Body temperatures of an intertidal barnacle and two whelk predators in relation to shore height, solar aspect, and microhabitat

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ABSTRACT: Accurate predictions of species responses to climate change require a detailed understanding of the temperatures that organisms experience in the wild. We developed biomimetic physical models of 3 common northeastern Pacific intertidal species: 2 predatory dogwhelks, *Nucella ostrina* and *N. lamellosa* and their barnacle prey, *Balanus glandula*. We established 42 biomimetics in up to 11 different microhabitats within an approximately 100 m^2 region of the shoreline on San Juan Island, Washington, USA. Average temperatures were recorded at 15 min intervals over 3 successive summers. We found large differences in temperatures of *N. ostrina* biomimetics when placed in different microhabitats; as much as 8°C difference in mean daily maximum temperature and over 30 °C differences on individual days. Solar refuges and differing solar aspects reduced body temperatures, relative to more sun-exposed locations at the same shore height, by as much as moving 0.5 m lower on the shore. When biomimetics of the 3 species were placed in the same habitat, average daily maximum temperatures differed by <0.2°C, a surprisingly small amount. Yet because these species differ greatly in known thermal tolerances, the temperatures imply large differences among species in daily risk of thermal stress (0 to 33.8%). Further, *N. ostrina* could halve its risk of thermal stress on the high shore by moving between solar aspects. The ability of mobile predators such as *Nucella* spp. to exploit spatio-temporal variation in temperature likely influences their ability to regulate sessile prey such as *B. glandula*.

KEY WORDS: Intertidal · Temperature · *Nucella* · *Balanus* · Solar aspect · Microhabitat · Foraging

INTRODUCTION

Predicting the consequences of climate change for natural communities is perhaps the greatest challenge facing ecologists today. Rocky intertidal communities have immense potential for the development of mechanistic, predictive models of community responses to climate change (Helmuth et al. 2006, Denny et al. 2011). Their long history of experimental study within ecology (e.g. Connell 1961, Paine 1966) has revealed strong relationships between physical factors and species distributions. The intertidal zone is characterized by steep vertical gradients in temperature and desiccation stress, controlled by tidally driven increases in the duration of exposure to aerial conditions at higher shore heights. A species' upper vertical limit is generally thought to be determined by its direct physiological tolerance and its lower limit is typically controlled indirectly by the physiological tolerances of its 'enemies', such as predators or competitors (Levinton 2013). Thus, a species' ability to persist locally under warming temperatures

depends on how both limits respond to warming. Local extirpation will occur when a species is more sensitive to warming than its lower shore enemies and its vertical range compresses towards zero (Huey et al. 2002, Stillman 2003, Harley 2008). Vertical range compression has been identified as an important cause of geographic range boundaries in several species (Wethey 2002, Harley 2013); thus, understanding the influence of temperature on local-scale patterns of distribution and persistence is key to developing general predictions of the effects of climate change on intertidal communities (Huey et al. 2002, Denny et al. 2011).

Predicting a species' response to rising temperatures requires understanding not only its physiological tolerances (Pörtner et al. 2006, Angilletta 2009), but also determining the actual body temperatures the species experiences in the field (Chapperon & Seuront 2011, Potter & Woods 2013). Intertidal species are poikilothermic, meaning that their body temperatures are determined by a combination of environmental conditions, such as air temperature and solar radiation, and the physical properties and behaviors of individual organisms. Accurate estimates of field body temperatures require either mathematical modeling of the relevant physical processes (Porter & Gates 1969, Helmuth 1998, Miller & Denny 2011) or the construction of physically matched ('biomimetic') temperature sensors (Fitzhenry et al. 2004, Lima & Wethey 2009, Szathmary et al. 2009, Lathlean et al. 2014). Regardless of the method chosen, each species has a unique set of energy transfer relationships (Porter & Gates 1969, Broitman et al. 2009), and thus the method must be repeated for each member of a community of interest. However multi-species studies of thermal niches remain rare in intertidal ecology (e.g. Broitman et al. 2009, Miller & Denny 2011). Without a general understanding of the magnitude of interspecific variation in body temperatures, it will be difficult to make accurate predictions of responses to warming.

Rocky intertidal shores are also characterized by high levels of small-scale thermal heterogeneity, which can exceed latitudinal scale thermal differences (Seabra et al. 2011, Lathlean et al. 2012). In addition to the vertical clines in temperature driven by tidal exposure, rocky shores also show smaller-scale temperature changes from variation in solar radiation. For example, animals in crevices or under canopy-forming algae are sheltered from direct sunlight and thus experience cooler body temperatures and reduced desiccation stress during low tide. These solar refuges can be exploited by mobile consumers to forage in areas higher on the shore than they could normally tolerate (Fairweather 1988). Similarly, rocks with different solar aspects may show large differences in thermal environments, which can influence species composition (Vaselli et al. 2008, Lathlean & Minchinton 2012). Although these microhabitats are known to affect community interactions and composition, the magnitude of their thermal differences has rarely been quantified (Chapperon & Seuront 2011).

Here we report on the results of a 3 yr study of temperatures recorded by biomimetic thermal sensors of the barnacle *Balanus glandula* and 2 dogwhelks, *Nucella ostrina* and *N. lamellosa* on San Juan Island, Washington, USA. All 3 species are common members of northeastern Pacific rocky intertidal communities, and have been studied extensively in this region (e.g. Connell 1970, Spight 1982, Palmer 1984). Both species of dogwhelk prey on *B. glandula*, and their population sizes are likely influenced by barnacle supply (Spight 1982), although *N. lamellosa* prefers the larger *Semibalanus cariosus* (Palmer 1984). The 3 species occupy overlapping vertical distributions on the shore, with *B. glandula* being highest and *N. lamellosa* lowest. *B. glandula*'s lower limit is strongly influenced by dogwhelk predation (Connell 1970, Spight 1982) and thus its ability to persist under warming temperatures will depend on the balance between the vertical space it can occupy under warming temperatures and that of the dogwhelks.

We address 3 related questions in this study. First, for a single species (*N. ostrina*), how do shore height, solar aspect, month, and solar refuge influence daily maximum body temperatures? Second, how much does body temperature vary among the 3 species when in the same microhabitat? Third, how does the range of temperatures experienced by each species compare to its thermal tolerance?

MATERIALS AND METHODS

Development of biomimetics

We constructed biomimetics of *Nucella ostrina*, *Nucella lamellosa* and *Balanus glandula*, each housing a small thermocouple to record long-term temperature in a specific microhabitat (Fig. 1). We used biomimetic models instead of live animals because the thermocouple probes are invasive in small-shelled organisms and impractical for mobile snails. Each biomimetic was individually wired to a central datalogger.

Fig. 1. Example of deployed biomimetics. The 6 biomimetic physical models deployed at the south-mid-exposed microhabitat, left to right: *Nucella lamellosa, Balanus glandula, N. ostrina, N. lamellosa, N. ostrina, B. glandula.* Snail biomimetics were made from empty snail shells filled with epoxy. Barnacle biomimetics consist of small dots of a different epoxy. A thermocouple sensor was inserted into each biomimetic and connected to a datalogger on land. See 'Materials and methods: Development of biomimetics' for complete details of biomimetic construction

To construct the snail biomimetics, *N. ostrina* and *N. lamellosa* shells (15–20 mm and 25–30 mm in length, respectively) were air-dried and emptied. A small thermocouple made from 24 gage type T wire (FF-T-24-SLE, Omega Engineering) was threaded through a ~2 mm hole drilled on the lateral side of the largest whorl and centered in the approximate position of the extracted snail. The shell was flooded with epoxy (Devcon 2-Ton, ITW Polymers Adhesives North America) using a syringe and needle inserted in a 0.8 mm hole drilled in a smaller whorl on the ventral side, thereby minimizing air pockets. The biomimetics were adhered to the rock with a small pad of epoxy (Fig. 1; Z-Spar A-788 Splash Zone Epoxy, Carboline). Barnacle biomimetics were constructed from white epoxy (PC Marine, Protective Coating). A thermocouple was inserted into a small ball (~0.25 g) of mixed epoxy, adhered directly to the rock and molded into a volcano shape similar to a live barnacle (Fig. 1).

The biomimetics were tested against live organisms as they heated up in a laboratory wind tunnel similar in construction to that of Bell (1995). Five hundred watt PAR64 incandescent lights were mounted over a water bath above the tunnel to provide radiant energy similar to noontime summer sun (~1000 W m^{-2}). A steady gentle breeze (10 cm s^{-1}) was generated by a low-speed blower. Similar sized pairs of biomimetics and live organisms were initially submerged in seawater at 11 to 12°C and then placed in the working section of the wind tunnel for comparison. Five *N. ostrina* biomimetics were placed next to live *N. ostrina* on a 28 × 28 × 1 cm granite tile. Separately, 4 barnacle biomimetics were molded adjacent to live *B. glandula* growing on small cobbles. Thermocouples were inserted into live organisms through small holes drilled on the side of the shell and all temperatures were recorded every minute by a datalogger (21X, Campbell Scientific). Biomimetics and organisms were heated until equilibrium temperature was reached, typically around 2 h. Temperatures were recorded every minute and the maximum temperature of each sensor was calculated.

Biomimetic deployment and data collection

The field study was conducted at the University of Washington's Friday Harbor Laboratories Biological Preserve (FHL) on San Juan Island in the Salish Sea (48.5461° N, 123.0078° W) during the summers of 2010–2012. Biomimetics of the 3 species (Table 1) were deployed in up to 11 microhabitats, representing combinations of 3 shore heights (high, mid, low), 2 solar aspects (south, east), and 3 microclimates (sun exposed, under *Fucus*, crevice). In some cases, 2 replicate biomimetics were placed within 5 to 10 cm of each other (e.g. Fig. 1). The biomimetics were re-established in May of each summer, and checked for damage (e.g. cracked or eroded shells, loss of *Fucus* cover, broken wires) every 1 to 7 d until at least August 31 of each year. The period from May to August represents the time of year during which warm daytime low tides are most common at FHL. Dogwhelk

Table 1. Summary of biomimetic deployments. Species-number: species (O = *Nucella ostrina*, B = *Balanus glandula*, L = *Nucella lamellosa*) and number of replicate biomimetics

Aspect	Height	Micro-habitat	Shore height (m)	Species-number
South	High	Exposed	1.23	O-2, B-2, L-2
		Crevice	1.23	O-2
	Mid	Exposed	0.69	O-2, B-2, L-2
		Crevice	0.69	O-2
		Fucus	0.73	O-2, B-2, L-2
	Low	Exposed	0.30	O-2, B-2, L-2
		Crevice	0.30	O-2
East	High	Exposed	1.40	O-1, B-1
	Mid	Exposed	0.89	O-2, B-2
		Fucus	0.89	O-1, B-1
	Low	Exposed	0.40	O-2, B-1, L-1

foraging is also greatest during this time (Spight 1982, H. Hayford pers. obs.), most likely because barnacle settlement peaks in spring (Strathmann 1987) and the metabolic demand of the snails is greatest in the summer.

The 3 tidal heights were selected to encompass most of the vertical range of *B. glandula*. The high shore biomimetics (1.23 to 1.4 m +MLLW [mean lower low water]) coincide roughly with mean sea level (1.387 m +MLLW, National Ocean Service 2003). This region is characterized by barnacles and littorine snails alternating with bare rock. *Nucella* spp. rarely occur above this height, although *B. glandula* may extend up to 2.0 m +MLLW (Connell 1970). The mid region (0.69 to 0.89 m +MLLW) consists of interspersed patches of *B. glandula* and *Fucus* spp. *N. ostrina* was most common in this region. Our low sites (0.30 to 0.40 m +MLLW) fall in a region of turf algae with few *B. glandula* or *Fucus* spp. *N. ostrina* was rare here. *N. lamellosa* was only observed in the low zone, primarily during neap tides.

Each thermocouple wire was anchored flush to the rock using restraining clips and strung 15 to 20 m upshore through a 5 cm diameter PVC conduit pipe. The terminal of each thermocouple was connected to a multiplexer that was sampled every minute by a datalogger (AM-25T Multiplexer and CR1000 datalogger, Campbell Scientific) and average temperatures were recorded at 15 min intervals. Data were exported to a web browser (Vista Data Vision, Vista Engineering) for near real-time display.

Recorded data were checked for errors in 2 ways. First, when physical damage was observed in the field, we spliced in a new biomimetic and deleted all temperature data recorded from the last time the sensor had been observed undamaged through the time of repair. The causes of physical damage included logs, wave action, and, in one case, a lightning strike. Second, all raw data were plotted in 2 wk intervals and days with unrealistically extreme values (<5°C or >45°C), likely caused by loose wiring or electrical noise, were identified visually and excluded. Where data were available for more than one intact biomimetic of the same species and microhabitat, we averaged each time point.

We selected the daily maximum temperature as our metric for all temperature analyses, as this is often more biologically relevant than mean temperature (Camacho et al. 2015). We considered a range of other metrics, including daily mean temperature, daily 97th percentile and the daily duration of time above 25°C; all calculated both for all daily observations and for only emersed observations. Initial comparisons revealed a high degree of correlation (r = 0.77 to 0.99) among these different metrics, and so it is unlikely a different metric would change our conclusions.

Statistical analyses

All statistical analyses were conducted in SAS v.9.3 (SAS Institute). To evaluate the magnitude of intraspecific temperature variation, we compared the effects of height, solar aspect, shading, and month on recorded *N. ostrina* temperatures using a mixed-model ANOVA in SAS Proc Mixed. The main factors were shore height (high, mid, low), month (May, June, July, August), and habitat (south-facing exposed, east-facing exposed, or south-facing crevice), and all possible interactions were included. We also examined interspecific differences among only south-facing biomimetics in a second mixed-model ANOVA. The main factors were month (as above), species (*B. glandula*, *N. lamellosa*, or *N. ostrina*), and height-habitat (high exposed, mid exposed, mid under-*Fucus*, and low exposed), and all possible interactions were included. For both ANOVAs, year and day within year were included as random replicates. We controlled for non-independence of errors by using an autocorrelated (Toeplitz) error model (Littell et al. 2006). Residuals were significantly heterogeneous among factor levels. Due to computer limitations, we were not able to model the heterogeneous variance directly; however, because the magnitude of the variance was positively correlated with the sample size (*N. ostrina* model: r = 0.58, p = 0.0002; all-species model r = 0.13, p = 0.36) we expect our analyses are conservative (Glass et al. 1972). Additionally, the residuals showed significant non-normality, based on a Shapiro-Wilk, test. No corrections were attempted, because sample sizes were very large and the distribution of errors was symmetric. Under these conditions, ANOVA should be robust to non-normality (Underwood 1997, Zar 2009). The Tukey-Kramer method was used to correct for multiple comparisons.

We used linear regression in SAS Proc Reg to determine if the midpoint time of each low tide exposure was associated with the observed relative temperature differences between south- and east-facing sun-exposed biomimetics at the same shore height. The previous day's temperature was included as a covariate to eliminate autocorrelation of errors. The start and end of daily low tide exposure was calculated by comparing our surveyed heights of each

habitat (Table 1) to the observed tidal height at 15 min intervals recorded by a water level sensor on the FHL main dock maintained by NOAA's National Water Level Program (http://co-ops.nos.noaa.gov/nwlon.html). We calculated the midpoint of low tide by averaging the start and end times of each habitat's emersion period.

Finally, we estimated the frequency of lethal events for each species by comparing its daily temperature maximum to the measured LT_{50} (the temperature lethal to 50% of individuals) for a 4 h low-tide exposure. For these calculations, we replaced missing values in the daily maximum temperature dataset with predicted values from the 2 ANOVA models described above (7.8% of observations in the all-species model, 9.6% in the *N. ostrina* model). We used LT_{50}s of 34 and 30°C for *N. ostrina* and *N. lamellosa*, respectively (Bertness & Schneider 1976), and 40.5°C for *B. glandula* (S. Gilman unpubl. data). All LT_{50}s were measured in the summer (Bertness & Schneider 1976, S. Gilman unpubl. data), and thus should match thermal tolerances in the season of this study. We label these 'near-lethal' events, rather than lethal events, because we are comparing the daily maxima, which may have been recorded for as little as 15 min, to a 4 h LT_{50}. This is necessary because LT_{50}s were not available for *B. glandula* for a period shorter than 4 h.

RESULTS

Laboratory comparison of biomimetics to live animals

Correlation coefficients—from the 1 min data—between each of the 9 biomimetic-animal pairs exceeded 0.99 in all cases (n = 260 for each barnacle pair, n = 104 for each snail pair). At equilibrium, the average (±1 SD) difference between the maximum temperature of each barnacle and its paired biomimetic was −0.10 ± 0.30°C. The instantaneous difference between biomimetics and live barnacles was always less than 2°C, and biomimetics reached equilibrium at roughly the same time as live barnacles, suggesting similar response times. The average difference (±1 SD) for the snail pairs at equilibrium was 2.60 ± 0.85°C. Instantaneous differences during heating were within ±3°C. Although the mean equilibrium difference for snails was larger than that for barnacles, it was comparable to those reported for other molluscs (Fitzhenry et al. 2004, Lathlean et al. 2014).

Table 2. *F*-test for ANOVA models comparing daily maximum body temperatures of (A) *Nucella ostrina* biomimetics in south- and east-facing habitats, and (B) biomimetics of all 3 species (*N. ostrina*, *N. lamellosa* and *Balanus glandula*) in south-facing habitats. Significant p-values are in **bold** (p < 0.05)

Effect	df	*F*	p
A. *Nucella ostrina*			
Habitat[a]	2, 38.2	63.71	**<0.0001**
Height	2, 38	366.97	**<0.0001**
Month	3, 236	8.17	**<0.0001**
Habitat × Height	4, 38.1	5.34	**0.0016**
Habitat × Month	6, 64.9	3.74	**0.0029**
Height × Month	6, 64.9	3.87	**0.0023**
Habitat × Height × Month	12, 69.7	0.98	0.4749
B. All species			
Species	2, 61.8	0.43	0.6540
Height-habitat[b]	3, 61.7	526.24	**<0.0001**
Month	3, 313	5.65	**0.0009**
Species × Habitat	6, 61.6	2.56	**0.0282**
Species × Month	6, 171	0.45	0.8467
Habitat × Month	9, 174	6.77	**<0.0001**
Species × Habitat × Month	18, 176	0.41	0.9840

[a]Habitat contains 3 categories: south facing and sun exposed, east facing and sun exposed, south facing and crevice
[b]Height-habitat contains 4 categories: high shore and sun exposed, mid shore and sun exposed, low shore and sun exposed, mid shore and under *Fucus*

Thermal variation among *Nucella ostrina*

Overall, *Nucella ostrina* body temperatures differed significantly among habitats (combinations of aspect and shelter), shore heights, and months (Table 2A). All 3 of the possible 2-way interactions were also significant. Body temperature increased significantly with height. Daily maximum temperatures high on the shore averaged 7.0°C warmer than low on the shore (Fig. 2) and this difference was as much as 30°C on some individual days. The mid-shore biomimetics were intermediate, averaging 4.6°C cooler than the high shore and 2.3°C warmer than the low shore. Among habitats, the south-facing crevice habitat averaged 2.4°C cooler than the south-facing sun-exposed biomimetics and 2.8°C cooler than east-facing sun-exposed biomimetics. These differences are roughly comparable to those between adjacent heights. On average there was a 0.5°C difference between south- and east-facing sun-exposed habitats, a difference that was not statistically significant. Finally, significant, but slight, differences in average biomimetic temperatures among months were detected. Overall, July was 1.9 to 4.1°C warmer
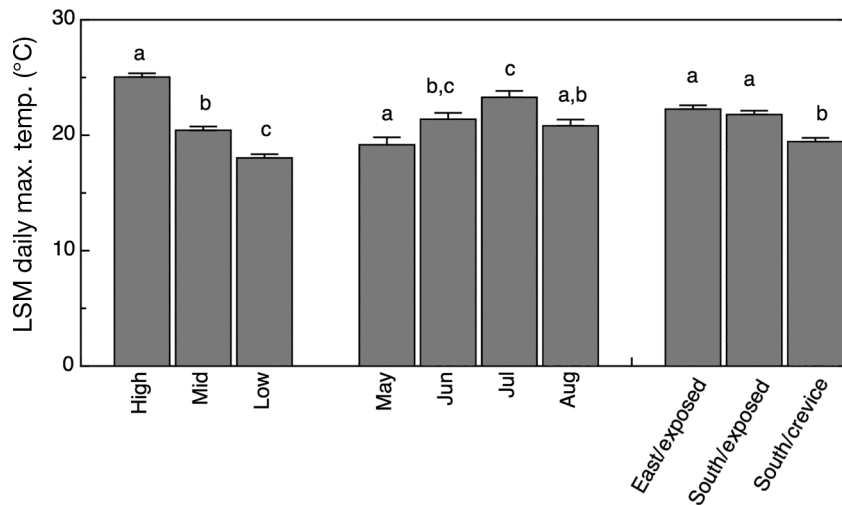
Fig. 2. Main effects of habitat, shore height, and month on *Nucella ostrina* daily maximum temperature. Values are least squared means (+SE) generated from the ANOVA model. Different letters indicate bars that are significantly different from each other (p ≤ 0.05, Tukey's HSD; comparisons made only within each main effect)

than the other 3 months, but only significantly warmer than May and August. May was also significantly cooler than June, by 2.2°C.

The 3 significant 2-way interactions (Table 2A) all reflected only minor variations on the patterns of the main effects. The height by month interaction (Fig. 3A) was driven by the high shore, the only height at which July was significantly warmer than June. However, July remained the warmest month and May the coolest month at all 3 heights. The significant interaction between height and habitat (Fig. 3B) was driven mainly by a smaller difference between crevice and exposed habitats at higher shore heights. Specifically, in the high shore, crevice was not significantly different from south exposed (p = 0.052). However, within each height the crevice was always the coolest habitat; and within each habitat the 3 heights always showed the same rank order. Finally, we also found a significant habitat by month interaction (Fig. 3C). The relative rank of the 2 sun-exposed habitats changed with month. The east-facing sun-exposed biomimetics were slightly, but not significantly, cooler in May than the south-facing sun-exposed biomimetics. By August, the east-facing habitat was significantly warmer than the
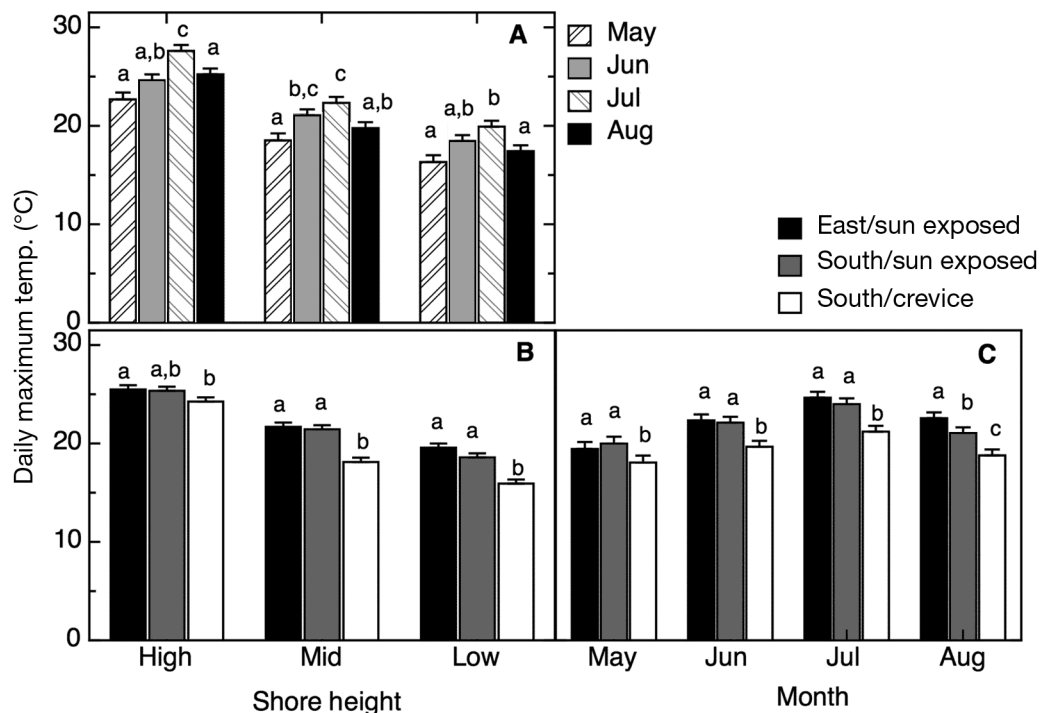

Fig. 3. *Nucella ostrina* daily maximum body temperatures recorded by biomimetics, partitioned among 3 interaction terms: (A) shore height × month, (B) shore height × habitat, and (C) month × habitat. Values are least squared means (+SE) generated from the ANOVA model. Different letters indicate bars that are significantly different from each other (p ≤ 0.05, Tukey's HSD; comparisons made only within each height or month)
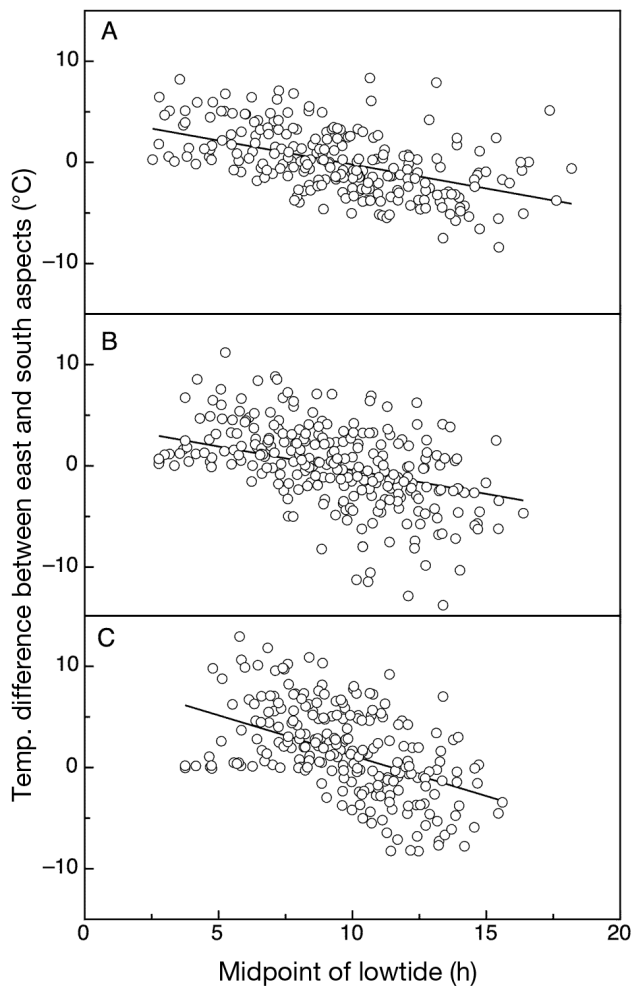
Fig. 4. Net difference in daily maximum body temperature between east-facing and south-facing sun-exposed *Nucella ostrina* biomimetics at the (A) high, (B) mid, and (C) low shore heights plotted against the median time (hour of day) of low tide for each shore height. The solid line is the best fit line from the multiple linear regression (see 'Results: Thermal variation among *Nucella ostrina*' for equations)

south-facing habitat, although the mean temperature difference was only 1.5°C. The crevice habitat was consistently the coldest of the 3, regardless of month.

To determine if the month by habitat interaction reflected differences in patterns of solar radiation on the 2 aspects, we regressed the daily temperature difference between east- and south-facing biomimetics at the same height to the time of day of the midpoint of low tide exposure for each height (Fig. 4). These regressions all showed a significant negative relationship ($p < 0.0001$ for all 3 slope terms), indicating that the later in the day that the midpoint of low tide exposure occurred, the more likely the south-facing site was warmer (high: $y = 4.53 - 0.47$midpoint $+0.08$lag(y), $r^2 = 0.25$; mid: $y = 4.26 - 0.47$midpoint $+0.40$lag(y), $r^2 = 0.36$; low: $y = 9.15 - 0.8$midpoint $+0.26$lag(y) $r^2 = 0.37$). This effect was greatest in the low zone, where a low tide exposure occurring 1 h later raised the south-facing biomimetic's temperature by 0.80°C (95% CI: 0.55–1.05) relative to the east-facing biomimetic. Individual daily differences could exceed 10°C (Fig. 4).

Thermal differences among species

The comparison of all 3 species among sun-exposed and sheltered south-facing habitats (Table 2B) was similar to the single-species analysis in many regards. Temperatures differed significantly among shore height-habitats (Fig. 5), with high-shore sun-exposed biomimetics averaging 4.6 and 7.7°C warmer than mid- and low-shore sun-exposed biomimetics, respectively. The mid-shore under-*Fucus* biomimetics were also significantly different from all sun-exposed biomimetics. They were cooler than high- or mid-shore sun-exposed biomimetics, by 7.1 and 2.4°C
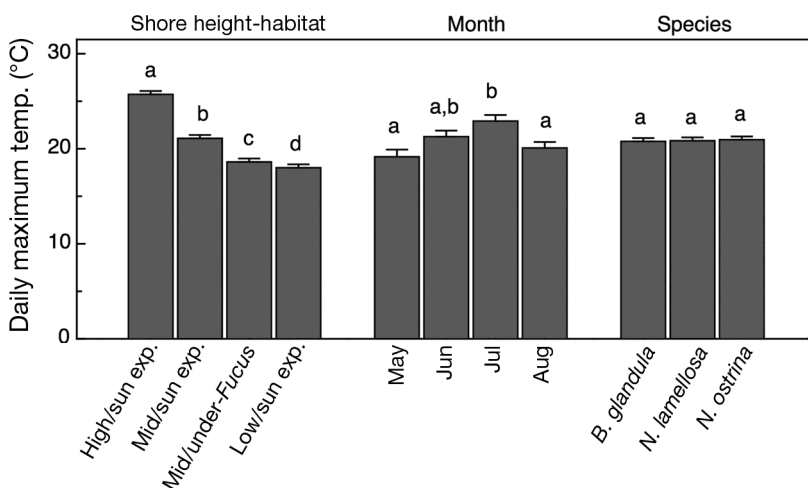

Fig. 5. Summary of main effects of the comparison of shore height-habitat, month, and species (*Nucella lamellosa*, *N. ostrina*, *Balanus glandula*) on daily maximum body temperature for south-facing biomimetics. Values are least squared means (+SE) generated from the ANOVA model. Different letters indicate factor levels that are significantly different from each other ($p \leq 0.05$, Tukey's HSD; comparisons made only within each main effect)
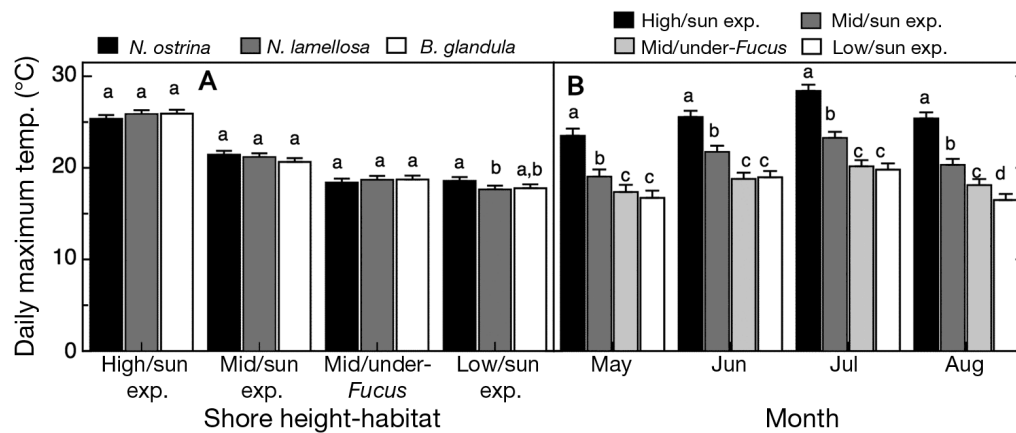
Fig. 6. Significant interactions in the 3 species (*Nucella lamellosa*, *N. ostrina*, *Balanus glandula*) analysis of daily maximum body temperature of south-facing biomimetics: (A) Shore height-habitat × species and (B) Shore height-habitat × month. Values are least squared means (+SE) generated from the ANOVA model. Different letters indicate bars that are significantly different from each other (p ≤ 0.05, Tukey's HSD; comparisons made only within each cluster of bars within each panel)

respectively, but 0.6°C warmer than the low-shore sun-exposed habitat. July was again the warmest month and this pattern did not differ among species.

The main effect of species was not significant, and average overall body temperatures differed by <0.2°C between any pair of species. However there was a significant interaction between species and height-habitat (Fig. 6A). *Nucella ostrina* was significantly warmer than *N. lamellosa* in the low-shore sun-exposed habitats, but this difference was less than 1°C.

Finally, there was also a significant height-habitat by month interaction (Fig. 6B). In August the mid-shore under-*Fucus* habitat was slightly (1.7°C) but significantly warmer than the low-shore sun-exposed habitat. In all other months they did not differ significantly.

Body temperatures and the frequency of thermal stress

Although body temperatures were similar among species in the same habitat, because known tolerance limits differ markedly among these species, the observed temperatures resulted in strikingly different frequencies of near-lethal events (Table 3). Over all 343 d of observations, *Balanus glandula* exceeded its 4 h LT_{50} (40.5°C, S. Gilman unpubl. data) only in the sun-exposed high-shore zone, and then only on 5 days (or 1.5% of days). In contrast, *N. lamellosa* exceeded its 4 h LT_{50} (30°C, Bertness & Schneider 1976) in all 4 habitats, including under *Fucus* in the mid-shore zone in the mid-shore zone. The fre-

quency of near-lethal events for *N. lamellosa* ranged from 33.8% of all days in the sun-exposed high-shore zone down to 2.6% of days in the mid-shore under-*Fucus* zone. *N. ostrina* also frequently exceeded its 4 h LT_{50} in the high-shore zone (34°C, Bertness & Schneider 1976), with near-lethal events occurring on 14.5% of the days, but in all other habitats the frequency was 3.8% or less.

The preceding results consider only south-facing sun-exposed and under-*Fucus* habitats. For *N. ostrina*, we also quantified the frequency of near-lethal events on east-facing and crevice habitats. There were fewer overall events on east-facing sun-exposed habitats than south-facing sun-exposed habitats (Table 4). Moreover, these events were not always synchronized between aspects. In the high-shore zone, roughly half of the events on the south-facing aspect and 24% of those on the east-facing aspect were unique to that aspect (Table 5). In the mid-shore zone, this increased to 85% of south-fac-

Table 3. Percent of days exhibiting near-lethal events (daily maximum temperature > 4 h LT_{50}) for all 3 species (*Nucella ostrina*, *N. lamellosa* and *Balanus glandula*) in south-facing habitats, pooled across all 3 summers (n = 343 days). See 'Materials and methods' for further explanation

Shore height	Habitat	*B. glandula*	*N. ostrina*	*N. lamellosa*
High	Sun exposed	1.5%	14.6%	33.8%
Mid	Sun exposed	0	3.8	14.6
Mid	Under *Fucus*	0	0.3	2.6
Low	Sun exposed	0	2.0	4.7

Table 4. Number and percent (in parentheses) of days exhibiting near-lethal daily maximum body temperatures for *Nucella ostrina* biomimetics in 3 different habitats, by shore height, pooled across all 3 summers (n = 343 d)

Shore height	East-exposed	South-exposed	South-crevice
High	34 (9.9)	50 (14.6)	35 (10.2)
Mid	10 (2.9)	13 (3.8)	0 (0.0)
Low	5 (1.5)	7 (2.0)	0 (0.0)

Table 5. Number of unique and co-occurring near-lethal daily maximum body temperatures on south- and east-facing exposed habitats, by shore height, pooled across all 3 summers (n = 343 d)

Shore height	East only	South only	Both habitats
High	8	24	26
Mid	8	11	2
Low	5	7	0

ing events and 80% of east-facing events. In the low-shore zone, 100% of near-lethal events were unique to one aspect.

Of the 26 high-shore *N. ostrina* near-lethal events that co-occurred on both aspects (east-facing and south-facing), 6 did not extend to the high-shore crevice habitat. Thus, in the high shore, *N. ostrina* experienced a total of 20 unavoidable near-lethal events, representing 5.8% of all summer days. This is 4 times the frequency of near-lethal events experienced by *B. glandula* in the sun-exposed high shore. In the low and mid shore no near-lethal temperatures were recorded in refuges for *N. ostrina* on any day.

DISCUSSION

The ability of an intertidal species to persist on the shore depends on its ability to carve out a zone of 'enemy-free space', within its low-tide tolerances but above those of its predators and competitors (Connell 1961, Paine 1966, Huey et al. 2002, Wethey 2002, Harley 2011). This depends, in part, on each species' individual experience of temperature. In this study, we monitored the temperatures of biomimetic physical models of 3 interacting species over 3 successive summers in 11 intertidal microhabitats. In contrast to some past studies (e.g. Broitman et al. 2009), we found very little difference in body temperature among species living in the same microhabitat. However, the recorded temperatures likely translate into

greater thermal stress for the 2 snail species, due to their lower thermal tolerance relative to the barnacle. Exactly how much more stress is experienced by the snails depends on their choice of microhabitat. While the barnacles are sessile, the snails are able to move between microhabitats both across and among shore heights, and the risk of near-lethal stress varied as much 10-fold between some microhabitats.

The observed minimal difference among species was expected in the sheltered, under-*Fucus* habitat, where all species were shielded from solar radiation at low tide, but in the sun-exposed habitats we had expected that differences in the size and shape of the 3 species would drive differences in body temperature. For example, Broitman et al. (2009) found that the low tide body temperatures of the intertidal mussel *Mytilus californianus* consistently exceeded those of its predator, the sea star *Pisaster ochraceus*, often by as much as 10°C. Yet other studies (Miller & Denny 2011, Lathlean et al. 2014) have found only modest interspecific differences, if any. The Broitman et al. (2009) study may be unique in that their 2 study species differ appreciably in morphological aspects that influence evaporative cooling and conduction to the ground (e.g. shells, shape, attachment structures). In contrast, our 3 species, and those in the other studies mentioned above, are morphologically more similar. They are all shelled, leaving little opportunity for the differences in evaporative cooling seen in Broitman et al. (2009).

It is worth noting that our laboratory measurements revealed that the snail biomimetics underheated by about 2°C relative to live animals, while the difference for the barnacles was less than 0.1°C. These results are in line with other mollusc biomimetics (Fitzhenry et al. 2004, Lathlean et al. 2014), and may be a limitation of the biomimetic approach. If so, live snails could actually be experiencing 2°C warmer temperatures than barnacles in sun-exposed locations.

It is also possible that the biomimetics did not capture behavioral differences among the species that could influence body temperature. For example, *Balanus glandula* can form a pneumostome during aerial exposure (S. Gilman pers. obs.), which could be used for evaporative cooling, but this has never been tested. For littorine snails, Miller & Denny (2011) have shown that altering either the proportion of the foot in direct contact with the surface or the orientation of the shell can reduce body temperatures by up to 4°C. Similar behaviors may be possible in *Nucella ostrina* and *N. lamellosa.* Thus there may be more difference between species in the same habitat than our biomimetics suggest.

Although we measured similar body temperatures for all 3 species, the physiological and ecological consequences of these temperatures are likely to be quite different for each species. We estimated the stressfulness of each species' daily maximum temperature by comparing it to its LT_{50} for a 4 h aerial exposure. Our results are consistent with what is already known of their vertical distributions. For example, *N. lamellosa* is generally found at or below the lowest of our 3 shore heights (Connell 1970). If *N. lamellosa* occurred in the high zone, it would experience near-lethal conditions on one out of every 3 days during the summer. In contrast, *B. glandula* naturally occurs at and above the highest of our sensors. Over all 3 summers, near-lethal conditions for *B. glandula* were limited to 2% of all summer days on the high shore and never occurred at all in lower habitats. *N. ostrina*, with intermediate tolerance, would rarely experience lethal conditions, except in the high zone, where *B. glandula* is most abundant. Clearly temperature limits the snails' opportunities to forage in the high zone, yet this is where their prey species is most abundant (Connell 1970, Hayford et al. 2015).

Snails may be able to extend their mid- and high-shore foraging opportunities by taking advantage of solar refuges provided by crevices and canopy-forming algae. The importance of these refuges to intertidal predators has long been noted in marine ecology (Connell 1970, Fairweather 1988). Here we have documented the thermal benefits of these refuges. We found that shifting into a crevice or under *Fucus* reduced daily maximum body temperatures of animals by 2.2 to 2.4°C on average. Refuge temperatures were typically as cool or cooler than sun-exposed temperatures one zone lower. For *N. ostrina*, judicious refuge use could reduce the risk of near-lethal exposure by up to 30% in the high shore and eliminate it completely in the low and mid shore. Such thermally dependent foraging behavior has been observed in both *N. ostrina* (Vaughn et al. 2014, Hayford et al. 2015) and other *Nucella* species (Burrows & Hughes 1989).

This study also demonstrated the ability of solar aspect to create spatio-temporal patterns in organismal body temperature. Solar aspect has previously been recognized to influence body temperature (Helmuth & Hofmann 2001, Seabra et al. 2011), but prior studies have looked for consistent effects of aspect across time. In contrast, we have shown that thermal differences among aspect can have large seasonal and daily fluctuations (see also Denny et al. 2011). For example, we found that east-facing sites were warmer than south-facing sites in May, but cooler in

August. This is because east-facing biomimetics receive a greater amount of solar radiation than south-facing biomimetics on early morning low tides, which are more common at FHL earlier in the summer. Similarly, over a tide series, there is a predictable daily increase in south-facing temperature, relative to east-facing, as low tide progresses an hour later each day.

Aspect-associated variation in thermal conditions could expand foraging opportunities for *N. ostrina* and *N. lamellosa*. For example, in the high shore, near-lethal conditions occurred in 14.6% of days on the south face and 9.9% on the east face. But if snails could anticipate these events and shift between exposures, they could reduce this number down to 7.6%. This seems likely, given that our south- and east-facing sites were within 5 m of each other, well within distances that *N. ostrina* and *N. lamellosa* can routinely crawl within a day or two (Emlen 1966, Bertness & Schneider 1976). A separate behavioral study on *N. ostrina* found that dogwhelks correctly chose among west and east aspects separated by shorter distances (Hayford et al. 2015), indicating that snails can anticipate the daily variation in temperature among aspects and use it to extend foraging opportunities within the barnacle zone.

Finally, it is important to note that this study measured temperatures only during the summer (May to August). This is the period when the animals are most likely to experience heat stress during emersion. In other seasons air temperatures are lower and daytime low tide exposure is much less frequent. Superficially, this would suggest greater foraging opportunities for the snails in the months when heat stress is reduced; however, both species of snails are much less abundant in barnacle beds in the fall and winter than in the spring and summer (Emlen 1966, Connell 1970, Spight 1982, H. Hayford pers. obs.). There are several reasons why this might be. Foraging during winter could be prohibited by the risk of exposure below freezing during nighttime low tides (H. Hayford unpubl. data), or the colder fall and winter water temperatures (≤6°C, National Oceanographic Data Center 2015) may limit activity levels of the snails. More likely, however, is that summer consumption of barnacles by dogwhelks removes most of the *B. glandula* population by early fall (Spight 1982, H. Hayford pers. obs.) leaving snails with little reason to forage during winter and early spring. Thus, summer foraging may be the most critical period for snail and barnacle population dynamics.

In summary, this study has documented the thermal environment of 3 interacting species across 11

different microhabitats on a single rocky shore. Our results suggest that, while all 3 species experience similar temperatures when in the same microhabitat, they are subjected to very different levels of thermal stress. We have also shown that thermal constraints on dogwhelk foraging are likely fluid. Upper shore regions alternate between tolerable and lethal to these snails over daily to annual time scales. Ultimately, predicting community-level responses to climate change requires understanding not just the thermal niche of each species, but also how mobile consumers, like *Nucella* spp., respond to thermal risk when making foraging decisions. Their decisions are influenced not only by temperature (Burrows & Hughes 1989, Yamane & Gilman 2009, Hayford et al. 2015), but by a range of other factors such as resource availability, refuges (Menge et al. 2002), digestive physiology (Burrows & Hughes 1991), and intraspecific competition (Robles et al. 2009). Disentangling these decisions will be critical to correctly predicting the effects of climate change on all 3 species in this system.

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