



## Aerial exposure and body temperature of the intertidal sea anemone *Anthopleura elegantissima*

Brian L. Bingham,<sup>1,a</sup> Ileana Freytes,<sup>2</sup> Meredith Emery,<sup>3</sup> James Dimond,<sup>4</sup>  
and Gisèle Muller-Parker<sup>5</sup>

<sup>1</sup> Department of Environmental Sciences, Western Washington University, Bellingham, Washington 98225, USA

<sup>2</sup> Department of Biology, University of Puerto Rico, 00931 Río Piedras, Puerto Rico

<sup>3</sup> Department of Biology, Western Washington University, Bellingham, Washington 98225, USA

<sup>4</sup> Shannon Point Marine Center, Anacortes, Washington 98221, USA

<sup>5</sup> Division of Graduate Education, National Science Foundation, Arlington, Virginia 22230, USA

**Abstract.** The sea anemone *Anthopleura elegantissima* is a common member of intertidal communities along the west coast of North America, and can experience extended periods of increased temperature during summertime low tides. Internal body temperatures of emersed individuals of *A. elegantissima* were monitored in a laboratory wind tunnel and in the field, and factors influencing the anemones' thermal experience were examined. Larger body size and aggregation with conspecifics slowed body temperature increases in controlled wind tunnel conditions. In the field, anemones in the interior of an aggregation stayed cooler than those on the edges, and microhabitat features related to light exposure and surface orientation overshadowed any direct effects of body size. In the warmest month only (July), aggregations of *A. elegantissima* were significantly larger at the upper limit of their distribution than they were at the mid and lower limits, suggesting aggregation in high intertidal zones may be a behavioral response to desiccation and temperature stress. As this sea anemone can host multiple species of symbiotic algae with different thermal tolerances, the ability to slow body heating may affect the type of algae hosted and thus the potential contribution of this abundant anemone to primary production in the intertidal zone.

*Additional key words:* thermal tolerance, desiccation, aggregation, symbiosis

The sea anemone *Anthopleura elegantissima* (BRANDT 1835) is an important member of many rocky intertidal communities along the west coast of North America, with extensive aggregations of these clonal animals stretching from high to low intertidal zones (Dayton 1971; Sebens 1982a). Even where they co-occur with spatially dominant mussels, densities of *A. elegantissima* can reach 500 individuals m<sup>-2</sup> (Sebens 1982b). Hosting symbiotic green chlorophytes (*Elliptochloris marina* LETSCH) and brown dinophytes (*Symbiodinium* spp.), members of *A. elegantissima* contribute significantly to intertidal productivity; in Southern California, their photosynthetic contribution is on par with that of intertidal seaweeds (Fitt et al. 1982).

Organisms living in intertidal zones experience dramatic fluctuations in physical conditions as receding

waters expose them to a terrestrial environment. The effects of the exposure are related to its duration, which can range from a few minutes to many hours depending on the location of the organism and the magnitude of the tidal exchange. In the northern part of the distribution of *A. elegantissima*, tidal ranges are large, averaging 2–3 m in many areas of the Salish Sea and exceeding 4 m in the waters of British Columbia and Alaska (NOAA 2010). The effects of tidal exposure are compounded by their timing. In the Salish Sea, summertime low tides occur during the warmest daylight hours, exposing intertidal organisms to the most extreme conditions. On a warm summer day, an organism's ambient thermal environment may change 20°C or more within a matter of minutes as the falling tide exposes the habitat to wind and sun (BL Bingham & J Dimond, unpubl. data), and the exposure may persist for many hours.

Data loggers are useful tools for measuring temperatures in the intertidal zone, but the data rarely

<sup>a</sup> Author for correspondence.

E-mail: brian.bingham@wwu.edu

reflect the actual thermal experience of organisms, whose shape, size, color, water content and behaviors vary considerably (Helmuth 2002). Live animals and biomimetic models provide much more accurate thermal data. Studies on mussels (Elvin & Gonor 1979; Helmuth 1998; Helmuth & Hofmann 2001; Helmuth et al. 2006), gastropods (Tomanek & Somero 1999; Dahlhoff et al. 2001; Denny et al. 2006), and the sea star *Pisaster ochraceus* (BRANDT 1835) (Pincebourde et al. 2008) have shown that natural heating during intertidal aerial exposure can have important physiological and ecological effects. Temperature stress can affect cellular structures, enzyme function, and energetics (reviewed by Hoffman 2005). Snyder & Rossi (2004) found that individuals of *A. elegantissima* exposed to sunny low tide conditions produce heat shock proteins (HSP70 family) in response to warming, suggesting that the anemones were under stress. As these shell-less, soft-bodied invertebrates are routinely exposed to low tide conditions, it is important to study their actual changes in body temperature. Our goals were (i) to measure body temperatures of emersed individuals of *A. elegantissima* under controlled laboratory and natural field conditions and (ii) to determine what features of the habitat or of the anemones themselves affect their thermal experience.

## Methods

### Wind tunnel experiments

Individuals of *Anthopleura elegantissima* were collected from Cattle Point, San Juan Island (48°27'N, 122°57'W) and from Shannon Point, Fidalgo Island, Washington, USA (48°30'N, 122°41'W) during January 2009. Clonal groups of similar-size individuals and isolated anemones of varying size were carefully detached from intertidal rocks, cleaned of attached debris, and transferred to a flow-through sea table at the Shannon Point Marine Center. To minimize disturbance and permit easy transfer of anemones during experiments, they were allowed to attach to slate tiles (4.7 × 4.7 × 0.8 cm) that mimicked natural substrate. Tiles had been previously weighed dry, soaked in seawater for 24 h, blotted dry and reweighed to determine dry, and blotted wet weights.

To measure body temperature during emersion, individual anemones were placed in a wind tunnel illuminated only by overhead fluorescent lights. Therefore, laboratory results demonstrate the effects of desiccation and ambient air temperature on the warming of anemones without the added effects of sunlight. Light intensity during the experimental runs

averaged 16–18  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . This approximated maintenance conditions of the anemones in flow-through sea tables, but was lower than field light levels (average ambient dawn to dusk PAR values on the study dates ranged 220–429  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; Padilla Bay NERR Monitoring Program; <http://cdmo.baruch.sc.edu>).

The working section of the wind tunnel held a Plexiglas platform suspended by narrow metal rods ~25 cm from the top and 11 cm from the bottom of the wind tunnel. Air temperature during all trials was 21–22°C and airflow at the platform was 0.5 m s<sup>-1</sup>, values typical of summertime conditions at the collection sites. Relative humidity in the wind tunnel averaged 34.8% during experiments (SD=2.7%, U12 HOBO data logger; Onset Corp., Bourne, MA, USA), compared to 70.2 ± 9.7% for the field during the same period (Shannon Point Marine Center database). Anemones and the test platform were initially immersed in a seawater bath that could be lowered and removed to start a trial. Temperature of the water bath at the beginning of trials ranged 10.5–12°C.

Anemone temperatures were recorded using 25-G, Type T, Teflon-coated thermocouples (Omega Engineering, Inc., Stamford, CT, USA) connected to a digital single-input thermometer (Omega HH25) through a multiprobe switchbox (Omega HH21A). Thermocouples were threaded through hollow plastic pipettes fixed to the top of the wind tunnel housing, allowing precise insertion in the anemones' mouths. To track ambient air temperature, one thermocouple was positioned 1 cm above the platform, ~6 cm behind the anemones.

We weighed anemones before and after trials to measure their water loss. Anemones and tiles to which they were attached were blotted with a paper towel to remove surface water and weighed. Because blotted weight of the tiles had been previously determined, anemone weights could be determined by subtraction. At the end of the exposure, tiles and the attached anemones were again weighed. As tiles were dry after 9 h, their dry weights (determined earlier) could be subtracted to determine post-exposure anemone weight. Testing effects of aggregation required placing all anemones on a single large tile (7.2 × 14.6 × 0.8 cm), so weights could not be determined the same way. Initial weights of those anemones were determined 2 d before trials by carefully loosening the anemones from the sea table, gently blotting and weighing them, then allowing them to attach to the larger tiles used in the aggregation experiment. Individual weights of the aggregated anemones were not measured after trials as

dislodging them from the tile would have caused expulsion of gastrovascular water, changing final weights.

To determine how body size affects *A. elegantissima* body temperature, four anemones of different sizes were arranged on the wind tunnel platform ~6 cm apart. Thermocouples were placed 2 mm from the bottom of the gastrovascular cavity and temperature readings were taken every 10 min for 9 h, after which the anemones were removed and weighed. A second trial was done 1 d later with four new anemones, under the same conditions of light, temperature, and wind.

Effects of aggregation were tested with a clonal group of similar-sized anemones attached to a single slate tile. Thermocouples were inserted into the mouths of five of 12 closely-spaced individuals and temperatures were recorded every 10 min for 9 h. With respect to wind direction, anemones at the front, back, center, and either side of the aggregation were monitored. Three days later, another trial was done with a second group of 12 anemones under the same conditions.

A repeated-measures analysis of variance (ANOVAR; SPSS Version 18, IBM North America, New York, NY, USA) was used to compare internal body temperatures of anemones tested individually and in an aggregation. Treatment (isolated or aggregated) and trial (2 levels nested in treatment) were the between-subject factors, and time was the within-subject factor. The dependent variable was the difference between wind tunnel and body temperature. To account for differences in anemone body size, anemone wet weight was included as a covariate (after verifying that the covariate assumption of parallel slopes was met).

To evaluate the role of evaporative cooling in the temperature response, five isolated anemones (ranging 1.4–11.7 g wet weight) on tiles were wrapped in plastic wrap and placed in the wind tunnel. Thermocouples were inserted into the anemones' gastrovascular cavity through a small hole in the wrap, and body temperature was measured at 10-min intervals for 4 h.

### Temperature measurements in the field

All field measurements were done on a bedrock outcrop exposed to moderate wave activity, where *A. elegantissima* is abundant (Cattle Point, San Juan Island, Washington). Anemone body temperatures were monitored during three low tides between July 21 and 24, 2009, as described above. We also attached thermocouples within 1 cm of the rock

surface with modeling clay to measure ambient temperatures. These thermocouples were shaded with opaque white tape to prevent direct solar heating. Therefore, the data show only the combined effects of ambient air temperature plus any heat energy re-radiated or conducted from the rock surface. Every 30 min, wind speed and irradiance were recorded 1–3 cm above the anemones. Wind speed was measured with an Alnor ThermoAnemometer (Model 8575), and irradiance with a Biospherical Instruments 4 $\pi$  PAR sensor (model QSL 100; spectral response 400–700 nm). Because the PAR instrument measured only part of the solar spectrum (300–1100 nm), values are used only for comparative purposes, not to calculate heat flux. When measurements were completed, all monitored anemones were collected, placed in seawater, and returned to the laboratory, where they were blotted dry and weighed.

To determine how position in an aggregation affects the temperatures of individuals of *A. elegantissima*, we located an aggregation of ~75 anemones and placed thermocouples in five individuals in the interior and five on the edges of the group. A final thermocouple was placed just outside the aggregation to measure ambient temperature. The aggregation was in a nearly horizontal rock depression that stayed damp during the low tide. Anemone temperatures were recorded every 10 min for 3.7 h.

We next tested the effect of orientation on body temperature. We identified two aggregations (each composed of 40–50 individuals) of *A. elegantissima* within 1 m of each other and at the same approximate tidal height. One group was attached to an unshaded, horizontal surface; the other was on a vertical, north-facing wall. Thermocouples were placed in five non-edge individuals of each group. Additional thermocouples were placed adjacent to each aggregation. Temperatures were monitored every 10 min for 4.3 h. Data collected for each comparison (interior vs. edge of an aggregation, horizontal vs. vertical substrate) were analyzed with ANOVAR including anemone body size as a covariate. Because ambient temperatures differed slightly for the comparison groups, it was inappropriate to simply compare body temperatures of anemones in the various treatments. Instead, the deviations of the anemone body temperatures from ambient were used as the dependent variable. This allowed us to test whether the ability of the anemones to control their body temperature relative to ambient was related to location in a group or surface orientation.

On July 24, 2009, we tested the relationship between body temperature, wind speed and irradiance

by monitoring the internal temperatures of 10 similar-sized anemones in microhabitats that experienced different levels of wind and sunlight. Internal body temperature was measured every 30 min for 4 h, as were wind speed and irradiance immediately adjacent to each individual. All measurements were pooled in a single dataset and analyzed with partial correlations testing the relationship between body temperature and wind speed while controlling irradiance, then testing the relationship between body temperature and irradiance while controlling wind speed. Because pooling measurements violates the assumption of independent data points, results are only approximations.

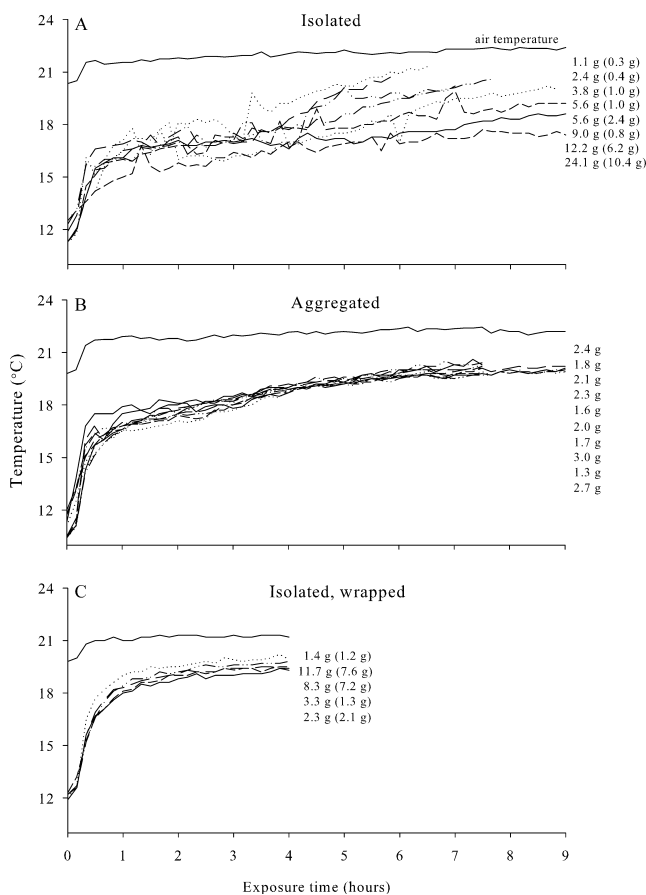
To look for patterns of aggregation potentially linked to temperature and desiccation, populations of *A. elegantissima* were randomly sampled at the Cattle Point study site twice in 2008 (July 16 and November 11) and twice in 2009 (February 6 and April 27). During low tides on those dates, 25 randomly chosen positions were sampled along permanent transects +0.2 m, +1.2 m, and +2.0 m above mean lower low water. The individual of *A. elegantissima* closest to each position was located, and the size of the aggregation in which it was found was determined. Anemones in tidepools were excluded from the data set. A 2-way ANOVA was used to determine whether aggregation size was affected by month or tide height.

## Results

### Wind tunnel experiments

Isolated individuals of *Anthopleura elegantissima* in the wind tunnel warmed 5–6°C in the first hour, then more gradually thereafter (Fig. 1A). Smaller individuals dried and warmed faster; some appeared completely desiccated after only 6.5 h (these were removed from the experiment). The largest anemone (24.1 g wet weight) stayed nearly 6°C below ambient air temperature throughout the 9 h exposure period. Over the 9 h exposure period, anemones lost 49–91% of their wet body weight, with loss rates near 11% h<sup>-1</sup> for smaller and 6% h<sup>-1</sup> for larger individuals.

Aggregation slowed the rate of heating (Fig. 1B). Although individual anemones in the aggregations were small, heating resembled that of much larger isolated individuals (Fig. 1A). Body temperatures stayed >2°C below ambient temperature over the 9 h exposure, despite a warming rate that initially exceeded that of isolated individuals. The rate decreased dramatically after the first hour, remaining below 0.5°C h<sup>-1</sup> for the remaining 8 h of



**Fig. 1.** Gastrovascular temperatures of individual *Anthopleura elegantissima* in a wind tunnel held at 21–22°C, with air flow of 0.5 m s<sup>-1</sup>. **A.** Isolated anemones. **B.** Aggregated anemones. **C.** Isolated, wrapped anemones. Initial anemone temperatures ranged 10.5–12°C. Individual anemone pre-exposure wet weights are listed in the same order as the temperature traces they represent. The upper solid lines in each plot are wind tunnel air temperatures. Numbers in parentheses show the final weights of the individual (A) and the individual, wrapped anemones (C).

monitoring. Warming patterns lacked the abrupt fluctuations seen in isolated individuals. ANOVAR comparing data shown in Fig. 1A and 1B showed multiple significant effects (Table 1). The time × weight interaction indicated that anemones of different sizes warmed at different rates. More importantly, the time × treatment interaction showed that, independent of body size, aggregated anemones warmed more slowly than did isolated individuals. The time × trial interaction resulted from slight differences in initial anemone temperature.

Anemones covered with plastic wrap lost significant amounts of water after only 4 h (mean weight loss was 26 ± 21%, N=5). Because the wrap prevented



**Table 1.** ANOVA for the effects of aggregation on internal body temperature of *Anthopleura elegantissima*. Because smaller individuals desiccated and were moribund after only 6.5 h, only data collected before that time point were used in the analysis. Anemone wet weight was used as a covariate. Huynh-Feldt adjusted df indicate adjustment for violation of the ANOVA sphericity assumption. Partial  $\eta^2$  values ( $\eta^2_p$ ) give the proportion of the total temperature variation explained by each factor (calculated as though the factor and its error were the only model terms). Bold p values indicate significance at  $\alpha = 0.05$ .

Source	SS	df	F	p	$\eta^2_p$
Between-subject factors					
Weight	111.5	1	24.4	<b>&lt; 0.001</b>	0.65
Treatment	6.4	1	1.4	0.25	0.09
Trial (treatment)	3.5	2	0.4	0.69	0.05
Anemone	59.4	13			
Within-subject factors					
Time	696.1	5.8	105.7	<b>&lt; 0.001</b>	0.89
Time $\times$ Weight	43.5	5.8	6.6	<b>&lt; 0.001</b>	0.34
Time $\times$ Treatment	36.7	5.8	5.6	<b>&lt; 0.001</b>	0.30
Time $\times$ Trial (treatment)	62.5	11.6	4.7	<b>&lt; 0.001</b>	0.42
Time $\times$ Anemone	85.6	75.6			
Total	1105.2	719			

evaporation and allowed only convective cooling, the anemones heated rapidly, approaching maximum temperatures after only 1–2 h (Fig. 1C). The rate of warming in the first hour was comparable to that of unwrapped anemones (6–7°C), but continued at a relatively high rate ( $\approx 2.5^\circ\text{C h}^{-1}$ ) until monitoring was stopped (4 h). Anemone size had no obvious effect on temperature change.

### Field monitoring

Location in an aggregation affected warming; individuals in the interior of the aggregation stayed cooler than those on the edges (Fig. 2). Body temperatures of all edge anemones reached or exceeded ambient temperature, and the pattern of warming was statistically different for interior and edge anemones (indicated by a significant time  $\times$  treatment interaction, Table 2). Body weight again had no significant effect ( $F_{1,7}=0.18$ ,  $p=0.69$ ) and was not used as a covariate.

Temperatures of anemones on horizontal and vertical surfaces also differed significantly (Table 2). Ambient temperatures were  $\approx 5^\circ\text{C}$  higher on the horizontal than on the vertical substratum, yet anemones on the horizontal surface stayed below ambient temperature through the emersion period (Fig. 3). Anemones on vertical surfaces exceeded ambient temperature within 30 min, and body temperatures continued to rise thereafter. Wet body weight again had no significant effect on warming ( $F_{1,7}=1.35$ ,  $p=0.28$ ).

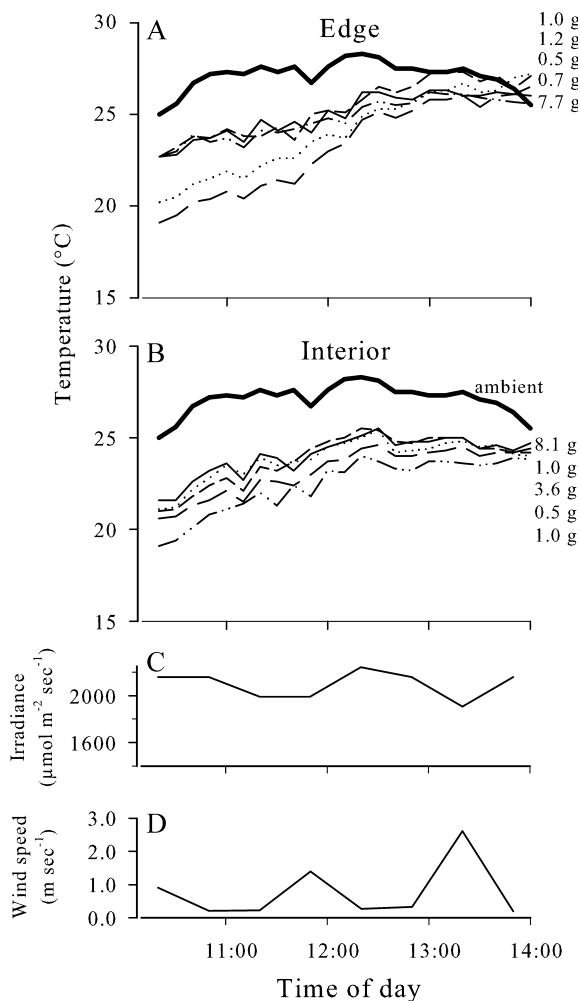
Sampling anemones across multiple microhabitats yielded a range of body temperatures, wind

exposures, and irradiance levels (Fig. 4). A partial correlation between body temperature and wind speed (controlling irradiance) was not significant ( $r_{w,i}=-0.16$ ,  $p=0.13$ ,  $df=87$ ). However, a partial correlation between body temperature and irradiance (controlling wind speed) was significant ( $r_{i,w}=0.63$ ,  $p<0.01$ ,  $df=87$ ), indicating that body temperature was more closely connected to irradiance than to wind exposure.

Field sampling showed distinct patterns of aggregation at the Cattle Point study site (Fig. 5). ANOVA showed a significant month  $\times$  tide height interaction ( $F_{6,261}=6.27$ ,  $p<0.01$ ), and Bonferroni-adjusted simple main effects contrasts (comparing tide heights within months) revealed differences only in the July samples. In that month, aggregations of *A. elegantissima* were significantly larger along the +2.1 m transect than they were on the +1.2 or +0.3 m transects (Fig. 5).

### Discussion

Duration of exposure, ambient temperature, relative humidity, wind speed, irradiance, and microhabitat can all affect the thermal response of individuals of *Anthopleura elegantissima* to low tide exposure. Under conditions of high humidity and moderate illumination, for example, aerally-exposed individuals of *A. elegantissima* stay fully expanded and irrigate the oral disk with gastrovascular water, enhancing aerobic respiration (Shick & Dykens 1984). However, when humidity is low, the anemones respond with water-conserving behaviors:



**Fig. 2.** Internal body temperatures of members of a field aggregation of *Anthopleura elegantissima* (July 21, 2009) as a function of position in the aggregation. Anemones were monitored from 10:20 to 14:00 (total emersion period: 6:30–14:00). Wet body weights of individual anemones are given. **A.** Individuals on the edge of the aggregation. **B.** Individuals in the interior of the aggregation. Heavy solid lines in A and B show ambient temperatures. **C.** Irradiance (mean  $\pm$  SD) adjacent to the aggregation, measured every 30 min. **D.** Wind speed (mean  $\pm$  SD) adjacent to the aggregation, measured every 30 min. Because all monitored anemones were within a single small area, ambient temperature, irradiance, and wind speed were measured at only one adjacent location.

closing the mouth, retracting the tentacles, and contracting the upper body column sphincter to completely enclose the oral disk, producing a cylindrical or hemispherical mass with minimal surface area (Shick 1991). As outer body surfaces dry, diffusion of gastrovascular water across the body wall (including through the numerous thin-membraned verrucae) or by release from the mouth keeps the tissues moist (Hart & Crowe 1977; Shick 1991).

Bell (1995) demonstrated that the temperature experience of the intertidal alga *Mastocarpus papillatus* KÜTZING is directly coupled to water loss. As long as the algal thalli held water, evaporative cooling kept temperatures low. When the water supply was exhausted, however, thallus temperatures skyrocketed, exceeding air temperatures by nearly 20°C. The capacity of members of *A. elegantissima* to control body temperature is similarly limited by the water they hold during periods of aerial exposure. Small individuals, with low gastrovascular volumes, heated quickly and showed abrupt changes in body temperatures (Fig. 1A). The sudden temperature changes corresponded to releases of water through the anemone's mouth. Eventually, however, small anemones exhausted their supply of water and suffered the effects of desiccation and steadily increasing temperature. Larger individuals retained substantial water even after 9 h of exposure, and remained several degrees below ambient air temperature. Wrapping individuals of *A. elegantissima* to prevent evaporation in the wind tunnel had dramatic effects on body temperature. Although the anemones released water, it could not evaporate so body temperatures quickly rose to near ambient.

Ottaway (1973) studied temperature responses of the temperate-zone anemone *Actinia tenebrosa* FARQUHAR 1898 and found that thermal stress became a major mortality source when temperatures exceeded 25°C. Members of *A. elegantissima* can tolerate much higher temperatures, at least for short periods. Dayton (1971) monitored internal body temperatures of *A. elegantissima* in the field and found that anemones could survive body temperatures as high as 33.6°C with no apparent negative effect. Over 3 d of field study, with different levels of sunlight and wind, body temperatures of *A. elegantissima* in our treatments often exceeded 24°C, and reached 32°C in the most extreme cases. Although not lethal, temperatures in this range induce the production of heat shock proteins in *A. elegantissima* (Snyder & Rossi 2004), which may involve significant metabolic costs (Somero 2002).

Members of *A. elegantissima* undergo regular cycles of asexual fission, often producing large clonal groups and leading to the common name of "aggregating anemone." Sebens (1979, 1980) suggested that, by dividing, individuals of *A. elegantissima* maintain an optimal body size for prey capture, maximizing energy available for sexual reproduction. Smaller body size, however, could increase the risk of desiccation and temperature stress. Sebens (1982a) monitored multiple field populations of

**Table 2.** ANOVAR tests for the effects of aggregation, position in a group, and surface orientation on body temperature of *Anthopleura elegantissima* during low tide exposure.

Source	Position (interior vs. edge)			Surface orientation (horizontal vs. vertical)		
	df	F	$\eta^2_p$	df	F	$\eta^2_p$
Between subjects						
Treatment	1,8	4.4	(0.36)	1,8	77.2***	(0.91)
Within subjects						
Time	1.9, 15.1	59.2***	(0.88)	7.1, 56.5	26.9***	(0.77)
Time×Treatment	1.9, 15.1	4.8*	(0.38)	7.1, 56.5	25.1***	(0.76)

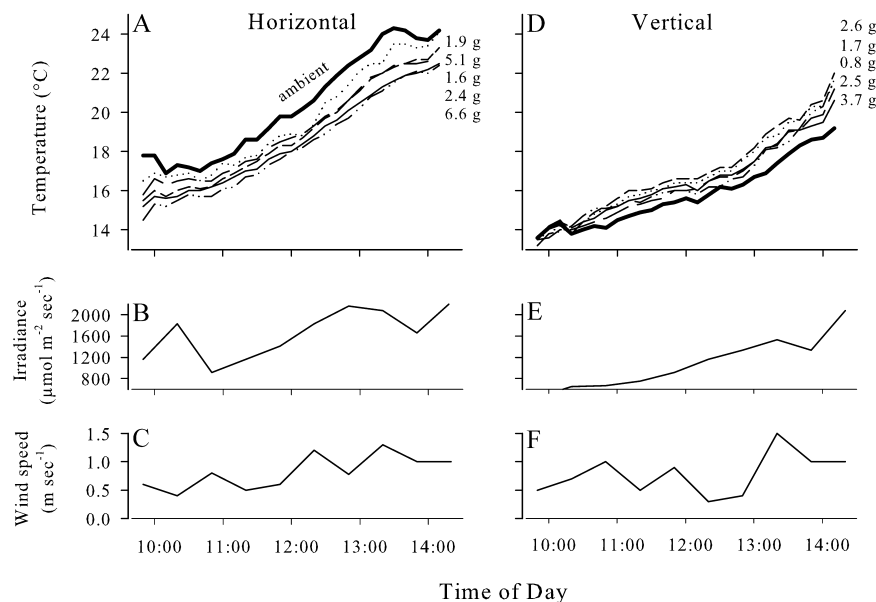
\*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ .

*A. elegantissima* on San Juan Island, Washington, and found that fission rates increased dramatically in August, the same season that mid-day low tides in the Salish Sea become much less frequent. While the timing of fission is likely controlled by food availability (Sebens 1982a), it may have the added benefit of maintaining larger body size through the warmer summer months when small size could be a desiccation and temperature liability.

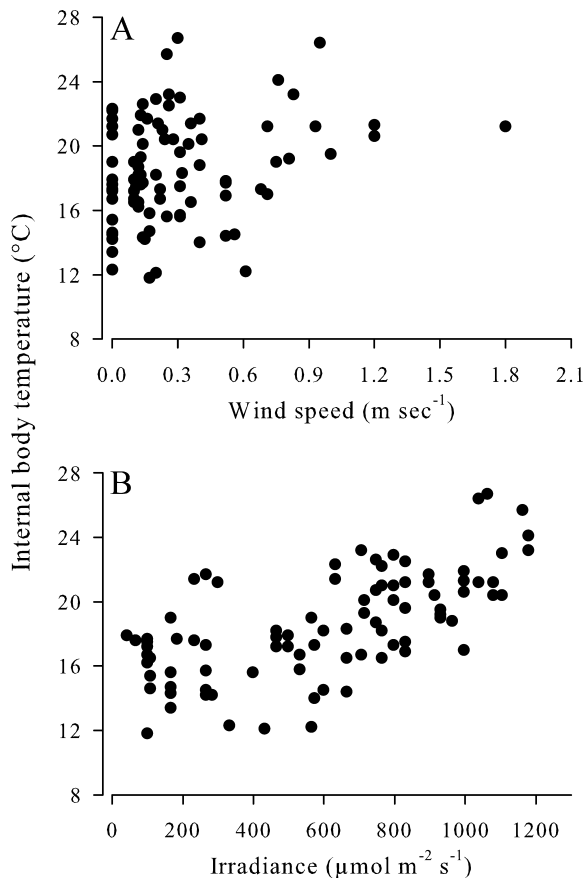
In the laboratory, aggregated anemones functioned thermally like a single large individual,

warming gradually, showing few sudden temperature changes, and remaining much cooler than isolated individuals of similar size. Aggregated individuals benefitted from the numerous water-filled spaces created by the aggregation itself. Extracorporeal water kept surfaces moist, with slow evaporation passively cooling the aggregation, allowing anemones to retain water held in their gastrovascular cavity.

Aggregation is important to the thermal experience of many intertidal organisms, but the effects



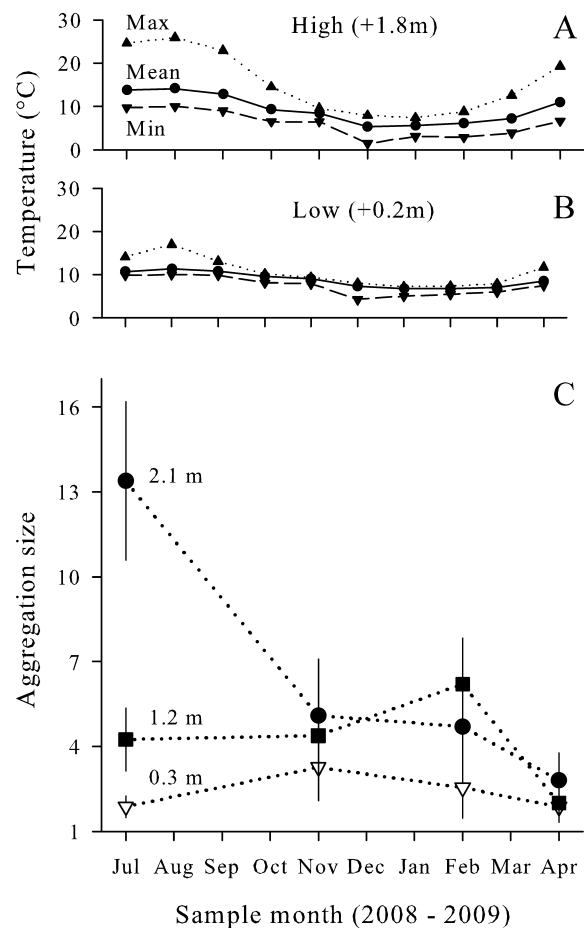
**Fig. 3.** Internal body temperatures of *Anthopleura elegantissima* as a function of surface orientation, in the field (July 22, 2009). Anemones were monitored over the total emersion period, from 9:50 to 14:10. **A.** Individuals found on a horizontal surface. **B.** Irradiance (mean  $\pm$  SD) adjacent to the horizontal surface, measured every 30 min. **C.** Wind speed (mean  $\pm$  SD) adjacent to the horizontal surface, measured every 30 min. **D.** Individuals found on a vertical surface. **E.** Irradiance (mean  $\pm$  SD) adjacent to the vertical surface, measured every 30 min. **F.** Wind speed (mean  $\pm$  SD) adjacent to the vertical surface, measured every 30 min. In A and D, heavy solid lines show ambient temperatures.



**Fig. 4.** Internal body temperature of individuals of *Anthopleura elegantissima* found in a range of field microhabitats (July 24, 2009), as a function of wind and irradiance. Data are pooled observations ( $n=90$ ) of 10 similarly sized anemones measured at 30-min intervals for 4 h. **A.** Wind speed. **B.** Irradiance.

are likely to be complicated by other microhabitat features (Garritty 1984; Chapman & Underwood 1996; Helmuth 1998; Munoz et al. 2008). Hart & Crowe (1977) studied survival of *A. elegantissima* under desiccation stress and found that isolated individuals suffered significantly higher mortality than did those living in aggregations. However, the effect was only apparent at higher intertidal heights, in exposed sites and during warmer summer months. Seasonal surveys at our field site revealed larger aggregations of *A. elegantissima* in the high intertidal zone than at lower tidal elevations, but only in the summer when temperatures were highest (Fig. 5), suggesting that aggregation in high intertidal zones may be a behavioral response to desiccation and temperature stress.

Although aggregation has clear benefits for offsetting temperature increases, the benefits may not be shared equally by all members of the group; anemones on the edges of the clone, with their more



**Fig. 5.** Environmental temperature and sizes of randomly sampled aggregations of *Anthopleura elegantissima* at the Cattle Point, San Juan Island, study site in 2008 and 2009. **A.** Temperature at +1.8 m above mean lower low water (recorded by an anchored Hobo Temp Pro water temperature data logger, with measurements made at 5-min intervals). **B.** Temperature at +0.2 m above mean lower low water. **C.** Aggregation sizes at three tidal elevations. Values range from one (for an isolated individual anemone) to 25 (the maximum size of sampled aggregations). Standard errors are shown.

exposed body surfaces, experienced more extreme temperatures than did individuals inside the aggregation. Individuals on the edges of clonal aggregations of *A. elegantissima* function as warriors, developing large acrorhagi (specialized organs filled with nematocysts) to defend the boundaries of the clone (Francis 1976). The warriors are smaller, have lower fission rates, and lack gonads, presumably because energy is diverted to defensive activities (Francis 1976). Temperature-related metabolic costs could also contribute to lower rates of growth and reproduction in these edge individuals. To estimate the energetic cost of higher body temperatures, we



used the temperature-related respiration data published by Verde & McCloskey (2007) for submerged, fully expanded *A. elegantissima* to produce a linear equation relating temperature to respiration. We then used our field data to estimate total energy expenditure of each individual of *A. elegantissima* shown in Fig. 2. Because both immersion and expansion state affect energy consumption in *A. elegantissima* (Shick et al. 1979; Shick & Dykens 1984), our calculations provide only very approximate comparisons of respiration. Within these constraints, the estimates suggest that, over the 3.7 h of monitoring, anemones on the edges of the aggregation respired about 5% more carbon than individuals located nearer the center (9.0 vs. 8.5  $\mu\text{g C mg}^{-1}$  protein). Persistent differences in body temperature during summertime low tide exposures could contribute to the lower rates of growth and reproduction reported for the warriors.

The rocky intertidal is a mosaic of habitats (Helmuth & Hofmann 2001) where minor movements can change an organism's microclimate, altering its thermal experience (e.g., Garrity 1984). Tidepools are refuges from desiccation, but may expose residents to extreme temperatures. At a location near our Cattle Point site, Jensen & Muller-Parker (1994) reported that tidepool temperatures increased from 14 to 31°C in just 3 h, and extensive bleaching of individuals of *A. elegantissima* in high tidepools at Cattle Point (unpubl. data) confirm the stressful summertime temperature conditions there. Isolated individuals of *A. elegantissima* are likely to move under conditions of stress (Pineda & Escofet 1989), and our results indicate that moving from a vertical to a horizontal surface could allow them to better tolerate low tide conditions. On a vertical surface, water left by the receding tide or released from the gastrovascular cavity will tend to drain quickly away, limiting the potential for evaporative cooling. Anemones on a horizontal surface, in contrast, can benefit from water that remains pooled on their surfaces. This is unlike the pattern reported for most shelled intertidal invertebrates (e.g., barnacles, snails, mussels) where vertical habitats, which can provide shading, may be more favorable sites (Miller et al. 2009). This difference may be related to the ability of invertebrates with shells to better retain water regardless of position, limiting evaporative water loss.

Although both wind and irradiance can influence the temperature of individuals of *A. elegantissima*, irradiance was a much better predictor of body temperature under the summertime field conditions we tested (Fig. 4). In the laboratory wind tunnel without solar heating, the rate of body warming was high

for the first hour (3–6°C), and decreased sharply thereafter (Fig. 1). In sun-exposed field conditions, warming rates in the first hour of emersion were somewhat lower (2.5–3.5°C, BL Bingham & J Dimond, unpubl. data), possibly compensated by the thermal mass of the bedrock to which the anemones were attached, but body temperature continued to increase at a fairly consistent rate throughout the exposure period (e.g., Fig. 3). Marshall et al. (2011) suggest that direct solar irradiance and re-radiative heating from rock surfaces are the primary features driving thermal adaptation of intertidal invertebrates. Members of *A. elegantissima* may attach gravel, shell, and other debris to their outer body wall to protect themselves from the effects of wind and sun (Dykens & Shick 1984), significantly reducing the rate of evaporative water loss (Hart & Crowe 1977) and, presumably, their overall rate of warming during the exposure period.

The thermal biology of members of *A. elegantissima* likely also affects the symbiotic algae they host. Moderate temperature increases can actually increase productivity of the symbiotic algae (Verde & McCloskey 2001; Muller-Parker et al. 2007), potentially benefitting the anemone, but symbiont health is compromised by persistent high temperatures (Saunders & Muller-Parker 1997; Muller-Parker et al. 2007). The thermal experience of individuals of *A. elegantissima* can also change the identity of the symbionts they host. At northern latitudes, members of *A. elegantissima* may host two distinct photosynthetic symbionts: the green alga *Elliptochloris marina* and the brown dinophyte *Symbiodinium muscatinei* LAJEUNESSE & TRENCH. Individual anemones can host one or the other symbiont, or both simultaneously. Anemones in cooler, low-light habitats tend to host *E. marina*, while those in warmer, sun-exposed sites host *S. muscatinei* (Secord 1995; Secord & Muller-Parker 2005). High temperatures significantly decrease growth, density, and chlorophyll content of cells of *E. marina* (Saunders & Muller-Parker 1997; Verde & McCloskey 2001) and can cause “browning” of the anemones as the symbiont population shifts toward *S. muscatinei* (Saunders & Muller-Parker 1997; Bates 2000). If the body temperature patterns we saw in our study are consistent, we would predict, over time, that elevated body temperatures would increase productivity and growth of *S. muscatinei* while decreasing performance of *E. marina*. Living solitarily, on the edge of an aggregation, or on a vertical substratum could push individuals of *A. elegantissima* with mixed symbiont complements toward dominance by *S. muscatinei*. This will be true, however, only if

body temperatures are not compensated for by anemone aggregation behavior, and, while exceeding threshold tolerances for *E. marina*, are not so high that they lead to complete bleaching of the anemone. Subtle changes in environmental temperature, if they translate to changes in anemone body temperature, could therefore fundamentally change the symbiotic relationships and the productivity of the anemone-symbiont association. Because of the tight coupling between temperature, symbiont complement, and symbiont productivity, it is critical to understand the complex thermal landscape in which *A. elegantissima* exists, particularly in the context of predicted changes to sea level and the global climate.

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