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RESEARCH ARTICLE

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Testing the effects of wave exposure, site, and behavior on intertidal mussel body temperatures: applications and limits of temperature logger design

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Abstract The rocky intertidal mussel *Mytilus californianus* is exposed to potentially damaging thermal conditions during low tide. However, because the temperatures of ectothermic organisms are driven by multiple climatic factors, we do not fully understand what the body temperatures of intertidal invertebrates are under field conditions, or how thermal stress varies between intertidal sites. We designed a temperature logger that thermally matches (similar size, color, morphology and thermal inertia) living mussels of the species *M. californianus*, and tested its ability to provide realistic measurements of body temperature in the field. As part of these tests, we examined the propensity of *M. californianus* to "gape," a behavior in which the mussel opens its shell valves, and which may permit evaporative cooling. Because our instruments were unable to mimic this behavior, we tested the degree to which gaping contributes to animal cooling by exposing *M. californianus* to a range of climatic conditions while recording body temperatures, gaping behavior and water loss. Results indicated no significant influence of gaping on body temperature. Tests comparing temperatures of loggers to those of real mussels under laboratory and field conditions showed that thermally matched loggers recorded temperatures within a few degrees of living animals and that unmodified loggers regularly incurred errors of up to 14°C. We then deployed a series of thermally matched loggers at two sites in central Oregon (Boiler Bay and Strawberry Hill) previously hypothesized to display site-specific differences in aerial temperature, and at various wave-exposure regimes within each site. Significant differences were demonstrated between sites using a subset of temperature metrics in a multivariate analysis. Yearly peaks in maximum temperature, average daily maximum temperature, and degree hours were useful in discriminating between sites. In 2001, wave-exposed sites at Strawberry Hill displayed fewer degree–hours than wave-protected sites, but an equivalent or greater maximum temperature. In 2002 both of these metrics were significantly lower in wave-exposed sites. Boiler Bay and Strawberry Hill differed in thermal regime, but not in a way that would indicate one was "hotter" than the other.

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Introduction

As climate changes throughout the world, thermal stress on organisms is becoming an increasingly important area of interest and concern to physiologists and ecologists working in intertidal ecosystems (Fields et al. 1993; Barry et al. 1995; Southward et al. 1995; Helmuth et al. 2002). Intertidal invertebrates must regularly contend with the terrestrial environment during low tide, although they evolved from marine ancestors. Thus they are generally believed to live very close to their thermal tolerance limits (Hofmann and Somero 1995; Stillman and Somero 1996; Tomanek 2002), though a suite of factors may set distribution limits (Southward 1958; Wolcott 1973; Harley and Helmuth 2003). Nonetheless, relatively few studies have attempted to measure long-term body temperature patterns in the field for intertidal organisms (Elvin and Gonor 1979; Helmuth and Hofmann 2001; Helmuth et al. 2002; Wethey 2002), or have been able to fully characterize how organismal body temperatures vary in space and time (Brawley and

Johnson 1991; Helmuth and Hofmann 2001). As a result we do not yet possess a good understanding of how often intertidal species encounter lethal, physiologically stressful, or optimal temperature conditions in the field.

This task is not as straightforward as it might seem. As has been shown now for a suite of terrestrial organisms, the body temperature of an ectotherm is driven by multiple, interacting climatic factors, and is often quite different from the temperature of the organism's surroundings (e.g., Porter and Gates 1969). Furthermore, heat fluxes are affected by the animal's size and shape, and two organisms exposed to the same climatic conditions can experience very different body temperatures (Helmuth 2002).

While these issues have been explored in considerable detail in terrestrial ecosystems (e.g., Porter and Gates 1969; Porter et al. 1973; Kingsolver 1989; Watt 1991) comparable studies in intertidal ecosystems have been relatively rare (Johnson 1975; Elvin and Gonor 1979; Bell 1995; Helmuth 1998, 1999, 2002; Helmuth and Hofmann 2001; Helmuth et al. 2002; Wethey 2002). To a large extent this lack of data from intertidal environments is a result of the difficulty in deploying instruments capable of withstanding severe wave action, fouling organisms, and corrosion from salt water. Thermocouple-based loggers, for example, have frequently been used in terrestrial studies, but are often difficult to maintain in wave-swept environments where the cables are easily broken or displaced (Helmuth and Hofmann 2001). An attractive alternative has emerged in recent years in the form of miniature, waterproof, self-contained data loggers (Fig. 1). These small instruments are relatively inexpensive, rugged, and are often capable of recording tens of thousands of temperature measurements during a single deployment. As a result, their recent use in intertidal studies has blossomed and permitted investigators to make quantitative comparisons of "temperature" over a wide range of spatial and temporal scales. Not only are these comparative measurements key for addressing questions related to climate change, but perhaps more importantly they serve as an important tool for linking studies of physiological thermal stress conducted at biochemical- and cellular-level scales with those at the scale of populations and ecosystems (Helmuth and Hofmann 2001; Halpin et al. 2002; Helmuth 2002; Menge et al. 2002; Somero 2002).

Fig. 1 A living *Mytilus californianus* mussel (*left*), an unmodified Onset TidbiT logger (*middle*) and "robomussel" logger (*right*), containing a TidbiT logger and thermally matched to the characteristics of a living mussel

One potential pitfall, however, is that the temperatures that a logger records may be specific to the thermal characteristics of the instrument itself. The flux of heat into and out of an organism (or any other object) occurs via several mechanisms, including solar radiation, convection, conduction, infrared radiation and the release of heat through the evaporation of water (Porter and Gates 1969). Significantly, most of these mechanisms of heat exchange are affected by the characteristics of the organism or object itself. Large organisms, for example, have a comparatively high thermal inertia, and require significant inputs of heat energy to enact small changes in temperature (Spotila et al.1973; Buatois and Croze 1978; Helmuth 1998, 2002). The absorptivity of an organism can significantly impact the amount of short-wave solar radiation absorbed (Kingsolver 1983, 1985) and an organism's shape affects the rate of convective and conductive heat exchange to and from its surface (Vermeij 1971; Wu and Gebremedhin 2001). The end result is that two organisms (or instruments) exposed to precisely the same environmental conditions can display markedly different temperatures (Helmuth 2002).

Here we describe a technique in which we match the thermal characteristics of a temperature-logging instrument to those of the organism being investigated, and explore the capacity of this logger to record realistic body temperatures under field conditions. We further compare these custom-designed instruments to an unmodified, "off the shelf" version as a means of exploring the potential pitfalls associated with the use of temperature loggers in the field when the experimental design fails to include some aspects of the organism's thermal characteristics. We then use a series of these thermally matched loggers to quantitatively investigate differences in the body temperatures of mussels in two wave-exposure regimes at two sites in Central Oregon (Boiler Bay and Strawberry Hill; Dahlhoff and Menge 1996; Menge et al. 1997a, 1997b; Dahlhoff et al. 2001). As part of this study, we additionally investigate the role of mussel gaping behavior in permitting this sessile organism to thermoregulate.

Organism

The California mussel, *Mytilus californianus*, inhabits rocky intertidal sites ranging from southern California

to southeastern Alaska (Seed 1992; Seed and Suchanek 1992), and is a competitive dominant for space in this ecosystem (Paine 1974). This species typically lives in large aggregated beds that provide habitat for a diversity of other organisms (Suchanek 1992), and is one of the most common constituents of hard-substrate communities at mid-tidal levels. Beds of *M. californianus* can exhibit high levels of productivity and may support a large proportion of the total productivity of the near-shore benthic environment (Leigh et al. 1987; Seed 1992). As a result, attempts to determine the growth and survival of *M. californianus* are extremely important due to the mussel's extensive impact on the intertidal community. Further, there is excellent background information on the thermal physiology of this species and its congeners (e.g., Bayne et al. 1976a; Hofmann and Somero 1995; Roberts et al. 1997; Buckley et al. 2001), and an understanding of mussel temperature patterns in situ is vital for providing an environmental context for these experiments.

Previous models of heat flux constructed for this and other species of *Mytilus* (Elvin and Gonor 1979; Helmuth 1998, 1999) have shown that, given accurate measurements of small-scale climatic conditions, body temperatures can be predicted within a few degrees Celsius. Realistically, however, obtaining measurements of the necessary microclimatic data (air and ground temperatures, solar radiation, wind speed, relative humidity and cloud cover) within the rocky intertidal over long periods of time is difficult. Thus other methods of estimating body temperature in the field are currently more tractable.

To obtain long-term records of body temperature in the field, Helmuth and Hofmann (2001), Helmuth et al. (2002) and Harley and Helmuth (2003) used temperature loggers that mimicked many of the thermal characteristics of real mussels (Fig. 1). Loggers were constructed of polyester resin and had a similar size, morphology and color to real mussels. Further, the thermal inertia (capacity to resist temperature change; Spotila et al. 1973) of each instrument was designed to be as similar as possible to that of living mussels by matching the product of their mass × specific heat (Fig. 2). Preliminary tests of this and other logger designs suggested that under most field conditions, thermally matched loggers displayed temperatures that were within 1.5–2.0°C of adjacent, living mussels (Helmuth and Hofmann 2001).

However, these instruments could not emulate cooling via evaporation of water, which has been shown to be important for other intertidal species (Vermeij 1971; Brawley and Johnson 1991; Bell 1995). Previous studies of the congener *M. edulis* have suggested that this species is able to lose water via gaping during low tide (Shick et al. 1986; Ameyaw-Akumfi and Naylor 1987; Guderley et al. 1994), but the capacity for *M. californianus* to cool by evaporation has never been fully assessed. Mathematical models (Helmuth 1998) have suggested that even a small amount of evaporation could lead to a significant loss of heat. The fact that the instruments used by previous studies were unable to account for any effects of evaporative cooling via gaping is thus a potentially significant liability. As part of our tests of the accuracy of these instruments, which do not hold water and thus do not cool by evaporation, we explored the tendency of *M. californianus* to gape and to cool via the evaporation of water. Furthermore, we tested the accuracy of our thermally matched logger design under a range of laboratory and field conditions as a means of better assessing their usefulness in predicting patterns in the field.

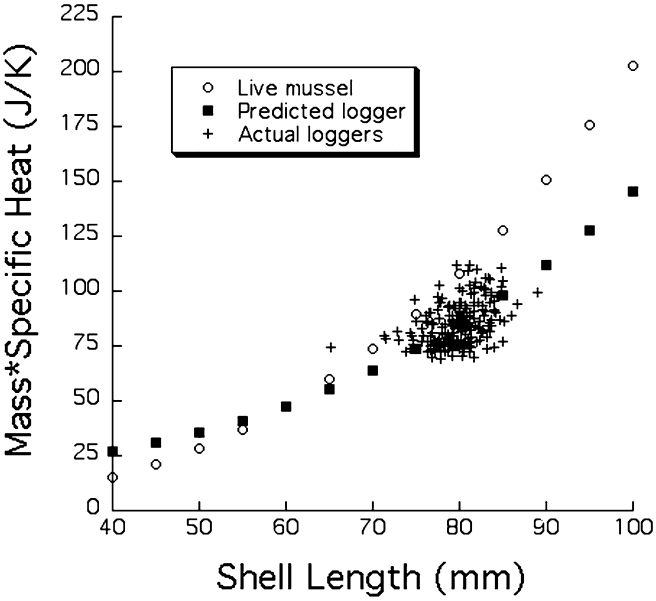

Fig. 2 Product of mass×specific heat capacity (a measure of thermal inertia) for epoxy (polyester) loggers shaped like mussels, and for living mussels, as a function of length. Instruments are most closely matched at a length of 60–65 mm, but because it was difficult to fit data-logging instruments in molds of mussels at this size, actual loggers (indicated by +) were based on a slightly larger (~80 mm) mussel

Study sites

As detailed below, our results show that thermally matched loggers are capable of recording temperatures that are representative of mussels in the field, and that evaporative cooling is not likely to occur in this species. Thus, physical models that mimic the thermal characteristics of living mussels can provide an accurate means of measuring body temperature in the field. Thermally matched temperature loggers ("robomussels") were thus deployed to study patterns of temperature exposure at two well-studied sites in central Oregon: Boiler Bay (44°15′N, 124°07′W) and Strawberry Hill (44°50′N, 124°03′W). Previous studies have shown that ecological and physiological patterns differ between these two sites. Menge et al. (1997a, 1997b) have shown that phytoplankton abundance and productivity are consistently

higher at Strawberry Hill than at Boiler Bay, and that as a result suspension feeders residing at Strawberry Hill are exposed to more food than those at Boiler Bay. Dahlhoff and Menge (1996) further showed that for *M. californianus*, higher metabolic rates and higher capacity for protein synthesis at Strawberry Hill corresponded to higher food levels at that site.

The authors of these studies (Dahlhoff and Menge 1996; Menge et al. 1997a, 1997b) noted that low zone temperature loggers at Strawberry Hill recorded hotter low tide (aerial) temperatures than those at Boiler Bay, and suggested that temperature may also play a role in site-specific differences in organismal physiology (Dahlhoff and Menge 1996; Dahlhoff et al. 2001). These measurements do not necessarily reflect organismal body temperatures, due to the multiple climatic factors that drive an organism's thermal regime, but the data of Dahlhoff and Menge (1996) and Menge et al. (1997a, 1997b) underscore the fact that even closely spaced sites may differ climatically (Helmuth 1999; Helmuth et al. 2002). More explicitly, Dahlhoff et al. (2001) were able to measure whelk temperatures in situ at Strawberry Hill and Boiler Bay, observing higher whelk body temperatures at Strawberry Hill. However, the temperatures were recorded for only one day, and not simultaneously, pointing to the need for deploying biologically accurate loggers that can record at multiple sites for long periods of time. We thus investigated whether mussel body temperatures, as measured by thermally matched loggers differed between sites and exposures at Boiler Bay and Strawberry Hill. We further investigated differences in the thermal regimes of wave-exposed and wave-protected subsites at these locations.

Materials and methods

Experimental animals

For the purposes of testing evaporative cooling rates and for comparisons of live mussel temperatures to logger temperatures under controlled conditions, we maintained living *M. californianus* in laboratory cultures. Mussels were collected from Strawberry Hill and transported to seawater facilities at the University of South Carolina, where they were kept in a flow-through tank at 12°C. All mussels were numbered and a small hole was drilled into their right side, just large enough to fit a small thermocouple wire (< 1 mm). No mortality was observed due to the drilled hole. Thermocouple wires were inserted into the approximate center of live mussels during each treatment, which allowed their body temperatures to be recorded by a Campbell data recorder (sample rate of 1 s).

Effects of temperature on gaping behavior

To determine effects of temperature on gaping behavior (defined as any measurable opening of the shell valves) and evaporative cooling, two treatments were used. In the first treatment, mussels were placed at varying distances from a heat lamp and their body temperature and gaping responses were recorded. In the second treatment, mussels were deployed in artificial beds composed of live mussels. Once again thermocouple wires were used to constantly measure body temperature. In this treatment, some mussels were allowed to gape, and others were prevented from gaping by holding the shells closed with a rubber band to serve as a control to ascertain if the observer was simply missing the gaping behavior. This second experiment allowed for a more realistic environment where mussels were in close proximity with their neighbors, and was designed to determine if mussels prevented from gaping achieved higher temperatures than those that were allowed to gape. Throughout each trial, air temperature, short-wave radiation, and relative humidity were monitored.

Thermally matched logger design

Commercially produced temperature loggers (TidbiT Loggers, Onset Computer, Pocasset, Mass.; diameter = 30 mm) were modified to match the thermal characteristics of living mussels as follows. Live mussels collected in California and Oregon during the course of other investigations were used to construct curve fits of tissue and shell mass versus shell length for *M. californianus*. Shell and body mass (m) as a function of length (L) were best described as a power function (length in m; mass in kg): body mass = $28.55\ L^{2.88}$, ($R^2 = 0.84$); shell mass = $28.73\ L^{2.71}$, ($R^2 = 0.80$). The specific heat capacity (c_p) of tissue was assumed to be equal to that of water, 4180 J/kg K; the c_p of shell was approximated as 815 J/kg K (Helmuth 1998). Thus, the sum of $m \times c_p$ for both shell and body for *M. californianus* was calculated as $y = (11.93\ 10^4\ x^{2.88} + 23.41\ 10^3\ x^{2.71})$, where y = weighted mass×specific heat of shell and body (J/K), and x = shell length in m (Fig. 2).

Temperature loggers designed to mimic real mussels were constructed of polyester resin (Evercoat) poured into molds created from *M. californianus* shells. Estimates of $m \times c_p$ of these instruments were based on the density (1,100 kg/m^3) and c_p (1,400 J/kg K) of polyester resin, plus that of a TidbiT logger (m = 19.3 g, c_p estimated as that of resin). Based on our calculations, and estimating mussel volume (in m^3) as a function of length (in m) as $V = 0.06\ L^{2.86}$ (Denny et al. 1985) we were then able to compare the thermal inertia of real mussels versus that of resin loggers as a function of length. The two estimates were equivalent at a shell length of ~60 mm (Fig. 2) but because it was difficult to fit a TidbiT logger into a mold of this size we created mussel mimics with a slightly larger length (~80 mm; Fig. 2).

For each "robomussel", a TidbiT logger was placed in the center of the mussel mold. Polyester resin with a black coloring agent was poured into the mold and allowed to harden. Each thermally matched logger was then smoothed and shaped to that of a real mussel using a Dremel tool (Fig. 1). Ratios of estimated thermal inertia of thermally matched loggers to that predicted for a mussel of identical length averaged 0.80 ± 0.09. As a result, thermally matched loggers had an estimated thermal inertia comparable to that of a real mussel ~74 mm in length. Logger data and launch parameters were transmitted through the instruments' LEDs, which were exposed on the outside of the robomussel (Fig. 1).

Laboratory tests of temperature loggers

To determine the effectiveness of our thermally matched logger design for estimating animal temperatures, live mussels were fitted with thermocouples and placed in beds composed of other live mussels. Two unmodified TidbiT loggers and two thermally matched loggers were then deployed alongside the live mussels. One unmodified logger was placed on the top of the bed; the other was placed at the bottom of the bed. The thermally matched logger was placed in a position similar to that of a living mussel, posterior-end upwards. Each logger was programmed to continuously record temperatures throughout the experiment at a frequency of 1 reading/s, and had an accuracy and resolution of ~0.3°C. A heat lamp was suspended above the bed and trials were run for 30 min. During each trial, mussels and loggers were exposed to constant

environmental conditions and temperatures were recorded simultaneously. After an initial rise in temperature at the beginning of each experiment, mussels and loggers maintained a relatively constant (equilibrium) temperature for the majority of the trial. These steady-state temperatures (e.g., Helmuth 1998) were used for statistical comparison of each logger design. Logger error was calculated as the difference between the temperature of the live mussel and that of each logger design (either modified or unmodified). Three paired *t*-tests were used to compare the body temperatures of the uninhibited (able to gape freely) living mussels to each logger treatment (thermally matched and in growth position, unmodified on the top of the bed, and unmodified on the bottom of the bed); when multiple loggers or multiple mussels were used in a single trial their temperatures were averaged to produce a single data point per treatment per trial.

Field tests of logger accuracy

During the week of 13–20 May 2002, comparisons were made in the field between thermally matched loggers and adjacent mussels living in growth position. During each trial, a single mussel was removed from a bed and replaced with a thermally matched logger that was placed in approximate growth position. The logger was programmed to record temperatures at a rate of 1 reading/min. Simultaneously, a thermocouple wire was inserted into the posterior margin of an adjacent, similarly sized living mussel within the bed. The thermocouple was connected to a Telatemp logger, Fullerton, Calif., that recorded animal temperatures at 1-min intervals. The mussel and logger temperatures were allowed to come to equilibrium (approximately 20 min). The maximum temperature recorded by the mussel mimic was then compared to that experienced by the mussel and the difference between the two was considered to serve as an estimate of maximum logger error. Five different thermally matched loggers were used for these trials and a total of 28 pairs of loggers and mussels were tested.

Measurements of field temperatures

To quantify patterns in mussel body temperature in the field, thermally matched loggers were deployed from May 2000 to August 2002 at Boiler Bay and Strawberry Hill. Each location was further divided into wave-exposed and wave-protected sites, based on previous work conducted at these locations (Menge et al. 1997a, 1997b; Dahlhoff et al. 2001, 2002). Strawberry Hill is a topographically complex site spanning a wide section of the intertidal zone. At low tide, landward sections are more than 50 m from the water's edge and are unlikely to experience wave splash at low tide. Strawberry Hill was thus divided into seaward (wave-exposed) and landward (wave-protected) sites, after Dahlhoff et al. (2001). Boiler Bay, in contrast, was divided into three gently sloping, topographically simple benches oriented perpendicular to the mainland. The seaward bench is generally considered to be the most wave-exposed, with the landward bench the most wave-protected (Menge 2000). Because of heavy instrument loss at the most wave-exposed bench in 2000, loggers were deployed only at the intermediate and protected benches in 2001–2002. Instruments at the two most seaward benches were thus assumed to be wave-exposed, while the most landward bench was considered to be comparatively wave-protected. (Later analysis, however, indicated no difference in wave splash between the protected and intermediate benches: see below). Between four and six thermally matched loggers were deployed at each wave exposure at each site and were exchanged at 3- to 6-month intervals. Each instrument was programmed to record average temperature at 10-min intervals. Loggers were deployed at a fixed tidal elevation of mean lower low water (MLLW) $+\sim 1.5$ m (approximately mid-tidal elevation); logger heights were confirmed using a laser level. Each instrument was placed in a bed of *M. californianus* and whenever possible was attached in approximate growth position (posterior end upwards) using Z-spar splash zone epoxy (Helmuth et al. 2002). With the exception of one 3-month gap due to logistical difficulties (5 January 2002–7 April 2002), continuous measurements of temperature were recorded from 20 May 2000–8 October 2002 at Strawberry Hill and from 14 October 2000–7 October 2002 at Boiler Bay.

In order to confirm that wave-exposed sites were indeed subject to higher levels of wave-splash than wave-protected sites, temperature data were also used to calculate the "effective shore level" (Harley and Helmuth 2003). This approach is described in detail in Harley and Helmuth (2003) but, in brief, it relies upon the sudden drops in temperature evident in logger records when the instrument is first inundated by the returning tide (during days with higher waves, a logger may be wetted when the still tide level is still far below the loggers' datum height; in other words, wave splash causes a high shore animal to experience thermal conditions similar to those experienced by an animal much lower on the shore during calm weather). Thus, we recorded the first instance of a drop in temperature of at least 3°C for each logger over the entire deployment period and then matched the time of the drop against the predicted still tidal height. We then calculated the linear regression between the effective shore level for each logger and the maximum significant wave height recorded by the nearest buoy (National Data Buoy Center No. 46050, Stonewall Banks, Newport, Ore.). These curve fits were used to compare the effective shore level of each microsite as a function of wave height.

Comparisons of effective shore level for each microsite showed that there was surprisingly little difference between the wave-protected (landward) and intermediate (more seaward) benches at Boiler Bay. Only the most seaward (exposed) bench displayed a marked drop in effective shore level. Because only one logger was recovered from this bench in 2000 (the remainder were lost to waves), statistical comparisons involving the wave-exposed treatment at Boiler Bay could not be completed. At Strawberry Hill, with one exception (a putative wave-exposed microsite that displayed an effective shore level characteristic of a wave-protected site), exposures conformed to expectations. Data from the outlying exposed microsite were grouped with those from the protected sites at Strawberry Hill.

Temperature data were summarized for comparisons between sites and wave exposures using four metrics. For each 24-h period, the 98th percentile of temperatures was calculated for each logger; this metric of "daily maximum" represents the highest temperature that each logger recorded for a period of at least 30 min for that day (usually, but not necessarily, sequentially). As a measure of more "chronic" thermal stress, we also calculated the "average daily maximum" on a weekly basis (the running average of the previous 7 days of daily maxima, a modification of the methods of Helmuth and Hofmann 2001). Because physiological thermal stress is generally thought to be greatest when organisms are exposed to temperatures comparatively much higher than those to which they are acclimated (Buckley et al. 2001; Halpin et al. 2002), for each day we calculated the difference between the daily maximum for that day and the average daily maximum of the previous week ("maximum difference"). The yearly peak values for each of these metrics (daily maximum, average daily maximum, and maximum difference) were then used for statistical analysis. Thus, for example, the peak daily maximum for a logger indicates the highest 30-min temperature recorded by that logger for the entire year, the peak average daily maximum indicates the hottest week of the year, etc. Finally, we calculated the total degree–hours for each logger for the months of May–September.

We chose the daily maximum and average daily maximum metrics because both acute and chronic high temperature exposures have been shown to produce cellular damage in intertidal organisms (Hofmann and Somero 1995; Buckley at al. 2001; Tomanek 2002). However, we acknowledge that the thermal environment and the physiological responses of organisms to it are quite complicated, and included the maximum difference as a measure of variability. We expect that as thermally matched loggers come into greater use, a clearer picture of what aspects of the thermal environment are relevant will emerge (i.e. distinguishing signal from

noise) and other metrics may be adopted. We offer these four metrics as an initial starting point as a means of comparing different thermal regimes.

We used discriminant analysis techniques to test which temperature metrics were most useful in contrasting the thermal regimes of our different sites. This approach also allowed multivariate analysis of correlated variables (the temperature metrics chosen). Because of high instrument loss at the Boiler Bay exposed site, we were unable to test for an exposure effect at both sites. Instead, we tested for differences between exposed and protected sites at Strawberry Hill in 2001 and 2002. To examine site effects, we tested for differences between Boiler Bay and wave-protected sites at Strawberry Hill in both years. After detecting no differences between the sites in each year, we pooled data for both years.

Results

Laboratory measurements

Gaping behavior was not observed during any trials. In several instances mussels died during the experiment, presumably due to temperature stress, but never exhibited the gaping behavior. Live mussels freely able to gape and live mussels restricted from gaping did not have temperatures significantly different from each other ($n = 22$; t-ratio $= -1.59$ and $P = 0.13$), and mussels prevented from gaping were not always hotter than those free to gape.

Thermally matched loggers had an average error ($\pm$1SD) of $+2.19 \pm 1.62$°C ($n = 23$) compared to live mussels; this difference was not statistically significant (t-ratio $= 1.63$, $P = 0.11$). Unmodified loggers on the top of the mussel bed had an error of $+14.61 \pm 3.65$°C ($n = 8$; t-ratio $= 12.02$, $P = 0.0001$); while unmodified loggers on the bottom of the mussel bed had an error of $+3.67 \pm 1.27$°C ($n = 9$; t-ratio $= 9.172947$, $P = 0.0001$). In sum, while the temperatures recorded by the thermally matched loggers were not significantly different from that of the surrounding bed of live mussels, the unmodified loggers were significantly different, incurring average errors of up to 14°C.

Field tests of logger design

The average absolute error (the absolute value of the difference between thermally matched logger and real mussel) for the 28 pairs recorded was 2.69 ± 1.99°C, and there was a significant correlation between live mussel temperature and thermally matched logger temperature ($F = 44.4$, $P \leq 0.0001$, $R^2 = 0.61$). However, absolute error also increased with animal temperature ($F = 18.2$, $P \leq 0.0002$, $R^2 = 0.41$). Somewhat surprisingly given their lower thermal inertia, loggers tended to record temperatures that were lower than those of living mussels. There was a subtle but significant negative correlation between unadjusted error and live mussel temperature ($F = 6.32$, $P \leq 0.02$, $R^2 = 0.20$) suggesting that the tendency for loggers to underestimate animal temperature increased with temperature.

Field patterns in mussel body temperature

Analysis of the effective shore levels of loggers at the two exposures from which loggers were retrieved at Boiler Bay (protected and intermediate benches) indicated that there was no difference in wave splash. We therefore pooled data from these two areas at Boiler Bay into the wave-protected category. Instruments were retrieved only from the Strawberry Hill wave-protected site ($n = 4$) and the Boiler Bay wave-exposed site ($n = 1$) in 2000; data for this year are thus presented in Table 1, but were not used for statistical analysis.

Discriminant analysis using the four temperature metrics indicated that degree–hours and annual peaks in daily maximum and weekly average daily maximum were all useful in discriminating between sites (Fig. 3); the maximum difference metric was never useful in discriminating between sites and this metric was therefore dropped from the analysis. In both 2001 and 2002, wave-exposed and wave-protected areas at Strawberry Hill were significantly different from one another, showing separation along the first canonical axis (Fig. 3; 2001: $P = 0.0376$; 2002: $P = 0.0189$). In 2001, degree–hours and yearly peak daily maximum temperatures allowed significant discrimination between wave-exposed and wave-protected areas (Fig. 3A, $P = 0.0376$). Interestingly, however, these metrics operated in opposite directions, with higher annual peak daily maximum temperatures at the wave-exposed site, but higher degree–hours at the wave-protected site (Table 1, Fig. 4). In 2002, all three temperature metrics allowed for significant discrimination between wave-exposed and wave-protected sites at Strawberry Hill (Fig. 3B, $P = 0.0189$). Here, all three metrics were higher in the wave-protected sites (Table 1, Fig. 4). The annual peak daily maximum temperature was most important in discriminating between protected and exposed sites in

Table 1 Summary statistics for wave-protected and wave-exposed sites at Boiler Bay (*BB*) and Strawberry Hill (*SH*). Data for annual peak values of daily maximum ("max"), average (weekly) daily maximum ("AD max."), and the maximum difference ("max. diff.") between the daily maximum and the average daily maximum for the preceding week are presented as mean ± 1SD. Degree–hours were calculated cumulatively from May to September of each year. (Loggers were not deployed until mid-May in 2000, so degree–hours for this year were not calculated)

Site	n	Max.	SD	AD max.	SD	Max. diff.	SD	Degree–hours	SD
2000									
BB exposed	1	33.00	·	27.06	·	11.92	·	·	·
SH protected	4	35.18	1.28	29.22	1.68	10.72	0.48	·	·
2001									
BB protected	2	33.32	1.94	29.83	1.89	11.42	0.87	45284	165
SH protected	4	35.34	3.76	29.19	2.52	12.45	1.83	46950	1916
SH exposed	2	37.74	0.69	30.53	0.55	15.14	1.33	43484	2334
2002									
BB protected	7	34.43	2.79	30.31	3.02	12.40	1.88	43091	1626
SH protected	4	34.95	2.85	29.39	1.54	12.26	0.96	44319	1301
SH exposed	2	26.95	2.93	21.39	1.80	9.46	1.94	38964	1155

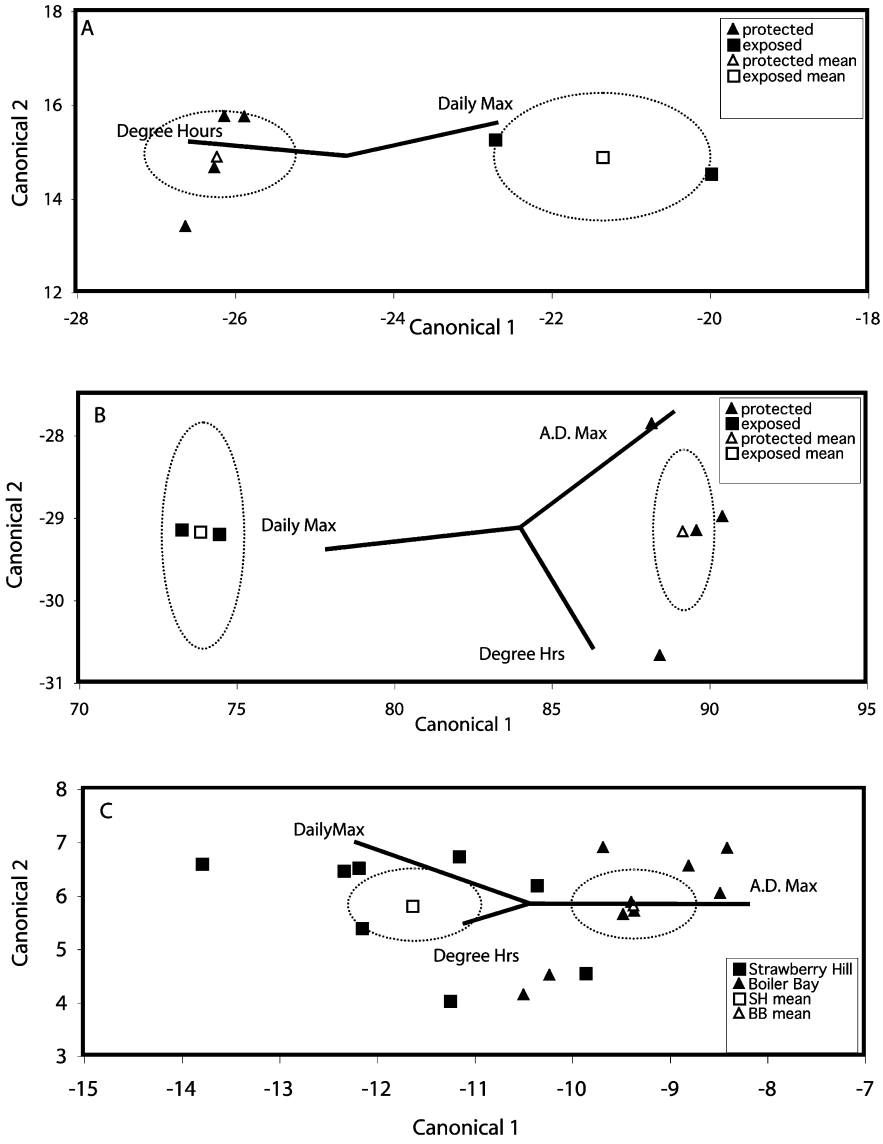

Fig. 3A–C Biplots showing separation of sites in multivariate space using three temperature metrics: annual peaks in daily maximum ("*daily max*") and weekly average daily maximum ("*AD max*."), and cumulative summertime degree–hours. *Graphs* show first and second canonical axes for wave-protected and wave-exposed sites at Strawberry Hill in 2001 (**A**); Strawberry Hill in 2002 (**B**); and at Boiler Bay and Strawberry Hill protected sites in 2001 and 2002 (combined) (**C**). *Ellipse*s show 95% confidence limits for the multivariate means. *Rays* represent loadings of variables in canonical space. Length of ray is proportional to loading; *direction* indicates axis of loading

2002, as indicated by its loading on the first canonical axis (Fig. 3B). Similarly, daily maximum, average daily maximum and degree–hours, but not maximum difference, provided significant discrimination between Boiler Bay and Strawberry Hill, along the first canonical axis (Fig. 3C, $P = 0.0072$). However, there were no clear indications of which site was "hotter" as peak daily maximum was highest at Strawberry Hill, but peak average daily maximum was highest at Boiler Bay (Table 1).

During 2001, annual peak values in the daily maximum temperature occurred in either mid-May (13–16 May) or in early June (7–12 June) at both Boiler Bay and Strawberry Hill; there were no obvious differences in the timing of these events between the wave-exposed and wave-protected sites (Fig. 4). Peak values in the average daily maximum also tended to occur at these same time intervals. Highest values of the maximum difference metric, i.e., times when the daily maximum was most different from the temperatures to which the animals were acclimated, occurred in either early April (11 April) or early June (7–8 June). The lowest temperatures of the year (~1–3°C) occurred on 16 January and 7 February 2001.

In 2002, yearly maximum values in the daily maximum and average daily maximum metrics for loggers at wave-protected sites were recorded during the first week of July at both Strawberry Hill and Boiler Bay (Table 1). However, timing of the peaks in these metrics at the Strawberry Hill wave-exposed site was more variable, occurring in either June or September. The timing of the peak values in the maximum difference was also variable. About half the loggers recorded peaks in this metric during the middle of April, but peak values also occurred during the months of May, June, July and (at wave-exposed sites) in September. Because of the 3-month gap in the data set in the winter of 2002, minimum values were not computed.

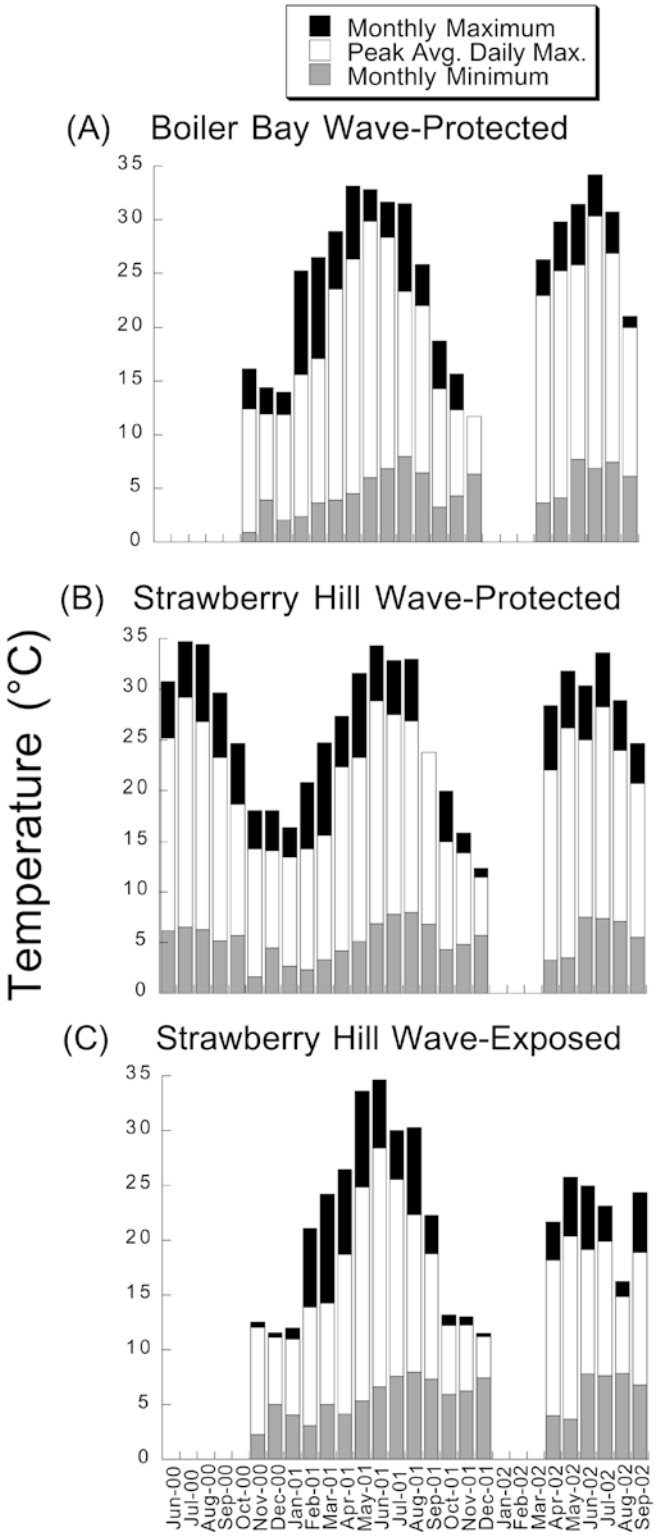

Fig. 4 Monthly temperature summary statistics [monthly maximum, peak average daily maximum (weekly average of daily maxima) and monthly minima] for **A** Boiler Bay wave-protected site, **B** Strawberry Hill wave-protected site, and **C** Strawberry Hill wave-exposed site

Discussion and conclusions

Relationship between temperature and mussel gaping behavior

We were unable to document any relationship between mussel gaping and body temperature of *M. californianus*. In trials, mussels actually died rather than gape, which suggests that evaporative cooling does not play a major role in *M. californianus* thermoregulation. These results are consistent with the findings of Elvin and Gonor (1979), who correlated environmental parameters with body temperature and found that including a term for evaporative cooling did not significantly improve the accuracy of their model. While failure to elicit gaping behavior by *M. californianus* under laboratory conditions does not necessarily mean that this behavior does not occur in the field, experiments conducted using the same methods with the mussel *Geukensia demissa* regularly produced this behavior (Fitzhenry, unpublished data), suggesting that our observations are not an artifact of our experimental conditions. The most likely alternative is that when gaping by *M. californianus* does occur it functions more as a means of increasing aerobic respiration (Lent 1968; Moon and Pritchard 1970; Bayne et al. 1976b).

Accuracy of mussel loggers

While our thermally matched loggers provide only an estimate of mussel temperatures in the field (within ~2–4°C), laboratory tests confirm that our design is still a much closer proxy for field temperatures than unmodified loggers. Further development of instrument design will likely increase the accuracy of field measurements. Two potential sources of error in our design are the infrared (long-wave) surface characteristics and the thermal conductivity of the resin. While the short-wave (visible) color of the loggers was close to that of real animals, we had no control over the tendency of our instruments to absorb and reflect infrared radiation. Indeed, measurements of logger emissivity (Helmuth, unpublished data) indicate that this parameter is lower for polyester loggers than for real mussel shells, suggesting that the logger's ability to gain and lose heat via infrared radiation may be lower than that of a real animal.

A second possible discrepancy between the logger properties and that of living animals lies in the thermal conductivity of the polyester. Previous models and measurements of heat flux within mussels (Helmuth 1998) have suggested that heat is circulated and conducted within tissue fairly rapidly, so that gradients of only a few degrees exist between different regions of the mussel. If heat were conducted more slowly in our thermally matched loggers, then it is possible that "core" temperatures of our instruments were not the same as those of living animals.

Finally, at least some of the error in our measurements may actually be a reflection of heterogeneity in temperatures within the bed, rather than a reflection of the inability of our loggers to record accurate temperatures. Variability in mussel temperature due to differences in shell absorptivity, angle relative to the sun, position within the bed, and body size all contribute to variability in body temperature. Thus, to some extent, our measurements under controlled laboratory conditions (where all of these variables were held constant) may serve as a more effective metric of logger accuracy (~2°C, not significantly different from live mussels) and our field measurements may serve more as an indication of natural variability within a bed. In either case, these results highlight the dilemma associated with making site-to-site comparisons within such a spatially and temporally heterogeneous environment (Underwood and Chapman 1996, 1998; Helmuth and Hofmann 2001; Helmuth and Denny 2003).

Previous versions of logger design incorporated real mussel shells filled with silicone, and these displayed errors of only 1.5°C (Helmuth and Hofmann 2001). However, this design was found to be far less rugged than the current method, and shells smaller than ~9 cm could not accommodate a TidbiT logger. While smaller loggers are available commercially, none have the memory capacity of the TidbiT logger, so loggers matched to smaller mussels must be retrieved at much more frequent intervals (e.g., Helmuth 2002).

While the accuracy of our design requires further testing, our results confirm that the design of a temperature logger can have a marked impact on the temperature that it records and that the deployment of a "generic" design without consideration of the animal in question can lead to large errors. We were able to regularly generate errors of >14°C using unmodified loggers; values that never occurred with our modified design. This study thus presents a strong caution to researchers working in intertidal environments to verify that the temperature being recorded is relevant to the organism in question. Our results thus strongly suggest that a single logger design is highly unlikely to provide accurate estimates of intertidal organismal body temperatures, with the likely exception of organisms with temperatures linked closely to that of the substratum (e.g., Wethey 2002; Harley and Helmuth 2003).

Perhaps the biggest challenge facing the use of these instruments is developing methods for more secure attachment to the substrate, and for incorporating smaller data loggers that still possess sufficient memory for long deployments. While the sample interval can be lengthened to increase deployment time, the increased time between samples will also tend to miss peaks, and in extreme cases may create sampling error by aliasing the data (Helmuth 1999).

Field patterns in body temperature

In some ways our comparisons of wave-exposed and wave-protected sites are not surprising. Wave splash tends to keep temperatures low even at high shore levels, and affords some protection during midday exposures. However, it should be noted that our designations of wave protected and wave exposed were based not only on visual assessment but also on direct quantification of wave splash effects by the use of effective shore level (Harley and Helmuth 2003). Notably, one putative exposed site at Strawberry Hill showed no more evidence of the effects of wave splash than did sites much farther inshore. Moreover, our results indicated no apparent difference between what are generally considered to be protected and intermediate exposure benches at Boiler Bay. While data from the single logger recovered from the most seaward bench suggest that this site does indeed experience higher levels of wave splash, our results emphasize the utility of direct measurements of wave splash and submersion time (Venegas et al. 2002; Harley and Helmuth 2003).

Our data set indicates year-to-year variability in the effects of wave splash. In 2001, extreme (rare) temperature events at the wave-exposed site at Strawberry Hill not only met, but slightly exceeded temperatures at the wave-protected site (Fig. 4, Table 1). Degree–hours, a more cumulative metric of the effects of temperature, was in contrast highest at the wave-protected site. In 2002, all measures of high temperature exposure were highest at the wave-protected Strawberry Hill site. These apparent differences are not easy attributable to interannual differences in wave height. During the months of May–September 2001, offshore significant wave heights (measured at National Data Buoy Center buoy 46050) averaged ($\pm$1SD) 1.80 ± 0.72 m. During the same interval in 2002, significant wave heights were slightly lower, with a mean of 1.69 ± 0.58 m. In other words, average wave heights were lower during a year (2002) when temperatures were comparatively highest at the wave-protected site than they were during 2001, when extreme temperatures at the wave-exposed site surpassed those at the wave-protected site. Thus, it would be difficult to predict relative levels of acute thermal stress between these 2 years based only on measurements of wave height. These results highlight the rare combination of hot terrestrial climate, midday low tides, and periods of low wave splash that must co-occur in order to produce high temperatures at wave-exposed sites. However, they also point to the fact that these combinations do occur, particularly at sites such as Strawberry Hill where midday low tides regularly occur during the summer months (Helmuth et al. 2002).

Our results suggest that such an event occurred at exposed sites on 12 June 2001, at Strawberry Hill. On this hot day, the maximum temperature recorded by a wave-exposed logger was recorded at the same time as

the peak temperatures recorded by instruments at wave-protected sites. On this particular day, the peak temperature recorded by all loggers occurred while the still tide level was approximately MLLW + 50 cm, approximately 20 cm lower than the effective shore level of the exposed loggers on that day, and well below the effective shore level of the more seaward, wave-protected loggers. In contrast, on 3 July 2002, when Strawberry Hill wave-protected loggers achieved the highest temperature of the year, wave-exposed loggers remained cool. On this day, low tide occurred at 1230 hours, and the peak temperature of the day was recorded when the still tidal level was MLLW + 75 cm, 10 cm above the effective shore level of the wave-exposed loggers.

The data from 12 June 2001 highlight some important points. First, in order for wave-exposed loggers to achieve high temperatures, a rather unusual set of environmental conditions needs to coincide. Nevertheless, such conditions do occur, and result in similar extreme thermal events in both wave-exposed and wave-protected sites. Mussels at exposed sites may be more vulnerable to the physiological effects of these rare, extreme temperature events, though they experience the same temperature as protected mussels, because they are thermally acclimated to an overall cooler environment.

Secondly, though such events may be difficult to predict, and depend upon terrestrial climate, wave splash, and the timing of low tide, they may not be all that uncommon at sites where midday tides occur in summer (Helmuth et al. 2002). While calm waves and hot terrestrial climate may be considered to be more or less stochastic events with little hope of accurate high resolution prediction, estimates of the timing of low tide are not. As such, animals living in wave-exposed locations where low tides never occur midday during the hottest months of the summer may be less likely to experience temperature extremes than are animals at locations such as central Oregon where midday summer tides occur regularly. On the west coast of the United States, midday exposures in summer occur primarily at more northern latitudes such as Oregon and Washington, and more southern, hotter locations typically display low tides at night in summer (Helmuth et al. 2002). Thus, not only are latitudinal patterns in body temperature complex (Helmuth et al. 2002), but as this study suggests, thermal differences between wave-exposed and wave-protected locations may change with latitude as well, and extreme events may be comparably more likely at more northern wave-exposed sites than at southern sites.

While these patterns are difficult to interpret, this study emphasizes the utility of direct, long-term measurements of temperature that are specific to the organism of interest, and highlights the concept that counterintuitive patterns in temperature often occur in nature, and can often only be discerned if we know how to look for them.

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