cover of *B. glandula* was 500% higher than that of *C. dalli* in the cool treatment, but only 16% higher in the warm treatment. Although it is tempting to attribute this change to competitive release, competition was not likely to have been strong because barnacle-free space did not become limiting (according to Dayton 1971, space becomes limiting when total barnacle cover exceeds 50%). The relative importance of interspecific competition among barnacles, differential effects of other interacting species (e.g. macroalgae; see above), and simple direct effects of warming on each species are difficult to tease apart in this instance.

### Response to a changing climate

As the climate changes, oceans will warm at a slower rate than the air (Sutton et al. 2007), but in the long term, both will be important to barnacle survival. Based on our results and those in previous studies (Barnes & Barnes 1956, Hines 1978, Pfeiffer-Hoyt & McManus 2005, Emllet 2006, Berger & Emllet 2007, Harley 2011), we predict that increasing aerial temperatures will be detrimental to these barnacle species in geographical areas where conditions will become more stressful as the climate warms (i.e. 'hot spots', including the location of our study). It is possible that barnacles will be able to adapt, but these species may not have scope to acclimate to future warming (Berger & Emllet 2007). In addition, given the steep genetic cline between barnacle populations north and south of San Francisco and the homo-

geneity of northern populations (Sotka et al. 2004), the probability of warm-adapted genotypes arriving in British Columbia from the south appears to be remote. It is also possible that barnacles may shift their distributions down-shore to compensate for higher temperatures, but there are limits to how successful this strategy can be because lower limits may be constrained by interactions with other species (Harley 2011). Field-based experiments like the one described here, that increase thermal stress (rather than decrease it with e.g. shades), are still rare due to logistic difficulties, especially in marine systems, but can enhance our understanding of these ecological effects of climate change.

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Kowloon, Hong Kong, SAR

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