

LETTER

Physical effects of habitat-forming species override latitudinal trends in temperature

L. J. Jurgens* and B. Gaylord

*Bodega Marine Laboratory and
Department of Evolution and
Ecology University of California at
Davis Bodega Bay, CA, USA*

**Correspondence and present
address: Smithsonian Environmental
Research Center, 3152 Paradise Dr.,
Tiburon, CA, USA. E-mail: ljur-
gens@temple.edu*

Abstract

Latitudinal and elevational temperature gradients (LTG and ETG) play central roles in biogeographical theory, underpinning predictions of large-scale patterns in organismal thermal stress, species' ranges and distributional responses to climate change. Yet an enormous fraction of Earth's taxa live exclusively in habitats where foundation species modify temperatures. We examine little-explored implications of this widespread trend using a classic model system for understanding heat stresses – rocky intertidal shores. Through integrated field measurements and laboratory trials, we demonstrate that thermal buffering by centimetre-thick mussel and seaweed beds eliminates differences in stress-inducing high temperatures and associated mortality risk that would otherwise arise over 14° of latitude and ~ 1 m of shore elevation. These results reveal the extent to which physical effects of habitat-formers can overwhelm broad-scale thermal trends, suggesting a need to re-evaluate climate change predictions for many species. Notably, inhabitant populations may exhibit deceptive resilience to warming until refuge-forming taxa become imperiled.

Keywords

Biogenic habitats, biogeography, ecophysiology, elevation, environmental gradients, facilitation, latitude, positive interactions, species ranges, thermal stress.

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INTRODUCTION

Understanding patterns of thermal stress in natural populations is an environmental linchpin for many studies of biogeography and ecology due to the fundamental role of temperature in regulating biological processes (Gillooly *et al.* 2001; Allen *et al.* 2006). Thermal conditions, especially stressful or lethal ones, can dramatically affect physiological rates, population demographics and distributions and species interactions (Allen *et al.* 2002; Enquist *et al.* 2003; O'Connor *et al.* 2007). Attempts to predict spatial patterns of thermal stress for free-living organisms, and associated climate-driven range shifts, have typically emphasised large-scale abiotic trends, most notably the latitudinal (LTG) and elevational (ETG) temperature gradients (Colwell *et al.* 2008; Deutsch *et al.* 2008; Chen *et al.* 2011). However, biogenic habitats – including forests, shrublands, macroalgal canopies, mangroves, coral and oyster reefs, seagrasses and mussel beds – provide living space for an enormous fraction of species globally and can markedly alter thermal conditions experienced by resident populations (reviewed in Stachowicz 2001; Bruno *et al.* 2003; Ellison *et al.* 2005). While examples of such effects are well studied in particular habitats, some of their broader implications have received relatively little attention. In particular, the extent to which biogenic habitats might alter the strength or shape of LTG and ETG-based trends in thermal stress for resident taxa remains underexplored. This research gap makes it difficult to accurately conceptualise key geographical trends in temperature exposure and to predict climate change responses for the many species that spend all or part of their life histories within such assemblages.

Much of our current understanding of the biogeography and population consequences of heat stresses has emerged

from studying rocky shore systems at the land–sea interface. In these ecosystems, marine organisms chronically encounter temperatures near their upper thermal tolerances during aerial exposure at low tide. Latitude and shore elevation are established drivers of variation in thermal stresses for species occupying exposed rock surfaces (Somero 2002). Other abiotic factors also modify LTG-based trends, especially the timing of low tides relative to periods of intense solar radiation, which can generate high-latitude 'hot spots' (Helmuth *et al.* 2002; Lathlean *et al.* 2014), and topographical variation that influences sun exposure (Seabra *et al.* 2011). An additional contrast with terrestrial environments is that shoreline ETGs manifest over hundreds of metres, such that small gains in elevation of a metre or less can substantially exacerbate heat stresses for intertidal taxa (Somero 2002).

Within these rocky shore systems, biogenic habitats, formed largely by mussel beds or seaweeds, dominate across a broad range of latitudes to the extent that bare rock is often scarce at all but the highest elevation zones. Such space limitation creates fierce competition for primary substrate (Stephenson & Stephenson 1949; Paine 1974). At the same time, these biogenic habitats typically shelter the majority of species present in a locality during one or more stages of their life cycles, often hosting orders of magnitude more species than are found on exposed rock surfaces (Bertness *et al.* 2006; Raffaelli & Hawkins 2012; Lafferty *et al.* 2016). In doing so, mussel and seaweed beds, like terrestrial plants, characteristically buffer local temperatures via shading and moisture retention (Jenkins *et al.* 1999; Stachowicz 2001; Burnaford 2004; Bertness *et al.* 2006; Jurgens & Gaylord 2016; Pocklington *et al.* 2017).

Despite widespread appreciation for such facilitative effects of foundation species (e.g. Suchanek 1992; Bertness & Leonard 1997; Hawkins *et al.* 2015), the extent to which thermal

buffering influences broader-scale patterns of thermal stress remains an open question. While small shifts in latitude ($< 2^\circ$) may alter the strength of facilitation (Leonard 2000; Bertness & Ewanchuk 2002), geographical trends in high-temperature exposure, and their demographic and ecological consequences, remain unclear for taxa that occupy biogenic habitats. For example if thermal buffering is spatially consistent and moderate in intensity relative to latitudinal trends in temperature, it could simply shift the latitudinal curve towards less frequent or intense thermal stress, while maintaining the same general biogeographical pattern. Alternatively, if the magnitude of thermal buffering within biogenic habitats shifts with latitude, it could alter the steepness or curvature of the operational LTG. Completely new patterns could also arise, such as a reversal or removal of typical latitudinal trends.

On the basis of these unknowns, we ask here how thermal effects of two ubiquitous foundation species, a bed-forming mussel and a common turf alga, interact with latitude and shore elevation to determine the frequency of stress-inducing high temperatures for intertidal invertebrates, and the associated implications for their survival. We address this question by measuring temperatures in these biogenic habitats and in rock clearings at two shore elevations in three regions along the west coast of North America. These regions span mid-temperate latitudes over which the sharpest gradients in the incidence of high-temperatures typically occur (Colwell *et al.* 2008). We then analyse the relative contribution of habitat type, site, elevation and latitude to the frequency at which temperatures in each location exceeded sub-lethal and lethal heat-stress thresholds of common rocky shore invertebrates. Our findings reveal that effects of biogenic habitats over the extent of our study were strong and consistent enough to negate the effects of latitude and elevation.

METHODS

Study locations and temperature measurements

We measured habitat temperatures from June to October of 2012 and 2013 (typically the warmest months) on horizontal surfaces in experimentally formed rock clearings and inside two different biogenic habitats dominated by the foundation species *Mytilus californianus* Conrad 1837, the California mussel, and the turf-forming 'black pine' alga, *Neorhodomela larix* (Turner) Masuda, 1982. These two species are common primary space holders on rocky shores of the northeastern Pacific Ocean, form habitats with different structural traits, and frequently co-occur on intertidal benches where their broad ranges overlap (Alaska to south-central California, USA). Both species shelter a wide array of taxa whose small size means their body temperatures closely track the immediate environment (Porter & Gates 1969; Vermeij 1972). Many of these inhabitant taxa are important community members and provide resources for higher trophic levels including shorebirds and terrestrial mammals (D'Antonio 1985; Menge *et al.* 1993; Lafferty *et al.* 2016).

Study sites were embedded within three regions: one identified previously as a high-latitude, high-heat 'hot spot' (*sensu* Helmuth *et al.* 2002) for adult invertebrates living directly on

rock surfaces (48° N, Washington, USA), a cooler mid-region (38° N, northern California) and a warm, lower latitude region (34° N, southern California). To account for potentially appreciable variation at the site level, we replicated measurements at two sites within each region that differed in wave exposure, directional orientation and bedrock type (see Appendix S1; Table S1 in Supporting Information). To avoid confounding strictly latitudinal effects with those related to local oceanography at our lowest-latitude region (34° N, southern California), we avoided locations inside the Southern California Bight (SCB) where warm-water retention could influence the thermal dynamics of rocky benches. Instead, we chose sites on Santa Rosa Island, where the cool California current maintains water temperatures consistent with those in the other study regions (typically $9\text{--}18^\circ\text{C}$). This current bathes the majority of the mainland coastline in regions both north and south of the SCB.

At each site, we measured habitat temperatures every 30 min for roughly 20 weeks in 2012 (June 3–October 15; 135 days) and 2013 (May 27–October 20; 147 days) with small temperature loggers (Maxim[®] DS-1922L iButtons, 1.6 cm in diameter), placed in *M. californianus* beds (4–6 cm deep), *N. larix* turfs (2–6 cm deep) and in bare rock clearings scraped of biota ($N = 4$ loggers per habitat per site). We affixed calibrated and waterproofed instruments with neutral-coloured marine epoxy (Z-Spar[®] Splash Zone Marine Epoxy; following the same procedures as Jurgens & Gaylord 2016) to horizontal substrate in each habitat. We deployed temperature loggers from late spring through early autumn to capture the months of highest solar radiation (mid-summer) and warmest air temperatures (typically early autumn) along northeastern Pacific shores. Sampling every 30 min captured variation similarly well to more frequent measurements (5, 15, 20 min) in a 1-month test deployment and allowed us to log temperatures over 5 months without disruption.

We used the broad elevation zones typical of mussel beds to examine effects of biogenic habitats relative to shore elevation (the alga *N. larix* generally occurs only in the lower zone occupied by mussels). To do this, we replicated measurements in mussel beds and rock clearings at two elevations spanning the upper and lower quartiles of mussel distributions. Since tidal range and wave exposure vary markedly across sites and regions, the difference in the vertical extent of mussel beds and their specific elevation relative to the lowest daily low tide ('MLLW') varied by location. Differences between the 'high' and 'low' quartiles of the mussel beds, and hence our shore elevation comparisons, ranged from 0.6 to 1.3 m by site, with all shore elevations between 0.8 m and 3.4 m above MLLW (measured with a portable sight level and grading rod).

We measured temperatures in five habitat types per site within an area 20 m (alongshore) by 12 m (cross-shore): (1) upper quartile 'high-zone' mussel beds, (2) high-zone rock clearings, (3) lower quartile 'low-zone' *N. larix* turf, (4) low-zone mussel beds and (5) low-zone rock clearings. However, two sites – Point of Arches (48° N) and Northwest Talcott (34° N) – had comparatively narrow mussel zones. We measured mussel bed temperatures only at high-shore elevations at these sites. To minimise spatial variation not associated with the parameters of interest, we spatially interspersed

temperature loggers among microhabitats within an elevation zone, allowed elevation zones to span a maximum vertical range of 6 cm, and placed each logger in a experimentally cleared rock clearing within 25 cm of one located inside a biogenic habitat.

Defining thresholds of thermal stress

To compare how latitude, shore elevation and habitat influence the occurrence of stressful high temperatures on rocky shores, we used ecologically relevant assays of physiological stress in intertidal invertebrates that occupy biogenic habitat. Most organisms have evolved to tolerate a range of temperature conditions, and physiological stress occurs when this tolerable range is exceeded (here, we are concerned with the high end of that range). We used published studies and experiments to select two temperature thresholds beyond which lethal and sub-lethal stresses were highly likely for multiple rocky shore taxa. We then determined lethal thresholds experimentally for sample populations of a subset of invertebrates commonly found in the relevant habitats: juvenile mussels, *Mytilus californianus*; the predatory whelks *Acanthinucella spirata* Blainville, 1832 and *Nucella ostrina* Gould, 1852; and the herbivorous chink snail, *Lacuna vincta* Montagu, 1803. Across latitudes, genetic variation and acclimatisation to local conditions can influence thermal tolerance, as researchers have demonstrated in *M. californianus* (Logan *et al.* 2012). We therefore collected organisms from each study region and tested thermal tolerances in the laboratory after a period in common conditions (see Appendix S1). Temperatures over 35 °C killed nearly all individuals of each species (Appendix S1, Table S1) and we therefore chose 35 °C as our lethal high-temperature stress threshold (also supported as a critical threshold for heart function in adult *M. californianus*; Logan *et al.* 2012). We assigned our lower stress threshold at 26 °C, which is a common induction threshold for heat-shock proteins marking sub-lethal thermal stress for various intertidal snails, limpets and mussels along northeastern Pacific shores (Buckley *et al.* 2001; Tomanek 2002; Dong *et al.* 2008; Miller *et al.* 2009). Temperatures above this threshold also indicate potentially lethal thermal stress for species with comparatively lower thermal tolerances, such as the chink snail *Lacuna vincta* (Appendix S1, Table S2).

Data analysis

We analysed patterns in the duration of exposure to habitat temperatures over the 35 °C and 26 °C thresholds by latitude, shore elevation and habitat type. We calculated this response metric as the cumulative hours that habitat temperatures exceeded each threshold over the duration of temperature measurements. For analysis, we used the total hours per 30 days of measurement that habitat temperatures exceeded each threshold because tidal differences in the two study years led to small differences in the number of days we deployed instruments (135 vs. 147 days). We pooled data from measurements in mussel beds and *N. larix* turf to analyse the relative importance of biogenic vs. abiotic habitats compared to latitude and shore elevation in driving the duration of

exposure to temperatures over 26 °C. For this analysis, we fit a linear mixed effects model using restricted maximum likelihood procedures in R with the nlme package (version 3.1; Pinheiro *et al.* 2015). We modelled latitude/region, shore elevation and habitat type as fixed categorical factors (including interactions), with year and site as random effects (random intercepts) and variance conditioned on habitat type. We inspected residual plots to confirm homoscedasticity and approximate normality, and obtained *P*-values for fixed effects with likelihood ratio tests (details of model selection and validation in Appendix S1).

We used chi-square and Fisher's exact tests to compare the occurrence of temperatures over 35 °C across latitude, elevation and habitat type, since data violated assumptions of more complex approaches (biogenic habitats essentially eliminated temperatures over 35 °C). We also used a Fisher's exact test to examine if the identity of the habitat-forming species affected whether, at any time during the deployments, temperatures over 35 °C occurred.

RESULTS

In all locations, mussel and seaweed beds substantially attenuated high-temperature extremes and thermal variability (e.g. Fig. 1), dramatically reducing the occurrence of temperatures that exceeded stress thresholds for intertidal invertebrates (Fig. 2). Thermal buffering by mussel beds and *N. larix* turfs reduced the duration of biologically stressful temperatures within their confines to zero or near zero for temperatures over 35 °C, and by an order of magnitude for temperatures over 26 °C, regardless of shore elevation or latitude (Fig. 2). Biogenic habitat effects were sufficiently strong and consistent that they eliminated the otherwise strong latitudinal differences in the occurrence of high temperatures over invertebrate stress thresholds that were apparent in rock clearings (Table 1).

Mussel beds so efficiently reduced stressful high temperatures that the 0.6 to 1.3 m differences in shore elevation at each site had no effect on high temperature patterns within the beds (Table 1; Fig. 2). Although mussel beds more consistently depressed temperature maxima below both thresholds than *N. larix* turf (Fig. 2), we found no evidence that the identity of the habitat-forming species had significant effects on exposure to temperatures over either stress threshold (26 °C: $F_{1,42} = 0.15$, $P = 0.70$; 35 °C: *FET*, $P = 0.53$).

Unlike temperatures in mussel beds and algal turfs, rock surface temperatures in open clearings frequently (Fig. 2), and sometimes dramatically (e.g. Fig. 1), surpassed lethal thresholds for rocky shore taxa (high-shore rock clearings reached up to 46.5 °C). Effects of latitude and shore elevation on the incidence of stressful temperatures were significant in abiotic (rock clearing) habitats (Table 1), consistent with prior findings for adult invertebrates living in such locations (e.g. Hel-muth *et al.* 2002).

DISCUSSION

Results of this study reveal that physical effects of biogenic habitats 2–6 cm deep can override large-scale geographical

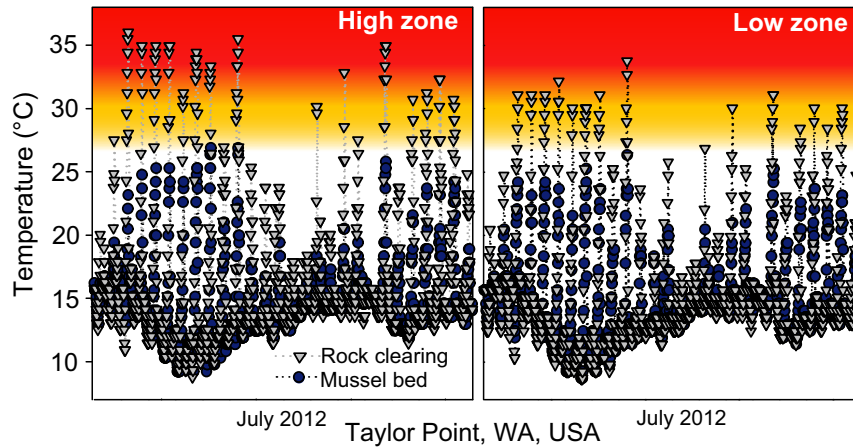


Figure 1 Temperatures measured every 30 min for the month of July 2012 in mussel beds and rock clearings at two shore elevations: high-shore (3.4 m above MLLW, left) and low-shore (2.1 m above MLLW, right) at one representative study site. Yellow shading denotes typical sub-lethal, and red indicates lethal, thermal stress thresholds for common invertebrates (see Appendix S1). For clarity, data depicted are from only one instrument per habitat and do not include algal bed temperatures (which followed similar patterns to mussel beds). Tide-driven fluctuations are apparent as roughly bi-monthly modulations of the time series. Variance and peak temperatures are greatest in rock clearings during low tide emersion, and are substantially reduced in mussel beds at both shore elevations.

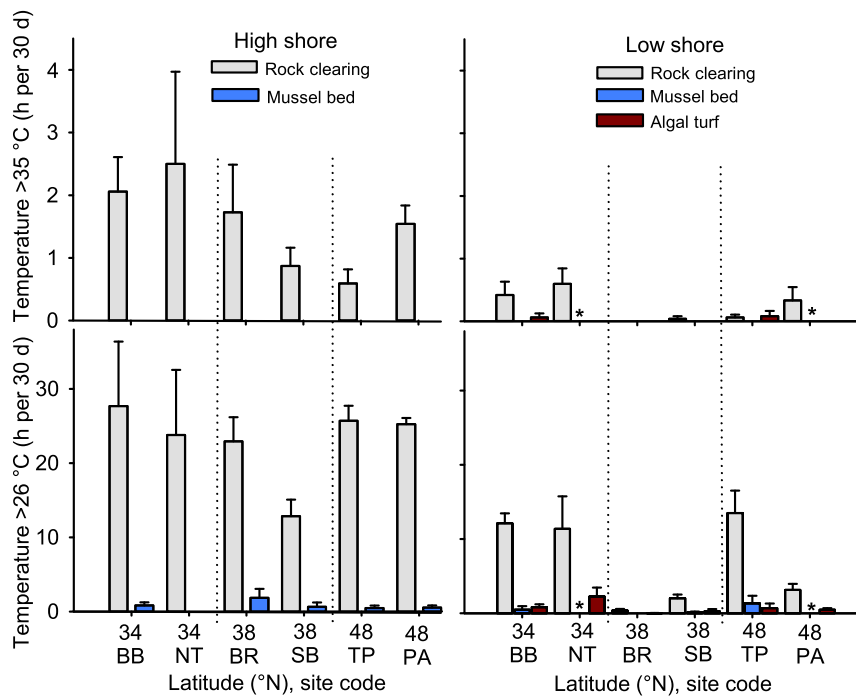


Figure 2 Measures of thermal risk appropriate to common intertidal invertebrates, shown as the duration of exposure to microhabitat temperatures exceeding two ecologically relevant thermal stress thresholds (in hours per 30 days + SE across replicate instruments; $N = 4$ per site per habitat per shore elevation). Results are partitioned by site within latitudinal regions, the latter separated by dashed lines. Upper panels depict exposure over a lethal threshold ($> 35\text{ }^{\circ}\text{C}$) for juvenile mussels and whelks. Lower panels depict exposure to temperatures $> 26\text{ }^{\circ}\text{C}$, a typical sub-lethal stress threshold for heat-tolerant species and a lethal one for the chink snail *Lacuna vincta*. Left panels show data from high-shore rock clearings and mussel beds, whereas panels to the right include data from the same habitats in low-shore zones where algal turfs are present (*Neorhodomela larix*). Asterisks indicate sites with no low-zone mussel beds; all other zeros are true zeros.

and mid-scale elevational patterns in thermal stresses on rocky shores, with implications for mortality and decreased fitness in associated organisms. We found that LTG and ETG-driven trends of thermal stress were not just diminished, but functionally eliminated within mussel beds and algal turfs, such

that neither latitude nor elevation had any effect on the frequency of exposure to stress-inducing temperatures (Table 1). Biogenic habitats overwhelmed latitude and shore elevation effects on both lethal and sub-lethal heat stresses, the latter of which is typically accompanied by important energetic costs

Table 1 Results of linear mixed effects model analysing the duration that microhabitat temperatures exceeded 26 °C, a common stress threshold for marine invertebrates, as a function of habitat type (biogenic: mussel and seaweed beds, vs. abiotic: rock clearings), latitude and shore elevation. Effects of latitude and shore elevation are significant only in rock clearings (significant terms are italicised). The model incorporated different variance structures by habitat type (std. dev. in abiotic habitats = 7.14 times that in biogenic habitats; see also Appendix S1, Figs S1, S2).

Fixed effects	Estimated effect	SE	<i>P</i> -value
<i>Habitat type (biogenic relative to abiotic)</i>	-17.19	2.48	< 0.0001
Latitude × habitat (reference: 38° N)			
<i>Abiotic habitat at 48° N</i>	+7.55	3.10	0.016
Biogenic habitat at 48° N	+0.24	0.41	0.57
<i>Abiotic habitat at 34° N</i>	+8.18	3.07	0.0085
Biogenic habitat at 34° N	+0.45	0.43	0.29
Elevation × habitat type (reference: high zone)			
<i>Abiotic habitat in low vs. high</i>	-16.55	2.54	< 0.0001
Biogenic habitat in low vs. high	-0.12	0.34	0.72
Random effects			SD
Intercept by year			0.73
Intercept by site			0.21

to organisms that can reduce fitness (Somero 2002). These findings suggest value in incorporating biogenic habitats more explicitly into existing conceptual models of biogeographical patterns in heat stress. For intertidal biota, for instance, a trend line that does not vary appreciably across latitude may be more relevant for a wide diversity of organisms that occupy such ubiquitous habitats, in comparison to standard LTG constructs, or even an LTG modified to incorporate tidal regimes (Fig. 3).

Similarly, our data suggest that concepts of vertical stress gradients associated with elevation, which dominate textbook descriptions of rocky shore ecosystems, may apply less strongly than is often anticipated, at least to the many species living in and among biogenic habitats. Indeed, for mobile species, our findings suggest that individuals encountering hot conditions on exposed rock surfaces could reduce the risk of thermal stress more by moving into an adjacent mussel bed than by descending a metre in shore elevation (e.g. Fig. 1). These results indicate that habitat-forming species may operate as ‘vertical equalisers’, largely eliminating otherwise significant differences in the incidence of high temperatures across substantial swaths of shore elevation (Table 1, Fig. 2). Of course this phenomenon is not likely to apply to primary substrate holders (such as adults of the habitat-formers themselves) or in locations where biogenic habitats are scarce, as may occur on tropical rocky shores (e.g. Lubchenco *et al.* 1984), although abiotic thermal refugia, such as shady crevices, may also play important roles for species regulating thermal exposure on rock surfaces (e.g. Seabra *et al.* 2011; Dong *et al.* 2017). Here, thermal buffering effects of mussel beds were consistently strong at all sites across the latitudinal range of the study, suggesting that these biogenic habitats may extend vertical ranges of heat-sensitive organisms (i.e.

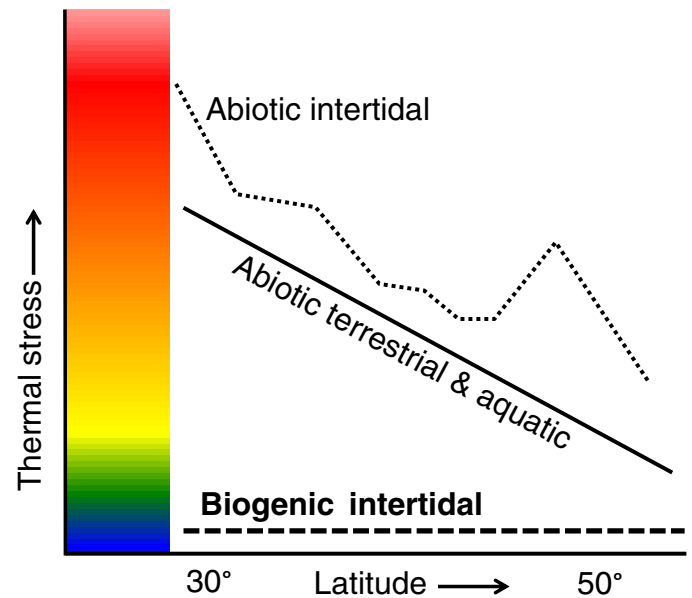


Figure 3 Data from this study indicate that biogenic habitats (mussel and seaweed beds; dashed line) functionally eliminate latitudinal patterns in the occurrence of stress-inducing high temperatures typical across temperate regions. In both aquatic and terrestrial systems unmodified by biogenic habitats (unbroken line), this trend often follows the traditional latitudinal temperature gradient (LTG). Effects of biogenic habitats complement other, previously identified factors that cause deviations from the LTG; for example patterns of thermal stress in abiotic (rock surface) intertidal habitats are often complicated by spatial anomalies associated with the timing of low tides (an example of which is depicted by the dotted line). There, rock temperatures also tend to exceed water and air temperatures under intense solar radiation during aerial exposure.

niche expansion, Bruno *et al.* 2003; and e.g. Moore *et al.* 2007) over large portions of species ranges.

Although research increasingly considers biotic interactions as potentially important modifiers of climate change outcomes (especially predation and competition; Poloczanska *et al.* 2008; Harley 2011; Zarnetske *et al.* 2012) our data reveal the extent to which facilitative interactions, or ‘ecosystem engineering’ (*sensu* Jones *et al.* 1997), can directly affect temperature patterns across multiple spatial scales. In particular, our findings highlight the climatic value of biogenic habitat and the potential for its preservation, restoration or enhancement to offer double benefits, at least in the short term, by reducing climate-driven thermal stresses for inhabitant taxa. Such stresses are capable, as are various other stressors, of inducing mass mortalities with long-term population consequences (e.g. Harley 2008; Jurgens *et al.* 2015), and any reduction in their occurrence may therefore increase population-level climate resilience. At the same time, activities that decrease foundation species cover – including harvest, trampling, pollution and coastal development (reviewed in Thompson *et al.* 2002) – could concomitantly reduce climate resilience in intertidal systems. Climate warming itself can also shift distributions of habitat-forming species (e.g. Southward *et al.* 1995; Helmuth *et al.* 2006; Sorte *et al.* 2017). Results here emphasise the importance of direct micro-climatic effects of habitat-forming taxa on inhabitant populations in these systems, providing further support for considering foundation species dynamics

as key factors influencing community and ecosystem responses to climate change (Hiscock *et al.* 2004; Hawkins *et al.* 2008, 2009; Wernberg *et al.* 2010). There is also the possibility that taxa not currently associated with facilitative habitats – but which face increasing climate variability and temperature extremes – may increase their use of biogenic habitat refugia. This concept is now receiving discussion if not yet wide investigation (Williams *et al.* 2008).

More broadly and perhaps most crucially from an applied perspective, our results emphasize the need to quantify habitat-level conditions explicitly when attempting to forecast species' responses to warming (see, e.g. analogous considerations for abiotic habitats; Kearney & Porter 2009). This approach could be critical to refining predictions from large-pixel analyses derived from satellite data, which include spatial projections of rates of movement of climatic parameters across the landscape ('climate velocity') (e.g. Loarie *et al.* 2009; Burrows *et al.* 2011). In particular, low-latitude and low-elevation range contractions predicted under climate change (Parmesan 2006; Chen *et al.* 2011) may not track thermal niches of many populations, but instead might apply most appropriately in cases where warming shifts the presence, extent, or thermal buffering capacity of a habitat-forming species. Populations buffered strongly from thermal stress may therefore appear deceptively resilient to warming temperatures until conditions reach a tipping point that removes or reduces the efficacy of biogenic thermal refugia.

While our results are most directly relevant for biogenic habitats on rocky shores, similar dynamics are likely in many other ecosystems, such as the variety of terrestrial ones where dense vegetation buffers both extreme low and high temperatures (Callaway & Walker 1997). Indeed, in any system where they occur, taxa that strongly modify temperatures may revise the applicability of typical latitudinal and elevational gradients in thermal stresses. Biogenic habitats therefore have the potential to influence dependent species' ranges, evolution of thermal tolerances, and responses to climate warming in a broad range of systems.

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AUTHOR CONTRIBUTIONS

LJJ designed the research with input from BG. LJJ conducted the experiments and analysed the data. LJJ and BG wrote the manuscript.

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