



Hidden signals of climate change in intertidal ecosystems: What (not) to expect when you are expecting

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ABSTRACT

One of the most significant biological impacts of global climate change is through alterations of organismal body temperature, which ultimately drives almost all physiological processes. Using a simple heat budget model ground-truthed using ~5 years of *in situ* temperature data collected using biomimetic sensors, we explored the sensitivity of aerial (low tide) mussel body temperature at three tidal elevations to changes in air temperature, solar radiation, wind speed, wave height, and the timing of low tide at a site in central California, USA (Bodega Bay). Results suggest that while increases in air temperature and solar radiation can significantly alter the risk of exposure to stressful conditions, especially at upper intertidal elevations, patterns of risk can be substantially reduced by convective cooling such that even moderate increases in mean wind speed ($\sim 1 \text{ m s}^{-1}$) can theoretically counteract the effects of substantial ($2.5 \text{ }^\circ\text{C}$) increases in air temperature. Simulations further suggest that shifts in the timing of low tide (+1 h), such as occur moving to different locations along the coast of California, can have very large impacts on sensitivity to increases in air temperature. Depending on the timing of low tide, at some sites increases in air temperature will primarily affect animals in the upper intertidal zone, while at other sites animals will be affected across all tidal elevations. Field measurements and model predictions show that animal temperatures are often high even when air temperatures are not, confirming the importance of solar radiation in the heat budgets of intertidal ectotherms. Conversely, body temperatures are not always elevated even when low tide air temperatures are extreme due to the combined effects of convective cooling and wave splash. The results of these simulations, coupled with ongoing field measurements, suggest that the timing and magnitude of warming will be highly variable at coastal sites, and can be driven to a large extent by local oceanographic and meteorological processes. Moreover, they strongly caution against the use of single environmental metrics such as air temperature as indicators of past, current and future physiological stress on the west coast of North America, and instead advocate for approaches that consider the interactive roles of multiple physical drivers.

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1. Introduction

Virtually every physiological process is affected by the temperature of an organism's body, and the field of marine physiological ecology has experienced a revitalization in recent years with the advent of new molecular and biochemical techniques for studying organismal responses to thermal stress (e.g. Hofmann and Place, 2007; Somero, 2010; Pörtner, 2010; Lockwood and Somero, 2011-this issue). Concomitantly, there has been a renewed interest in the effects of temperature extremes on the ecology and physiology of organisms given the observed and forecasted impacts of global climate change

(Kearney and Porter, 2004; Helmuth et al., 2006a; Lima et al., 2006; Mieszkowska et al., 2006; Harley and Paine, 2009; Jones et al., 2009). However, particularly in studies of intertidal ecosystems, there is often a potential disconnect between measurements of the “environment” and the actual drivers of physiological performance, i.e. body temperature (Kearney, 2006; Broitman et al., 2009; Helmuth, 2009; Denny et al., 2011-this issue). For example, many ecological studies, and particularly those focused on climate change impacts, have relied on measurements of air and water temperature as proxies for environmental stress (e.g., Jones et al., 2009; Fodrie et al., 2010; Lesser et al., 2010; van der Wal et al., 2010). In some instances, the disparity between these large-scale measurements of the environment and what the organism actually experiences at the cellular level may be relatively minor: in a well-mixed water column, sea surface temperature may be very similar to water temperature a few m beneath the surface. Likewise, the body temperature of animals in shaded environments may be similar to that of the surrounding air or rock. In contrast, body temperature can be significantly different from the

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temperature of the surrounding air or surface when organisms are directly exposed to solar radiation (Bell, 1995; Williams and Morritt, 1995; Williams et al., 2005; Denny and Harley, 2006; Marshall et al., 2010), for example when invertebrates and algae are aerially exposed at low tide. Subtidally, tissue temperatures can be hotter than water temperature when water flow is sufficiently slow (Fabricius, 2006; Jimenez et al., 2008), and depending on the levels of mixing and surface heating, temperature gradients of several degrees can occur over depths of only a few m (Leichter et al., 2006). The question remains, therefore, when can we use environmental data such as air or sea surface temperature as effective indicators of environmental stress for marine organisms, and when must we instead model or measure the body temperatures of organisms? (Kearney, 2006).

On the east coast of North America, air and water temperature have been used as an effective indicator of physiological stress in intertidal mussels, and have been used to successfully reconstruct current and historical range boundaries (Jones et al., 2009, 2010). In contrast, measurements and models of intertidal animal temperature (Helmuth et al., 2002, 2006b) and concomitant measurements of physiological stress (Place et al., 2008) conducted over geographic scales on the west coast of North America suggest that patterns of body temperature are at odds with patterns of air or water temperature. Specifically, because of the complex interplay of multiple environmental drivers – air and water temperature, wave height, wind speed, cloud cover, solar radiation, and the timing of low tide – in determining body temperature, intertidal animals on the west coast of North America (Helmuth et al., 2006b), and likely in other parts of the world (Finke et al., 2007; Mislan et al., 2009; Pearson et al., 2009) may exist over a series of “thermal mosaics” rather than simple latitudinal gradients that cannot be explained based upon measurements of air or water temperature. Exploring the relative importance of each of these drivers is therefore a key consideration if we are to understand how changes in any of these physical factors are likely to affect intertidal populations.

The use of heat budget modeling has long been used in terrestrial systems as a highly effective means of moving from large-scale measurements of the environment (air temperature, solar radiation, wind speed, etc.) to physiologically-relevant measurements such as body temperature and water balance (e.g. Porter and Gates, 1969; Mitchell, 1976; Kearney and Porter, 2009). These methods have been applied successfully in intertidal systems as well (Johnson, 1975; Bell, 1995; Helmuth, 1998; Denny et al., 2006; Wethey, 2002; Denny and Harley, 2006; Finke et al., 2009), albeit far less frequently. Here we use a simple heat budget model to explore the effects of changing weather conditions on the physiological performance of an ecologically important species of intertidal mussel, *Mytilus californianus*. We do so using 5 years of meteorological and oceanographic data from a single site in central California, combined with *in situ* measurements representative of mussel body temperature collected using biomimetic sensors. Our goal is to tease apart the relative importance of various drivers of body temperature as a means of exploring how future changes in those parameters may alter the survival and performance of this ecologically important species both at this site and at other locations along the Pacific coast of North America.

2. Modeling approach and field validation

We used a steady-state model of heat flux to calculate the hourly body temperatures of moderately-sized ($L = 7.5$ cm) mussels (*M. californianus*) at a wave-exposed site in Bodega Bay, California, US. The model assumes that animals reach equilibrium within an hour, which is probably a reasonable assumption given measured time constants of 20–30 min for animals of this size (Helmuth, 1998). The model calculates the surface temperature of a horizontal bed of mussels of uniform size using hourly average weather data as inputs, and estimates emersion and wave splash from measurements of

nearshore significant wave height (Harley and Helmuth, 2003; Gilman et al., 2006a). Based upon a model first presented in Helmuth (1999) and expanded upon in Kearney et al. (2010), the model is explained in detail in an online Appendix, where an executable Microsoft Excel version is also provided.

Weather data (wind speed, air temperature, and direct solar radiation) were obtained from the University of California Davis Bodega Ocean Observing Node (BOON) system (bml.ucdavis.edu/boon). Tidal height estimates were acquired from X-Tide, operated by the Wethey laboratory at the University of South Carolina (tbone.biol.sc.edu/tide). Wave data were obtained from the NOAA National Data Buoy Center (Station 46013; www.ndbc.noaa.gov). Simulations were not run for days lacking four hours or more of weather or wave data. A wind floor of 0.25 m s^{-1} was set for wind speed reported at the BOON sensor (height of ~20 m) because we assumed that wind was never truly still, and to account for free convection.

The model was used to predict the hourly aerial body temperatures of mussels at a mid intertidal height of Mean Lower Low Water (MLLW) + 1.5 m from January 1, 2004 to December 31, 2008. Daily maximum, minimum and average values during aerial exposure were then compared against comparable measurements made at this site during the period April 14, 2004–December 31, 2008, with gaps in the data from 8/29/06 to 9/25/06 and 4/28/08 to 9/19/08 due to instrument failure and loss. Biomimetic sensors ($n = 3$) designed to replicate the thermal characteristics of living *M. californianus* (technique described in Fitzhenry et al., 2004; and Helmuth et al., 2006a, 2006b) were deployed in natural growth position in mussel beds at the same tidal elevation. Data were collected at 10 min intervals, and instruments were downloaded approximately every 6 months. Each biomimetic sensor consisted of a Tidbit temperature logger (Onset Computer Corporation) embedded in polyester resin of similar size, shape, and color to a living mussel with a shell length of approximately 7.5 cm. Previous comparisons of these sensors against living mussels have shown that the instruments record temperatures within ~ 2 °C of living mussels, as opposed to unmodified Tidbits which were on average 14 °C different from living animals (Fitzhenry et al., 2004). Because topography in the rocky intertidal habitats can be highly variable, very large differences in temperature can occur between microsites, for example between shaded and unshaded surfaces (Helmuth and Hofmann, 2001, also see Denny et al., 2011–this issue). Sensors were therefore placed on horizontal, unshaded microsites as a means of standardizing for the effects of topography. A sample size of three microsites is likely insufficient to capture all of the variability within a site, especially when variability in substrate orientation is considered (see Denny et al., 2011–this issue). Therefore, the temperatures reported here should be considered as realistic examples of temperatures of animals on horizontal surfaces at a fixed tidal height, but not as representative of the full range of variability at the site.

Data were archived along with those from other study sites on a searchable database that separates aerial temperatures from aquatic temperatures based on still tidal height. Users of the database (climate.biol.sc.edu/data.html) are able to access data through a map-based interface, and can download summary data at intervals ranging from 10 min (raw data) to 24 h. Spatial standard deviations of records from the three loggers are also reported.

We used this database to calculate the maximum, minimum and average daily aerial temperature recorded by the temperature loggers. Each metric was recorded daily as the spatial average of all loggers (thus, for example, for each day we calculated the average of the daily maxima for all loggers). These spatial averages of daily maxima and minima are thus to some extent an underestimate of extreme temperatures; for example, in some cases loggers varied by 5 °C or more on hot days. For each day for which data were available (some instrument loss occurred), we calculated, for daily maxima, average, and minima, the average difference between the model and loggers, the absolute value of the difference between the model and the

loggers, and the root mean square error (RMSE). The average across all days was then used as a measure of model error.

As with previous attempts to model intertidal organisms (e.g., Gilman et al., 2006b; Denny and Harley, 2006; Szathmary et al., 2009), on average the model performed quite well in predicting daily average, maximum, and minimum values, although on some occasions predicted values could be substantially off. For example, we interpret many of the data points where predicted model temperatures are high but logger temperatures are ~12 °C as days when loggers were splashed by waves that were not accounted for in the model (Fig. 1A). Overall, however, average absolute error was reasonably small (~2 °C for average daily aerial temperature and ~2.8 °C for daily maximum temperature; Table 1), and the frequency distributions of values of maximum daily temperatures estimated from the model were similar to those measured in the field, especially at temperatures above 24 °C (Table 1, Fig. 1B). The comparatively large number of days with temperatures in the range of 12–15 °C is again likely an indication of times when the model failed to account for wave splash (Fig. 1B). Thus, the error in the model was similar to the ability of the instruments themselves to predict the temperature of living animals (Fitzhenry et al., 2004), and comparable to the spatial variability among instruments and living animals on hot days (Gilman et al., 2006b). The ability of the model to predict estimated mussel temperatures, and

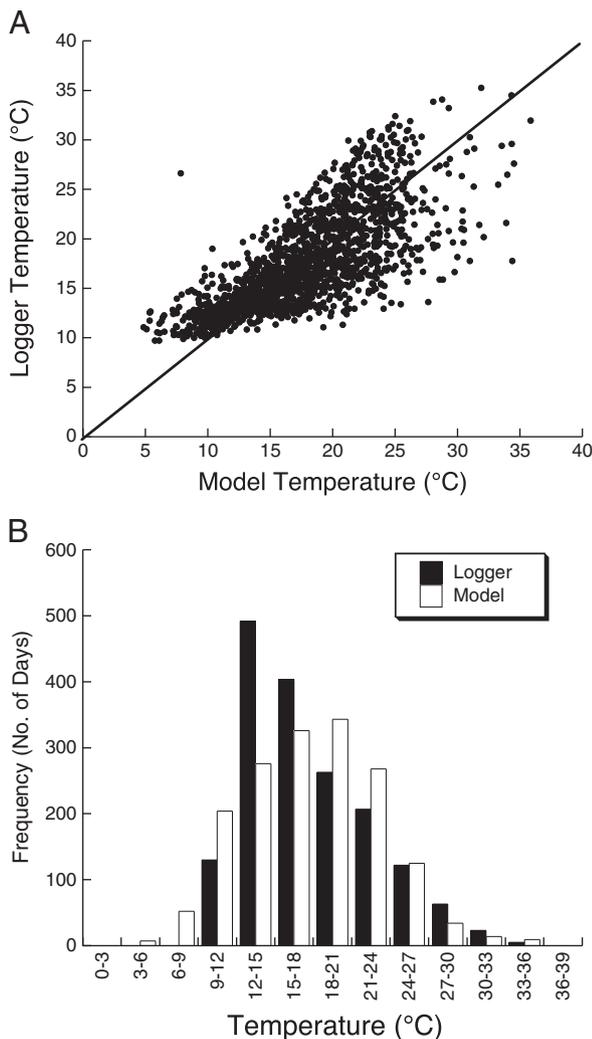


Fig. 1. Comparison of model predictions (daily maximum values) to biomimetic logger measurements (average of 3 loggers). (A) Daily maximum temperatures recorded by biomimetic sensors in mussel beds at MLLW + 1.5 m plotted as a function of model predictions. (B) Frequency distributions of logger temperatures and model outputs.

Table 1

Comparison of model simulations to field measurements collected using biomimetic sensors. A positive value in average difference indicates that the model overestimated logger (mussel) temperatures.

	Daily maximum	Daily avg	Daily minimum
Average difference	-0.22	-0.68	-2.29
Abs (Avg diff)	2.82	1.98	2.67
RMS error	3.60	2.50	3.13

particularly daily maximum temperatures ($R^2 = 0.55$), was therefore as good as our ability to record them in the field, despite daily fluctuations of 20 °C or more. Notably, the error in this relatively simple model compared very favorably to more sophisticated models (e.g. for daily maximum, average difference = -0.22, RMSE = 3.60 as compared to Gilman et al., 2006b: average difference = -1.71, RMSE = 4.12); it should be noted however that unlike the model presented in Gilman et al. the applicability of this model to sites other than Bodega Bay has not been verified.

During the period 2004–2008, air temperatures ranged from ~0 to 27.5 °C, maximum solar radiation recorded was ~1075 W m⁻² and wind speed at a height of 20 m ranged from near still (assumed as 0.25 m s⁻¹) to >20 m s⁻¹ with an average of 4.3 m s⁻¹. The tidal range at this site over the five years examined was MLLW -0.6 m to MLLW + 2.15 m, and significant wave heights ranged from 0 to 9.7 m with an average of 2.2 m. The maximum predicted mussel temperature over the time period examined was 35.8 °C; on that same day (May 15, 2008) the average daily maximum of the three loggers was 32.0 °C, although one of the three biomimetic sensors recorded temperatures in excess of 36 °C. Notably, maximum air temperature on this day was 27.2 °C, with a high level of solar radiation (939 W m⁻²), average mainstream wind speed (4.1 m s⁻¹) and average to low significant wave height (1.7 m). The highest temperature recorded by the biomimetic sensors (average of all loggers) was 35.3 °C on May 8, 2007; on this day the model predicted a maximum temperature of 34.2 °C. On this day maximum recorded air temperature was 18.5 °C and solar radiation was ~930 W m⁻² during a period of low tide (0.1 m) coupled with low wind (1.2 m s⁻¹) and low wave height (1.3 m).

We also compared biomimetic logger data against air temperatures recorded at the BOON station to determine the degree to which air temperature could serve as an indirect proxy for elevated body temperatures. A comparison of daily maximum logger temperature to daily maximum air temperature showed that mussel temperature differed substantially from air temperature ($R^2 = 0.14$), with differences (Air-logger) ranging from -19 to +11 °C, with an average of -3.7 °C and an average absolute error of 4.3 °C (Table 2). Errors actually increased when only air temperatures during predicted low tide were considered (Table 2), although a higher coefficient of determination was observed ($R^2 = 0.26$). We also examined the relationship between air temperature during low tide and logger temperature for days in which maximum logger temperature exceeded 30 °C (i.e., “When mussels are hot, does this only occur on days when air temperatures are high?”) Results showed that high

Table 2

Comparison of maximum air temperatures and maximum air temperatures recorded at predicted low tide to maximum mussel temperatures recorded by biomimetic loggers. Also shown are error statistics for the difference between air temperature during predicted low tide and logger temperatures for days when logger temperatures exceeded 30 °C (n = 24), and statistics for when air temperature at predicted low tide exceeded 20 °C (n = 14). In all cases a negative value in the average difference indicates that the logger was hotter than air temperature.

	Daily max. air temp	Max air at low tide	Low tide air, logger > 30 °C	Low tide air, air > 20 °C
Average difference	-3.72	-4.30	-15.23	-0.63
Abs (Avg diff)	4.33	4.52	15.23	4.77
RMS error	5.84	5.98	15.42	5.72

mussel temperatures occurred on days with a wide range of air temperatures. Low tide air temperatures during periods when loggers were hot ($>30^{\circ}\text{C}$) ranged from 11.9 to 24.5°C with an average of 16.2°C , and loggers were on average 15.2°C warmer than the air (Table 2). We also examined periods when air temperatures were unusually warm ($>20^{\circ}\text{C}$) to ask, “when air temperatures are high during low tide, will mussels always be hot?” Note that the two questions are explicitly not the same: while the former asks, “when mussels are hot, does it only occur on days when air temperature is hot? (If A then B)”, the second asks, “can high air temperatures be used as a reliable indicator of high mussel temperature? (If B then A)”. When air temperatures at predicted low tide were above 20°C (average of 21.8°C), the average temperature of the loggers was 21.59°C , and ranged between 13.7 and 33.4°C . Notably, loggers exceeded 30°C on only two days when air temperature at predicted low tide exceeded 20°C ; the other 22 recorded instances all occurred when air temperatures at low tide were below 20°C . Moreover, 16/24 of the events in which temperatures of 30°C were recorded occurred in 2007 and 2008, years in which summer air temperatures were on average lower than in the preceding 3 years.

In contrast, there was a fairly strong correlation ($R^2=0.51$) between maximum daily logger temperature and maximum solar radiation at low tide. The correlation between maximum solar radiation at low tide and maximum air temperature at low tide was considerably lower ($R^2=0.13$), likely a reflection of the tendency of wind to blow onshore at this site.

3. Simulations

We used environmental data from January 1, 2004 to December 28, 2008 (as described above) to conduct a series of sensitivity analyses in order to examine the separate and interactive influences of changes in air temperature, solar radiation, wind speed, and nearshore wave height on mussel body temperature for animals at tidal elevations of MLLW + 1 m, 1.5 m and 2 m, corresponding roughly to the “mid-lower”, “mid” and “upper-mid” regions of the mussel bed at this site, respectively. We used the predicted number of days in which body temperature was expected to exceed 30°C as an indicator of “high risk” because this temperature is sufficient to cause the production of heat shock proteins and to cause cellular damage (Halpin et al., 2004). We also tracked the number of days in which temperatures were predicted to exceed 38°C , the approximate lethal temperature for acute exposures (Smith, 2010; also see Denny et al., 2011–this issue), although as described below these body temperatures only occurred under extreme scenarios. While an effort was made to select ranges of environmental parameters values that fell within expected values for the next century, the goal of these simulations was to determine sensitivity to various environmental parameters that change not only in time but in space along the coast (e.g. due to patterns of local fog, timing of low tide, changes in wave height, etc.). Thus, no attempt was made to generate explicit predictions for Bodega Bay, but rather to explore the relative importance of various physical drivers, and how their importance might change with tidal elevation. We recognize that the choice of fixed thresholds for all tidal heights is simplistic, and that lower shore intertidal animals are likely to have lower lethal thresholds than upper intertidal animals (Tomanek and Sanford, 2003). Likewise, thresholds will likely change as animals acclimate throughout the year. However, fixing values of 30°C and 38°C allowed a direct comparison of sensitivity to changing environmental conditions without the additional confounding role of thermal history.

Perhaps not surprisingly, all environmental factors examined influenced body temperature. However, several notable patterns emerged. Increases in air temperature and solar radiation significantly increased the predicted number of days $>30^{\circ}\text{C}$ and were most pronounced at tidal elevations of MLLW + 1.5 and 2 m. At extreme levels predicted temperatures exceeded 38°C (Fig. 2A,B).

Interestingly, even a modest ($0.75\text{--}1\text{ m s}^{-1}$) increase in wind speed resulted in a significant decrease in the number of stressful days (Fig. 2C), primarily at the upper two tidal elevations tested. However, convective cooling via increased wind speed appeared to have an asymptotic effect and could not eliminate days $>30^{\circ}\text{C}$, even though air temperatures recorded at this site were always at least several degrees below 30°C . Increased wave height had only a modest effect on the number of “risky days” (i.e., days with body temperatures $>30^{\circ}\text{C}$) at the lowest and highest elevations, although increases in wave heights above 1 m were predicted to lead to a fairly substantial decrease in risk at the MLLW + 1.5 m elevation site (Fig. 2D).

The timing of low tide had a very significant impact on risk of exposure to high body temperatures at MLLW + 1 m and + 1.5 m, but fairly little impact on animals in the upper portions of the mussel bed (Fig. 3). For example, a shift in the timing of low tide of minus one hour led to little change in relative levels of risk at the three tidal elevations (Figs. 2A and 3A) so that, with increasing air temperatures, mussels at upper elevations were expected to experience significant increases in stress, whereas animals at lower elevations were predicted to experience only modest increases in risk of temperatures $>30^{\circ}\text{C}$. Thus, at Bodega Bay and at sites where the timing of low tide is shifted back by one hour, the difference in thermal stress between the high and low portions of the bed is expected to increase with increasing air temperatures. In stark contrast, with a plus one hour shift (Fig. 3B), mussels at MLLW + 1 m and + 1.5 m were expected to experience much higher levels of stress than those under the tidal conditions at Bodega Bay (Fig. 2A, “zero level”); however, the MLLW + 2 m site was relatively unaffected. Thus, at sites with a + 1 h shift, the difference in thermal stress between the upper and lower portions of the bed was significantly reduced. Moreover, under scenarios of increased air temperature, levels of stress at the site with a + 1 h tide increased at all tidal elevations, in contrast to predictions for Bodega Bay (Fig. 2A) or at sites with a – 1 h shift (Fig. 3A). Thus, at sites with a slightly different tidal cycle (+ 1 h), such as occur at other sites along the coast, the difference in the number of days with temperatures $>30^{\circ}\text{C}$ between upper and lower portions of the mussel bed is likely much smaller than it currently is at Bodega Bay. For example, in an embayment where the tide is delayed by one hour, mussels lower in the bed would be expected to experience more severe responses to increases in air temperature than animals at the same tidal elevation at a site where low tide occurs one hour earlier. Similarly, as tide cycles change with an ~18.6 year cycle at Bodega Bay (Denny and Paine, 1998), patterns of exposure to elevated body temperature may change as well. This effect has been previously described for other sites along the west coast of North America (Helmuth et al., 2002) and likely reflects the total amount of exposure to midday solar radiation.

Simulations examining the combined effects of increased air temperature and altered wind speed show the efficacy of convective cooling. Even under a scenario in which air temperature was increased by 2.5°C , increases in wind speed of $\sim 0.75\text{--}1\text{ m s}^{-1}$ were sufficient to drop the number of risky days to levels comparable to where they were with no increase in air temperature (as indicated by “X”s in Fig. 4). Notably, air temperatures recorded during the five year period only reached 27.5°C on one day, so that an addition of 2.5°C brought air temperature to 30°C only once. The observation that a number of risky days nevertheless occurred even under fairly high wind speeds is therefore a strong indication of the role of solar radiation in maintaining mussel body temperature well above ambient air temperature, and suggests that while convective heat exchange plays an important role in lowering mussel temperature, under days with high solar radiation, it cannot completely eliminate the incidence of high body temperatures. Conversely, however, results emphasize that days with low wind speed are likely to be highly stressful, particularly because they are likely to be correlated with conditions of low wave splash.

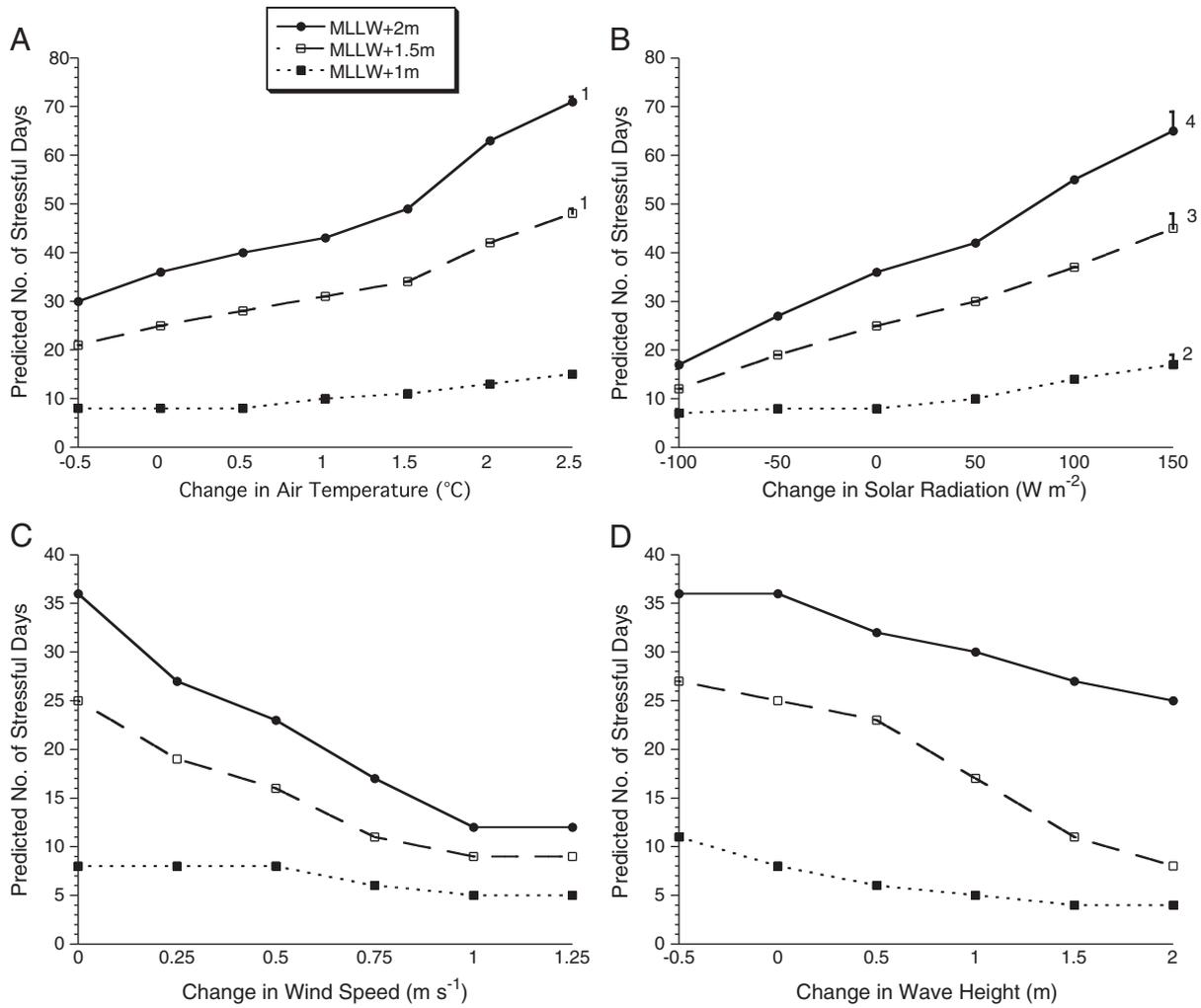


Fig. 2. Predicted number of “stressful days” as a function of changes in (A) air temperature, (B) solar radiation, (C) wind speed and (D) significant wave height. Data points indicate predicted number of days over a 5 year period where mussel temperature exceeded 30 °C; vertical bars stacked on top of lines (also noted by numbers) indicate additional days in which mussel temperatures were predicted to exceed 38 °C, the approximate lethal limit for acute exposures.

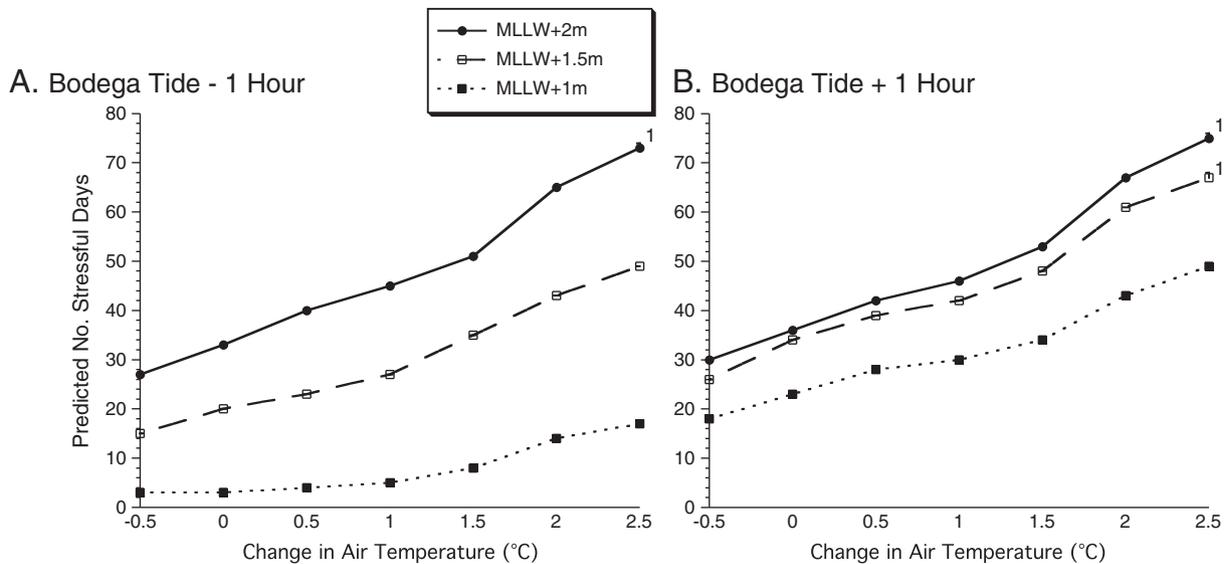


Fig. 3. Effect of increased air temperature at sites where low tide is shifted by (A) minus 1 h (relative to Bodega Bay) and (B) plus 1 h. At sites where low tide occurred one hour later than at Bodega Bay, levels of stress in the mid and lower intertidal sites were markedly higher as compared to Bodega Bay so that mid intertidal sites were nearly as stressful as upper intertidal sites, and the difference between lower intertidal and upper intertidal sites was smaller than at Bodega Bay.

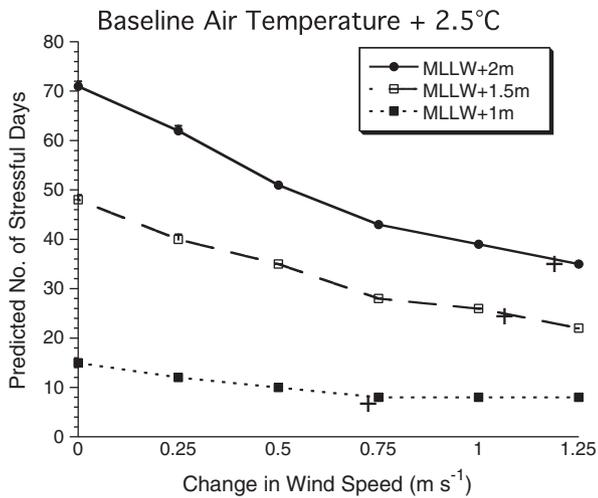


Fig. 4. Interaction of wind speed and increased air temperature (+2.5 °C). At wind speeds marked with “+”, levels of risk were equivalent to scenarios with no change in wind and no increase in air temperature; i.e. at these speeds convective cooling was able to counteract a 2.5 °C increase in air temperature.

4. Discussion

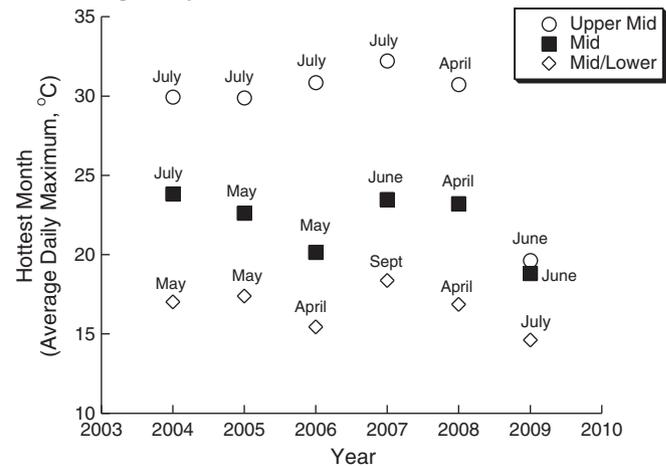
It is well established that the body temperatures of ectotherms such as intertidal invertebrates are driven by multiple interacting environmental factors. For example, previous models have shown the effectiveness of convective heat exchange on reducing body temperature, provided that body temperature is above that of the surrounding air (e.g. Helmuth, 1998; Lactin and Johnson, 1998; Denny and Harley, 2006). While many studies of the effects of climate change still tend to focus on large-scale measurements of air, land and sea surface temperature, and rely on correlations between these “habitat” level parameters and current and future species distributions (Pearson and Dawson, 2003; Hampe, 2004), a growing body of literature has promoted the use of modeling and measuring the effects of weather and climate at the level of the organism (Kearney, 2006; Kearney and Porter, 2004, 2009). These more mechanistic approaches take into account the role of an organism’s behavior, morphology and physiological tolerances, and, perhaps most importantly in the context of determining patterns of exposure to extreme conditions, generally use high frequency spatial and temporal data as inputs (Denny et al., 2009; Harley et al., 2009). In contrast, models that use monthly or even seasonal environmental data as inputs not only ignore the potential for organisms to modify or perceive those large scale signals in different ways, but they forego any possibility of detecting the coincidence of extreme events unless they co-occur over those same coarse temporal and spatial domains (e.g., as described in Kearney, 2006; Broitman et al., 2009; Denny et al., 2009; Helmuth, 2009).

Here we have shown that air temperature, solar radiation, wind speed, wave splash, and the timing of low tide all contribute to patterns of “risk” in intertidal ecosystems. Importantly, while solar radiation appears to be the dominant driver of body temperature, no single parameter is the sole determinant of organism temperature, and many variables potentially covary with one another (Denny et al., 2009). It is perhaps not surprising that mussels in the lower portions of the bed, which spend considerably less time in air than upper bed animals, are less affected by variation in weather conditions during aerial exposure at low tide. What is notable is that the sensitivity of animals to these parameters was drastically affected by the timing of day-time low tide (Helmuth et al., 2002; Finke et al., 2007). These results therefore suggest that altered climates not only will have very site-specific effects that will depend on local meteorological and oceanographic conditions, but that differential impacts across the intertidal zone will vary from site to site. At some locations, lower bed

mussels may be spared from significant risk of extreme temperatures, while at other sites, they may experience marked increases in risk along with upper intertidal organisms. At sites with tidal cycles shifted forward by just one hour relative to Bodega Bay, animals in the middle of the bed are predicted to experience extremes in body temperature that are nearly comparable to those in the upper portions of the mussel bed, and lower bed animals likewise are predicted to experience very high levels of potential stress (Fig. 3B). This pattern is in striking contrast to animals at Bodega Bay (Fig. 2A) or at sites where the tide is one hour earlier (Fig. 3A), where lower bed animals are predicted to experience substantially fewer incidences of elevated body temperature than upper bed animals. The ecological consequences of these contrasting levels of asymmetry in physiological stress between lower and higher portions of the mussel bed remain relatively unexplored (but see Engel et al., 2004) but predictions that they may be enhanced with climate change suggest that further exploration is certainly warranted.

These unusual patterns are mirrored in long-term data collected at Bodega Bay and other sites in California using biomimetic sensors (Fig. 5). For example, interannual variability in maximum temperatures (here quantified as the average of the daily maxima for the

A. Bodega Bay, CA



B

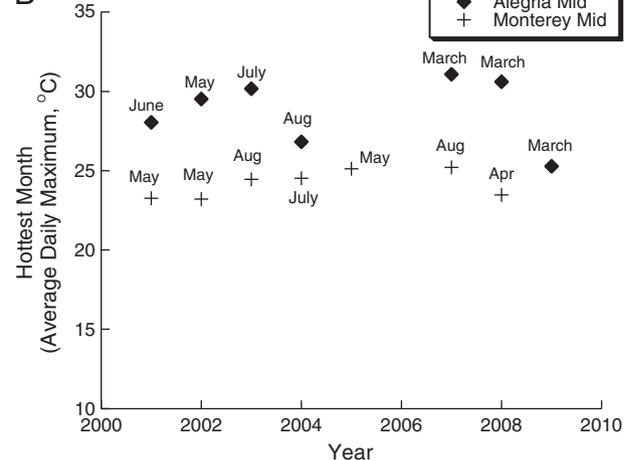


Fig. 5. Hottest months (month with highest average daily maxima) for (A) 3 tidal elevations at Bodega Bay and (B) mid tidal elevations at Alegria (southern California) and Monterey Bay. Note that the timing of when the hottest month occurred varied between heights and between sites, and was not always consistent within a site. Data for 2008 at Bodega (April) should be considered as minimum values as no data were collected between May and September of that year due to instrument failure and loss.

hottest month of each year) is not always consistent between tidal elevations within a site (Fig. 5A), or between sites (Fig. 5B). Moreover, the timing of when the hottest month occurs varies from year to year and between tidal elevations; at Bodega Bay, the hottest month for lower bed mussels tends to be in April or May, as compared to July in the upper portions of the bed (Fig. 5A). These measurements point to the difficulty of knowing when to expect maximal levels of thermal stress to occur; because thermal extremes are driven by the interaction of multiple factors, the timing of when they are most likely to occur will vary between sites, between years, and even between tidal elevations.

The results of this study emphasize the complexity of interpreting the ecological impact of changes using single environmental parameters. For example, a 1 °C change in air temperature at one location or tidal elevation may have very different consequences than the same change at another location or elevation. Moreover, comparisons of data from field instruments against weather data (Appendix Table A) suggest that high air temperatures are not necessarily a prerequisite for high animal temperatures, and point to the importance of solar radiation in driving body temperature (Marshall et al., 2010). Thus, for example, loggers were hot during periods when solar radiation was high and wind was blowing onshore such that the temperature of the air, which had not yet interacted with land, was a poor proxy for mussel temperature (Table A). Conversely, days with high air temperatures do not always correspond to extreme animal temperatures, likely because of unaccounted-for wave splash or changes in still tidal height due to variability in atmospheric pressure.

In many ways our results seem to contrast with those of Jones et al. (2009, 2010), who used both air and water temperature to successfully hindcast shifts in the distribution of the mussel *Mytilus edulis* on the east coast of the US. However, Jones et al. (2010) acknowledge that the use of air temperature as a proxy for aerial body temperature neglects the role of solar radiation (and other drivers), and therefore was only likely an effective proxy for animals in shaded environments. Their results suggested that air temperatures were sufficiently hot that even animals in the shade were expected to die in some instances; therefore animals in the sun would have died as well. Thus, air temperature may work as an effective proxy for body temperature when it is hot enough to kill both shaded animals and animals exposed to full sunlight but a modeling approach such as the one presented here is necessary when air temperatures are not that extreme.

Importantly, these analyses highlight the concept that while many physical parameters drive risk of extreme exposures, elevated risk occurs when several factors are in phase with one another (Denny et al., 2009; Firth and Williams, 2009; Helmuth et al., 2010). Thus, for example, an increase in air temperature *per se* does not increase the risk of lethal exposures, but rather it increases the risk that a sufficiently high air temperature will coincide with a period of low tide, low wave splash and high solar radiation. Our results thus caution strongly against the use of single parameters such as air temperature as indicators of physiological stress, or at the very least that this assumption must be tested. Our results also point to the importance of considering the interaction of multiple physical drivers when assessing the future impacts of climate change (Mislán et al., 2009; Marshall et al., 2010).

For example, largely as a result of the differential heating of land and the sea surface, mean wind speeds are expected to increase substantially (Snyder et al., 2003; Checkley and Barth, 2009). Such increases may offset much of the effects of increased air temperature through convective cooling, as may additional wave splash due to higher waves. These mechanisms will of course come at a cost: many species such as intertidal algae are at risk of desiccation and so may suffer damage despite reduced temperatures (Bell, 1993, 1995). Likewise, increased wave heights may increase rates of dislodgement and breakage of intertidal invertebrates and algae (Carrington, 2002;

Denny, 1995; but see Helmuth and Denny, 2003), but could potentially enhance feeding.

In summary, this study emphasizes the complex interactions between organisms and their environments, and cautions against making projections of the impacts of climate change based on single environmental variables, and against extrapolating from studies conducted at only one field site. A growing body of evidence confirms that coastal environments are spatially and temporally complex over a wide range of scales, from microscopic to latitudinal (Underwood and Chapman, 1996; Benedetti-Cecchi, 2001; Denny et al., 2004; Benedetti-Cecchi et al., 2005; Habeeb et al., 2005), and that biological and physical processes interact over these nested scales to drive observed patterns of abundance and biogeography (Burrows et al., 2009; Gouhier et al., 2010). Understanding the scales over which physical processes operate to drive physiological and ecological responses is therefore a key consideration if we are to forecast how ecosystems are likely to respond to changes in the physical environment. Here we have used large-scale weather data to examine patterns of “risk” at a series of fixed tidal elevations and a single substratum angle as a means of teasing apart the relative importance of multiple environmental variables. In reality, we know that nature is far more complex than this, and that subtle variability in the angle of the substrate and in boundary layer dynamics can lead to significant changes in microhabitats. For example, we did not predict any mortality events due to acute exposures (>38 °C) during the period 2004–2008. However, Harley (2008) reported a large mortality event of *M. californianus* at Bodega Bay in late April 2004. Our loggers recorded maximum temperatures of ~29.0–29.5 °C on these days on horizontal surfaces. However, as discussed by Harley, virtually all mortality occurred on surfaces with higher angles of incidence (e.g. vertical surfaces facing the sun). A true accounting of risk of mortality at an intertidal site would therefore require keeping track not only of physiological variability in susceptibility to stress, but also in variability in substratum angle and thus heterogeneity in body temperatures (see Denny et al., 2011–this issue). Moreover, an accurate accounting would include cumulative impacts of environmental stress, as well as the coupled effects of food supply (Kearney et al., 2010; Schneider et al., 2010). Finally, whereas we examined the roles of air temperature, wind speed, wave height, solar radiation, and the timing of low tide, changes in water temperature and rainfall are also likely to play a significant role (Firth and Williams, 2009). While time consuming, our confidence in our predictions of how, where and when organisms and ecosystems are most likely to respond to changes in climate will almost certainly increase when we can quantitatively tease apart the mechanisms by which organisms interact with their environment.

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References

- Bell, E.C., 1993. Photosynthetic response to temperature and desiccation of the intertidal alga *Mastocarpus papillatus*. Mar. Biol. 117, 337–346.

- Bell, E.C., 1995. Environmental and morphological influences on thallus temperature and desiccation of the intertidal alga *Mastocarpus papillatus* Kützinger. *J. Exp. Mar. Biol. Ecol.* 191, 29–55.
- Benedetti-Cecchi, L., 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. *Mar. Ecol. Prog. Ser.* 215, 79–92.
- Benedetti-Cecchi, L., Bertocci, I., Vaselli, S., Maggi, E., 2005. Determinants of spatial pattern at different scales in two populations of the marine alga *Rissoella verruculosa*. *Mar. Ecol. Prog. Ser.* 293, 37–47.
- Broitman, B.R., Szathmari, P.L., Mislan, K.A.S., Blanchette, C.A., Helmuth, B., 2009. Predator–prey interactions under climate change: the importance of habitat vs body temperature. *Oikos* 118, 219–224.
- Burrows, M.T., Harvey, R., Robb, L., Poloczanska, E.S., Mieszkowska, N., Moore, P., Leaper, R., Hawkins, S.J., Benedetti-Cecchi, L., 2009. Spatial scales of variance in abundance of intertidal species: effects of region, dispersal mode, and trophic level. *Ecology* 90, 1242–1254.
- Carrington, E., 2002. The ecomechanics of mussel attachment: from molecules to ecosystems. *Int. Comp. Biol.* 42, 846–852.
- Checkley, D.M., Barth, J.A., 2009. Patterns and processes in the California Current system. *Prog. Oceanogr.* 83, 49–64.
- Denny, M.W., 1995. Predicting physical disturbance: mechanistic approaches to the study of survivorship on wave-swept shores. *Ecol. Monogr.* 65, 371–418.
- Denny, M.W., Harley, C.D.G., 2006. Hot limpets: predicting body temperature in a conductance-mediated thermal system. *J. Exp. Biol.* 209, 2409–2419.
- Denny, M.W., Paine, R.T., 1998. Celestial mechanics, sea-level changes, and intertidal ecology. *Biol. Bull.* 194, 108–115.
- Denny, M.W., Helmuth, B., Leonard, G.H., Harley, C.D.G., Hunt, L.J.H., Nelson, E.K., 2004. Quantifying scale in ecology: lessons from a wave-swept shore. *Ecol. Monogr.* 74, 513–532.
- Denny, M.W., Miller, L.P., Harley, C.D.G., 2006. Thermal stress on intertidal limpets: long-term hindcasts and lethal limits. *J. Exp. Biol.* 209, 2420–2431.
- Denny, M.W., Hunt, L.J.H., Miller, L.P., Harley, C.D.G., 2009. On the prediction of extreme ecological events. *Ecol. Monogr.* 79, 397–421.
- Denny, M.W., Dowd, W.W., Bilir, L., Mach, K.J., 2011. Spreading the risk: small-scale body temperature variation among intertidal organisms and its implications for species persistence. *J. Exp. Mar. Biol. Ecol.* 400, 175–190 (this issue).
- Engel, C.R., Destombe, C., Valero, M., 2004. Mating system and gene flow in the red seaweed *Gracilaria gracilis*: effect of haploid–diploid life history and intertidal rocky shore landscape on finescale genetic structure. *Heredity* 92, 289–298.
- Fabricius, K.E., 2006. Effects of irradiance, flow, and colony pigmentation on the temperature microenvironment around corals: implications for coral bleaching? *Limnol. Oceanogr.* 51, 30–37.
- Finke, G.R., Navarrete, S.A., Bozinovic, F., 2007. Tidal regimes of temperate coasts and their influences on aerial exposure for intertidal organisms. *Mar. Ecol. Prog. Ser.* 343, 57–62.
- Finke, G.R., Bozinovic, F., Navarrete, S.A., 2009. A mechanistic model to study the thermal ecology of a southeastern Pacific dominant intertidal mussel and implications for climate change. *Physiol. Biochem. Zool.* 82, 303–313.
- Firth, L.B., Williams, G.A., 2009. The influence of multiple environmental stressors on the limpet *Cellana toreuma* during the summer monsoon season in Hong Kong. *J. Exp. Mar. Biol. Ecol.* 375, 70–75.
- Fitzhenry, T., Halpin, P.M., Helmuth, B., 2004. Testing the effects of wave exposure, site, and behavior on intertidal mussel body temperatures: applications and limits of temperature logger design. *Mar. Biol.* 145, 339–349.
- Fodrie, F.J., Heck, K.L., Powers, S.P., Graham, W.M., Robinson, K.L., 2010. Climate-related, decadal scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico. *Global Change Biol.* 16, 48–59.
- Gilman, S.E., Harley, C.D.G., Strickland, D.C., Vanderstraeten, O., O'Donnell, M.J., Helmuth, B., 2006a. Evaluation of effective shore level as a method of characterizing intertidal wave exposure regimes. *Limnol. Oceanogr. Methods* 4, 448–457.
- Gilman, S.E., Wetthey, D.S., Helmuth, B., 2006b. Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. *Proc. Natl. Acad. Sci.* 103, 9560–9565.
- Gouhier, T.C., Guichard, F., Menge, B.A., 2010. Ecological processes can synchronize marine population dynamics over continental scales. *Proc. Natl. Acad. Sci.* 107, 8281–8286.
- Habeeb, R.L., Trebilco, J., Wotherspoon, S., Johnson, C.R., 2005. Determining natural scales of ecological systems. *Ecol. Monogr.* 75, 467–487.
- Halpin, P.M., Menge, B.A., Hofmann, G.E., 2004. Experimental demonstration of plasticity in the heat shock response of the intertidal mussel *Mytilus californianus*. *Mar. Ecol. Prog. Ser.* 276, 137–145.
- Hampe, A., 2004. Bioclimate envelope models: what they detect and what they hide. *Global Ecol. Biogeogr.* 13, 469–476.
- Harley, C.D.G., 2008. Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. *Mar. Ecol. Prog. Ser.* 371, 37–46.
- Harley, C.D.G., Helmuth, B.S.T., 2003. Local and regional scale effects of wave exposure, thermal stress, and absolute vs. effective shore level on patterns of intertidal zonation. *Limnol. Oceanogr.* 48, 1498–1508.
- Harley, C.D.G., Paine, R.T., 2009. Contingencies and compounded rare perturbations dictate sudden distributional shifts during periods of gradual climate change. *Proc. Natl. Acad. Sci.* 106, 11172–11176.
- Harley, C.D.G., Denny, M.W., Mach, K.J., Miler, L.P., 2009. Thermal stress and morphological adaptations in limpets. *Func. Ecol.* 23, 292–301.
- Helmuth, B.S.T., 1998. Intertidal mussel microclimates: predicting the body temperature of a sessile invertebrate. *Ecol. Monogr.* 68, 51–74.
- Helmuth, B.S.T., 1999. Thermal biology of rocky intertidal mussels: quantifying body temperatures using climatological data. *Ecology* 80, 15–34.
- Helmuth, B., 2009. From cells to coastlines: how can we use physiology to forecast the impacts of climate change? *J. Exp. Biol.* 212, 753–760.
- Helmuth, B., Denny, M.W., 2003. Predicting wave exposure in the rocky intertidal zone: do bigger waves always lead to larger forces? *Limnol. Oceanogr.* 48, 1338–1345.
- Helmuth, B.S.T., Hofmann, G.E., 2001. Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. *Biol. Bull.* 201, 374–384.
- Helmuth, B.S., Harley, C.D.G., Halpin, P., O'Donnell, M., Hofmann, G.E., Blanchette, C., 2002. Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298, 1015–1017.
- Helmuth, B., Mieszkowska, N., Moore, P., Hawkins, S.J., 2006a. Living on the edge of two changing worlds: forecasting responses of rocky intertidal ecosystems to climate change. *Ann. Rev. Ecol. Evol. Syst.* 37, 373–404.
- Helmuth, B., Broitman, B.R., Blanchette, C.A., Gilman, S., Halpin, P., Harley, C.D.G., O'Donnell, M.J., Hofmann, G.E., Menge, B., Strickland, D., 2006b. Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. *Ecol. Monogr.* 76, 461–479.
- Helmuth, B., Broitman, B.R., Yamane, L., Gilman, S.E., Mach, K., Mislan, K.A.S., Denny, M.W., 2010. Organismal climatology: analyzing environmental variability at scales relevant to physiological stress. *J. Exp. Biol.* 213, 995–1003.
- Hofmann, G.E., Place, S.P., 2007. Genomics-enables research in marine ecology: challenges, risks and pay-offs. *Mar. Ecol. Prog. Ser.* 332, 249–255.
- Jimenez, I.M., Kühl, M., Larkum, A.W.D., Ralph, P.J., 2008. Heat budget and thermal microenvironment of shallow-water corals: do massive corals get warmer than branching corals? *Limnol. Oceanogr.* 53, 1548–1561.
- Johnson, S.E., 1975. Microclimate and energy flow in the marine rocky intertidal. In: Gates, D.M., Schmelzer, R.B. (Eds.), *Perspectives of Biophysical Ecology*. Springer-Verlag, New York, pp. 559–587.
- Jones, S.J., Mieszkowska, N., Wetthey, D.S., 2009. Linking thermal tolerances and biogeography: *Mytilus edulis* (L.) at its southern limit on the East Coast of the United States. *Biol. Bull.* 217, 73–85.
- Jones, S.J., Lima, F.P., Wetthey, D.S., 2010. Rising environmental temperatures and biogeography: poleward range contraction of the blue mussel, *Mytilus edulis* L., in the western Atlantic. *J. Biogeography* 37, 2243–2259.
- Kearney, M., 2006. Habitat, environment and niche: what are we modelling? *Oikos* 115, 186–191.
- Kearney, M., Porter, W.P., 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85, 3119–3131.
- Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species ranges. *Ecol. Lett.* 12, 334–350.
- Kearney, M., Simpson, S.J., Raubenheimer, D., Helmuth, B., 2010. Modelling the ecological niche from functional traits. *Philos. Trans. R. Soc. B* 365, 3469–3483.
- Lactin, D.J., Johnson, D.L., 1998. Conductive heat loss and change in body temperature of grasshopper and locust nymphs: relative importance of wind speed, insect size and insect orientation. *J. Thermal Biol.* 23, 5–13.
- Leichter, J.J., Helmuth, B., Fischer, A.M., 2006. Variation beneath the surface: quantifying complex thermal environments on coral reefs in the Caribbean, Bahamas and Florida. *J. Mar. Res.* 64, 563–588.
- Lesser, M.P., Bailey, M.A., Merselis, D.G., Morrison, J.R., 2010. Physiological response of the blue mussel *Mytilus edulis* to differences in food and temperature in the Gulf of Maine. *Comp. Biochem. Physiol. A* 156, 541–551.
- Lima, F.P., Queiroz, N., Ribeiro, P.A., Hawkins, S.J., Santos, A.M., 2006. Recent changes in the distribution of a marine gastropod, *Patella rustica* Linnaeus, 1758, and their relationship to unusual climatic events. *J. Biogeography* 33, 812–822.
- Lockwood, B.L., Somero, G.N., 2011. Invasive and native blue mussels (genus *Mytilus*) on the California coast: the role of physiology in a biological invasion. *J. Exp. Mar. Biol. Ecol.* 400, 167–174 (this issue).
- Marshall, D.J., McQuaid, C.D., Williams, G.A., 2010. Non-climatic thermal adaptation: implications for species' responses to climate warming. *Biol. Lett.* 6, 669–673.
- Mieszkowska, N., Kendall, M.A., Hawkins, S.J., Leaper, R., Williamson, P., Hardman-Mountford, N.J., Southward, A.J., 2006. Changes in the range of some common rocky shore species in Britain – a response to climate change? *Hydrobiologia* 555, 241–251.
- Mislan, K.A.S., Wetthey, D.S., Helmuth, B., 2009. When to worry about the weather: role of tidal cycle in determining patterns of risk in intertidal ecosystems. *Global Change Biol.* 15, 3056–3065.
- Mitchell, J.W., 1976. Heat transfer from spheres and other animal forms. *Biophys. J.* 16, 561–569.
- Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecol. Biogeogr.* 12, 361–371.
- Pearson, G.A., Lago-Leston, A., Mota, C., 2009. Frayed at the edges: selective pressure and adaptive response to abiotic stressors are mismatched in low diversity edge populations. *J. Ecol.* 97, 450–462.
- Place, S.P., O'Donnell, M.J., Hofmann, G.E., 2008. Gene expression in the intertidal mussel *Mytilus californianus*: physiological response to environmental factors on a biogeographic scale. *Mar. Ecol. Prog. Ser.* 356, 1–14.
- Porter, W.P., Gates, D.M., 1969. Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* 39, 245–270.
- Pörtner, H.-O., 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *J. Exp. Biol.* 213, 881–893.
- Schneider, K.R., Van Thiel, L.E., Helmuth, B., 2010. Interactive effects of food availability and aerial body temperature on the survival of two intertidal *Mytilus* species. *J. Thermal Biol.* 35, 161–166.
- Smith, K.A., 2010. Measuring and forecasting environmental conditions from the perspective of rocky intertidal organisms. PhD Dissertation, University of South Carolina, Columbia. 135 pp.

- Snyder, M.A., Sloan, L.C., Diffenbaugh, N.S., Bell, J.L., 2003. Future climate change and upwelling in the California Current. *Geophys. Res. Lett.* 30, 1823–1826.
- Somero, G.N., 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *J. Exp. Biol.* 213, 912–920.
- Szathmary, P.L., Helmuth, B., Wethey, D.S., 2009. Climate change in the rocky intertidal zone: predicting and measuring the body temperature of a keystone predator. *Mar. Ecol. Prog. Ser.* 374, 43–56.
- Tomanek, L., Sanford, E., 2003. Heat-shock protein 70 (Hsp70) as a biochemical stress indicator: an experimental field test in two congeneric intertidal gastropods (Genus : *Tegula*). *Biol. Bull.* 205, 276–284.
- Underwood, A.J., Chapman, M.G., 1996. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107, 212–224.
- van der Wal, D., Wielemaker-van den Dool, A., Herman, P.M.J., 2010. Spatial synchrony in intertidal benthic algal biomass in temperate coastal and estuarine ecosystems. *Ecosystems* 13, 338–351.
- Wethey, D.S., 2002. Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. *Int. Comp. Biol.* 42, 872–880.
- Williams, G.A., Morritt, D., 1995. Habitat partitioning and thermal tolerance in a tropical limpet, *Cellana grata*. *Mar. Ecol. Prog. Ser.* 124, 89–103.
- Williams, G.A., De Pirro, M., Leung, K.M.Y., Morritt, D., 2005. Physiological responses to heat stress on a tropical shore: the benefits of mushrooming behaviour in the limpet *Cellana grata*. *Mar. Ecol. Prog. Ser.* 292, 213–224.