Organismal climatology: analyzing environmental variability at scales relevant to physiological stress

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Summary

Predicting when, where and with what magnitude climate change is likely to affect the fitness, abundance and distribution of organisms and the functioning of ecosystems has emerged as a high priority for scientists and resource managers. However, even in cases where we have detailed knowledge of current species' range boundaries, we often do not understand what, if any, aspects of weather and climate act to set these limits. This shortcoming significantly curtails our capacity to predict potential future range shifts in response to climate change, especially since the factors that set range boundaries under those novel conditions may be different from those that set limits today. We quantitatively examine a nine-year time series of temperature records relevant to the body temperatures of intertidal mussels as measured using biomimetic sensors. Specifically, we explore how a 'climatology' of body temperatures, as opposed to long-term records of habitat-level parameters such as air and water temperatures, can be used to extrapolate meaningful spatial and temporal patterns of physiological stress. Using different metrics that correspond to various aspects of physiological stress (seasonal means, cumulative temperature and the return time of extremes) we show that these potential environmental stressors do not always occur in synchrony with one another. Our analysis also shows that patterns of animal temperature are not well correlated with simple, commonly used metrics such as air temperature. Detailed physiological studies can provide guidance to predicting the effects of global climate change on natural ecosystems but only if we concomitantly record, archive and model environmental signals at appropriate scales.

Key words: biogeography, climate change, ecological forecasting, intertidal zone, signal analysis.

Introduction

Several recent research reports and reviews have emphasized the importance of considering physiological mechanisms when forecasting the effects of global climate change on organisms and ecosystems (Chown et al., 2004; Kearney et al., 2008; Pörtner, 2002; Pörtner and Farrell, 2008). Specifically, these studies have highlighted a need to understand how environmental conditions vary in space and time as well as how organisms respond to those variables (Helmuth, 2009; Tewksbury et al., 2008), and have suggested that studies based on simple correlations between environmental measurements and species distributions may fail under the novel conditions presented by climate change (Kearney, 2006). While correlative approaches ('climate envelope models') may potentially serve as good 'first cut' approximations of ecological responses to climate change (Hijmans and Graham, 2006), predictions are likely to be significantly enhanced by: (i) comprehensive, spatially- and temporally-explicit measurements and models of current and future weather conditions; (ii) explorations of the mechanistic relationships between changes in abiotic variables and the changes experienced by organisms at the niche level ['organismal sensitivity' to environmental change (Gilman et al., 2006) or 'climate space' (Porter and Gates, 1969)]; (iii) a quantitative understanding of the physiological mechanisms underlying tolerance to abiotic stress ['organismal vulnerability' to environmental change

(Gilman et al., 2006; Tewksbury et al., 2008)]; and (iv) measurements of the indirect effects of physiological responses on species interactions, such as predation, competition and disease transmission (Davis et al., 1998; Pincebourde and Casas, 2006; Yamane and Gilman, 2009).

While global climate change is anticipated to result in an overall warming over the surface of the Earth, considerable variability in the magnitude and location of these changes has occurred in the past (Fang et al., 2008) and is predicted to continue into the future (Easterling et al., 2008; IPCC, 2007). Likewise, observed warming in the last century has not increased monotonically over time, and long-term trends can be temporarily overridden or augmented by processes, such as the El Niño Southern Oscillation (ENSO), the North Atlantic Oscillation (NAO) and the Pacific Decadal Oscillation (PDO) (Fang et al., 2008; Stenseth et al., 2003). In other words, 'environmental signals' such as air and water temperature comprise components fluctuating at varying spatial and temporal frequencies. Extremes in these drivers occur when multiple components, including those introduced by stochastic variability, are in phase with one another (Denny et al., 2009). Understanding the ecological impacts of these drivers becomes even more complex when one considers that behavior, size and morphology significantly affect how organisms perceive these environmental signals at a niche level (Kearney, 2006).

One of the most obvious examples of the complexity underlying organism–environment interactions is body temperature. The body temperatures of terrestrial ectotherms, and intertidal organisms during low tide, are driven by the interaction of multiple variables, including air and surface temperature, solar radiation, cloud cover, relative humidity and wind speed (Denny and Harley, 2006; Helmuth, 1998; Porter and Gates, 1969; Wethey, 2002), which can result in often poor correlations between body temperature and 'habitat-level' measurements of air or surface temperature (Southward, 1958). Even underwater, recent studies have shown that the body temperature of corals in shallow water is driven by the interplay of solar radiation and convection so that, depending on coral color and the characteristics of water flow, animal tissue can be 0.5–1.5°C warmer than the temperature of the surrounding water (Fabricius, 2006).

As a result of these interactions, spatial and temporal patterns of body temperature can be complex and even counterintuitive (Helmuth and Hofmann, 2001; Leichter et al., 2006). Pearson et al. found that maximum intertidal rock temperatures in the UK were similar to those in southern Portugal (Pearson et al., 2009). In intertidal ecosystems, maximum body temperature occurs when high solar radiation (especially at midday in summer) is coupled with low wave splash and high air temperature (Denny et al., 2009; Mislan et al., 2009). Thus, in part because low tides at the northern sites studied by Pearson et al. (Pearson et al., 2009) occurred more frequently during midday than at the Portuguese sites, rock temperatures at the two ends of this latitudinal gradient were very similar. Likewise, Helmuth et al. showed that intertidal mussels along the Pacific Coast of North America displayed a geographical thermal mosaic where animals at more poleward sites experienced extreme temperatures more often than animals at some of the more equatorial sites because of variability in wave splash, coastal fog and the timing of low tides (Helmuth et al., 2006a). These thermal patterns are also reflected in organismal physiology. For example, Sagarin and Somero found that patterns of heat shock protein (Hsp) expression in mussels and gastropods along the Pacific coast of the USA did not decrease with increasing latitude (Sagarin and Somero, 2006). Similarly, Place et al. simultaneously measured patterns of gene expression by intertidal mussels at four sites along the west coast of North America and showed that expression of genes related to thermal stress exhibited patterns that matched expectations based on measurements of aerial body temperature (Place et al., 2008). Specifically, animals from Oregon were more similar in gene expression to those in Mexico than they were to animals in central California. Thus, the interaction of organisms with their local environment can lead to unexpected patterns of where thermal stress is likely to occur (Gilman et al., 2006).

Understanding how current and future range boundaries are likely to be set by aspects of weather and climate thus demands that we understand how large-scale environmental 'signals' are downscaled to the level of the organism, namely to factors that define the organism's fundamental (physiological) niche (Kearney, 2006). Equally important to such an approach is a need to explore how physiological responses to these environmental drivers vary in space and time. Local patterns of acclimatization, phenotypic plasticity and genetic adaptation can cause different responses to changing environmental conditions among individuals within a population, among different populations and among closely related species (Bradshaw and Holzapfel, 2006; Helmuth et al., 2006a; Pearson et al., 2009; Stillman, 2003). For example, Pearson et al. showed that intertidal algae were more sensitive to thermal stress at their southern range edge (in Portugal) when compared with organisms from more poleward sites (UK), even though thermal regimes were similar (see above) (Pearson et al., 2009). Moreover, genetic changes and phenotypic plasticity can also occur rapidly in response to climate change (Bradshaw and Holzapfel, 2006), so that 'vulnerability' may vary not only in space but also in time.

Obviously, predicting patterns of physiological stress, and the subsequent effects of mortality and reproductive failure on species distributions, can be a complex task. However, if we rely upon broad-scale measurements of the physical environment, we run the risk of potentially making substantially inaccurate predictions of the future effects of climate change on natural communities (Buckley, 2008; Kearney, 2006; Kearney and Porter, 2009). By far the most frequent method of estimating future shifts in range boundaries due to climate change is to correlate large-scale habitat-level environmental parameters with on-the-ground measurements of contemporary range boundaries, and to then extrapolate to future conditions (for a review, see Pearson and Dawson, 2003). For example, large-scale, GIS-based measurements of monthly maximum and/or minimum air temperatures are frequently correlated with species' distribution patterns to estimate the ways in which climate drives the distribution of organisms (e.g. Kozak and Wiens, 2007). Such approaches are useful because they permit the rapid analysis of numerous species, given proper model tuning (Hijmans and Graham, 2006; Kearney and Porter, 2009). However, seldom is consideration given to the underlying physiological drivers that either directly set species' range limits or else serve to indirectly set limits through their impacts on species interactions (but see Buckley, 2008; Kearney and Porter, 2009; Kearney et al., 2008). It is thus difficult to mechanistically untangle what, if any, components of weather and climate (i.e. long-term trends in weather) set range edges. As a result, correlative approaches have been criticized for having potentially low predictive capacity in the novel environments presented by global climate change (Kearney, 2006; Helmuth, 2009).

By contrast, given the incredible complexity inherent in both physical and biological systems, using the results of controlled physiological and ecological experiments to predict ecological responses over large geographical scales is a time-consuming and data-intensive method (Davis et al., 1998; Hijmans and Graham, 2006). Moreover, such approaches require an understanding of how environmental parameters vary in space and time at scales pertinent to the organism (Broitman et al., 2009; Kearney, 2006) so that conditions in the lab can be extrapolated to those in the field. For example, experiments made under constant temperature treatments do not faithfully replicate natural conditions in environments where temperatures fluctuate, and thus may ignore the importance of factors such as the time history of thermal exposure (Tomanek and Sanford, 2003; Widdows, 1976). Conversely, whereas field studies provide important insight into physiological responses under natural conditions (Costa and Sinervo, 2004), it may be difficult to extract understanding of mechanistic underpinnings, especially given the interactive nature of multiple stressors (Crain et al., 2008).

An obvious drawback to the use of mechanistic approaches to understanding the current and future determinants of range boundaries is the need for fine-scale data, both environmental and physiological. One potentially fruitful approach is to design controlled experiments of physiological responses and the indirect effects on species interactions by first quantifying spatial and temporal patterns of environmental parameters that probably drive patterns of stress in the field. In other words, it may be possible to condense complex environmental signals into categories based on known or suspected physiological responses and to use these as

guides to further controlled experimentation. These metrics can then be used in either large-scale correlative models (Pearson and Dawson, 2003) or through finer-scale approaches based on *in situ* experimentation (Pearson et al., 2009). Importantly, by using such an approach, we can examine the potential for multiple stressors to act in setting species' range limits and patterns of abundance. For example, while extreme temperatures may set the range edge of a population of organisms at one location, longer-term, more chronic stressors may act to set limits at another location or at another time at the same location (e.g. Beukema et al., 2009; Hutchins, 1947). At yet another site or time, limits may be set by stressors acting upon a competitor or predator (Pincebourde et al., 2008; Wethey, 1983; Yamane and Gilman, 2009).

To some extent hybrids of these two approaches are being used to good effect (e.g. Buckley, 2008; Kearney et al., 2008; Kearney and Porter, 2009). For example, coral reef ecologists frequently use degree heating weeks (DHW) to predict large-scale patterns of bleaching (Gleeson and Strong, 1995). DHW are based on the difference between the observed sea surface temperature (SST) at any point in time and a bleaching threshold. This threshold is defined as 1°C above the highest historical monthly mean SST for that location, a condition shown to cause bleaching in laboratory conditions (Glynn and D'Croz, 1990). The cumulative effect of these extremes is then calculated using a running sum of 96 days (e.g. Peñaflor et al., 2009).

DHW is now the most widely used method for predicting patterns of coral bleaching over large geographical scales (Peñaflor et al., 2009). Other studies, however, have shown that SST-based statistics other than DHW may prove equally effective as predictors of bleaching (Berkelmans et al., 2004; Winter et al., 1998). Moreover, the use of DHW can very frequently result in false predictions (van Hooidonk and Huber, 2009). These analyses thus strongly suggest that we may be able to significantly improve our predictive capacity through a better understanding of how temperatures vary in the field (Leichter et al., 2006) and how those temperatures affect corals and their symbionts (Castillo and Helmuth, 2005; Helmuth et al., 2005). For example, SST can be very different from water temperature even the few meters below the surface where corals live (Leichter et al., 2006). Water flow also interacts with water temperature to drive patterns of coral bleaching, both through its effect on coral tissue temperature (Fabricius, 2006) and by the removal of oxygen free radicals (Finelli et al., 2006). Thus, while DHW may serve as an effective broad indicator of overall patterns of coral bleaching, and is based to some extent on physiological responses to temperature extremes, this method could almost certainly be improved through a better understanding of how coral temperature patterns (as opposed to SST patterns) vary in the field and of how corals physiologically respond to their localized environments.

Signal transduction

While climate change is a global phenomenon, to an organism, all relevant environmental changes are very local (Mislan et al., 2009; Russell et al., 2009) as the organism moves through space and time. Namely, the only factors that drive the physiological and behavioral responses of an organism are those in its immediate vicinity (Patterson, 1992), and thus the only aspects of weather and climate that affect an organism are those that directly drive its physiology, dispersal and fitness or else affect organisms with which it interacts (e.g. predators, prey, competitors and pathogens). For example, for sessile animals, differences in environmental conditions on the north and south faces of rocks, in and out of crevices or other shaded areas, or between different tidal elevations can be so large that they exceed those observed over a latitudinal gradient (Chan et al., 2007; Helmuth and Hofmann, 2001), which in turn can have significant consequences for population and community dynamics (Benedetti-Cecchi, 2001; Blockley and Chapman, 2007; Schmidt et al., 2000). Moreover, two organisms exposed to identical environmental conditions can experience very different patterns of body temperature depending on their size, morphology and color (Etter, 1988; Harley et al., 2009; Jost and Helmuth, 2007). The body temperature of ectotherms thus depends strikingly on these factors, and two organisms of different species exposed to the same microhabitats can have very different body temperatures (Broitman et al., 2009; Southward, 1958).

In all of these examples, interactive aspects of the 'environment', for example air temperature, wind speed and solar radiation, are thus 'translated' or 'transduced' through the organism's size, morphology and behavior into one or more axes of an organism's fundamental niche space (Kearney, 2006; Patterson, 1992). This phenomenon was perhaps most clearly described by Patterson, who envisioned scleractinian corals and their symbionts as a series of 'resistors', each of which 'filtered' different frequency components of a signal, either through membrane structure or through processes related to boundary layer diffusion (Patterson, 1992). Using this analogy, host–symbiont interactions could be understood from the ways in which corals 'filtered' aspects of their ambient environment through their morphology and behavior.

Niche-level parameters such as gas and nutrient concentrations and body (tissue) temperature then drive physiological processes that can be measured in the field and lab. For example, an increase or decrease in body temperature affects patterns of gene expression (Gracey et al., 2008; Hofmann et al., 2005; Place et al., 2008), which in turn can lead to the activation of a heat shock response (Tomanek, 2008) or can affect processes related to growth (Beukema et al., 2009; Schneider, 2008), metabolism (Dahlhoff, 2004; Vernberg, 1962), fecundity (Dillon et al., 2007; Petes et al., 2008) and survival (Chan et al., 2007; Harley, 2008; Jost and Helmuth, 2007). Changes in body temperature can also have significant effects on movement (Fangue et al., 2008) and foraging behavior (Pincebourde et al., 2008; Sanford, 2002; Yamane and Gilman, 2009).

Taken at a population level, the cumulative impact of physiological performance by individuals drives higher-level responses that are relevant for studies of biogeography. For example, Harley and Paine recently showed that population dynamics and distributions of intertidal algae were driven more by rare events rather than by slow changes in ambient environmental conditions (Harley and Paine, 2009). By contrast, Beukema et al. showed that warm temperatures experienced by bivalves living well within their range boundaries (several hundred kilometers poleward of their equatorial range edge) not only increased mortality but also reduced growth, suggesting that sublethal effects of increasing temperatures can be an important response to changing environmental conditions (Beukema et al., 2009). In other words, both 'chronic' (long term, low frequency) and 'acute' (extreme, high frequency) stressors (Helmuth and Hofmann, 2001) can contribute to ecological responses to climate change (Etter, 1988; Wethey, 1983).

In recent years the development of new tools has provided significant insight into how environmental processes drive cellular responses (Dahlhoff, 2004; Gracey et al., 2008; Hofmann and Gaines, 2008; Tomanek, 2008). For example, the expression of inducible forms of Hsp (Halpin et al., 2004) has been shown to exhibit threshold-like responses that occur only during extreme events but they can also respond to lower frequency changes *via*

acclimatization. Other physiological responses such as growth are probably best related to lower-frequency, dampened or time-averaged (integrated) measurements of the environment such as seasonal means (Bayne et al., 1976; Widdows, 1978). The time history of exposure is also important. Previous exposure to extremes can cold- or heat-harden individuals (Klok et al., 2003), and prior exposure to cyclic conditions can sometimes lead to higher performance than in animals exposed to constant conditions (Widdows, 1976) (but see Du et al., 2009). Repeated exposure to extreme conditions may also reduce performance in metrics, such as foraging behavior (Pincebourde et al., 2008), fecundity (Dillon et al., 2007) and survival (Jones et al., 2009). Finally, cumulative damage can occur, as discussed above in the example of DHW and coral bleaching. Thus, physiological responses vary in accordance with their sensitivity to different both 'chronic' and 'acute' aspects of stressors such as body temperature.

Quantifying environmental patterns relevant to physiological responses

Here we use a moderately long-term (nine years), nearly continuous, record of temperatures recorded by biomimetic sensors in intertidal mussel beds (*Mytilus californianus* Conrad 1837) at a site in central California (Pacific Grove, CA, USA) to explore temporal patterns that can potentially be linked to metrics of physiological stress. We then compare patterns measured in California with those at a site in Oregon (Boiler Bay, OR, USA) to show how this approach might be applied over geographical scales. Intertidal organisms are thought to be especially sensitive to changes in weather and climate (Helmuth et al., 2006b; Mieszkowska et al., 2006; Southward et al., 1995) because they frequently exist very close to their thermal limits in nature (Somero, 2005; Stillman, 2003). In addition, intertidal ecosystems have served as intellectual fodder for many ecological studies (Paine, 1994), making them an ideal study system for examining the effects of the physical environment on populations and communities. While we focus on the effects of climate change and variability on animal temperature, in principle the approach applies to other factors expected to change in the near future, including, for example, oxygen concentration, nutrient levels and wave forces (Denny et al., 2009; Harley et al., 2006).

Our goal is to explore how long-term records of body temperatures – as opposed to records based solely on habitat-level measurements such as air, surface or water temperature – can be used to calculate meaningful spatial and temporal patterns in physiological stress. Our ultimate goal is to explore how we can use physiological measurements as a guide to develop a 'climatology' of body temperatures (long-term trends in various aspects of body temperature such as means, maxima and cumulative measurements). We do so by first examining what the likely indicators should be and how these covary in time at a single site.

Body temperature climatology: how do we measure the environment?

Clearly we need to quantify environmental signals at temporal and spatial scales appropriate to multiple physiological responses. While this statement may appear obvious or simplistic, consider that often 'environmental' data collected by remote sensing platforms, buoys or weather stations are usually measured, archived and/or analyzed at intervals and spatial scales that may have little or nothing to do with organismal biology (IPCC, 2007). For example, monthly means may hide highly significant extreme events, and data collected over large spatial scales may ignore ecologically important patterns of smaller-scale heterogeneity (Benedetti-Cecchi et al., 2003).

Using biomimetic sensors ('robomussels') designed to mimic the thermal characteristics of the mussel *M. californianus*, we have recorded physiologically relevant temperatures at the Hopkins Marine Station in Pacific Grove, CA, USA (36.62°N, 121.88°W) at 10-minute intervals since 2000 (with a gap in 2006). These instruments record temperatures within ~1.5–2°C of living animals in the field (Fitzhenry et al., 2004). Data were recorded using 3–5 instruments placed in growth position in the mid-intertidal zone [mean lower low water (MLLW) +1.5–1.7 m]. Prior to analysis records were smoothed using a running average of 30 min in order to remove brief transients. This choice of filter length is somewhat arbitrary but falls within the range of induction times for Hsps for several intertidal species (e.g. Tomanek and Somero, 2000). We also recorded standard meteorological data at this site over the same period.

Our data show clear differences between estimates of physiological stress based on body temperature rather than on air temperature. First, yearly maximum logger (mussel) temperature is always higher than yearly maximum air temperature (Fig. 1). Whereas air temperatures seldom cross 30°C (the approximate temperature for Hsp production, see below), yearly maximum body temperatures regularly have exceeded this threshold at this site (Fig. 1). Likewise, maximum body temperatures have come very close to 36–37°C, the approximate lethal temperature (LT_{50}) for aerial body temperature for the related species *Mytilus edulis* (Jones et al., 2009) (the lethal aerial temperature for *M. californianus* has not yet been reported). While air temperatures suggest that 2003 was the hottest year for mussels at this site during the nine-year time interval examined, measurements made using biomimetic sensors show that this was not in fact an unusually hot year for mussels. By contrast, biomimetic sensors clearly show that 2007 was a hot year for these animals (based on extremes): a year with only modest air temperatures. A regression of maximum annual logger (body) temperature *vs* maximum yearly air temperature during low tide shows a correlation coefficient of only 0.08 (Fig. 1B). A comparison using a seven-day running mean (not shown) increases the fit of this relationship to 0.24. These results thus strongly suggest that estimates of stress in the field need to be derived from niche-level measurements or models relevant to physiological performance such as body temperature (Gilman et al., 2006; Denny et al., 2009; Jones et al., 2009; Southward, 1958) rather than habitat-level measurements such as air temperature.

How do we predict and measure patterns of stress in the field?

We used data from biomimetic loggers to calculate four physiologically relevant metrics of stress. First, we measured the incidence of events over 30°C, the approximate threshold for Hsp production in *Mytilus* spp. (Buckley et al., 2001; Halpin et al., 2004). Second, we calculated return times of biomimetic temperatures over 30°C, an indicator of repeated exposure to stressful conditions. Third, we estimated seasonal means in body temperature, a rough indicator of the effect of body temperature on processes such as growth (Blanchette et al., 2007). Finally, we calculated an estimate of degree heating hours (DHH) using a running 30-day sum of degree hours over 25°C. The physiological relevance of this latter metric to *Mytilus* spp. is unclear, but because similar metrics have been shown to be important for corals, we show these data for heuristic purposes.

Fig. 2 shows the number of days during which a 30°C threshold was crossed for at least 30 min in each year, along with (numbers in Fig. 2) the mean return time, defined as the mean number of days occurring between each high temperature event. When looking at
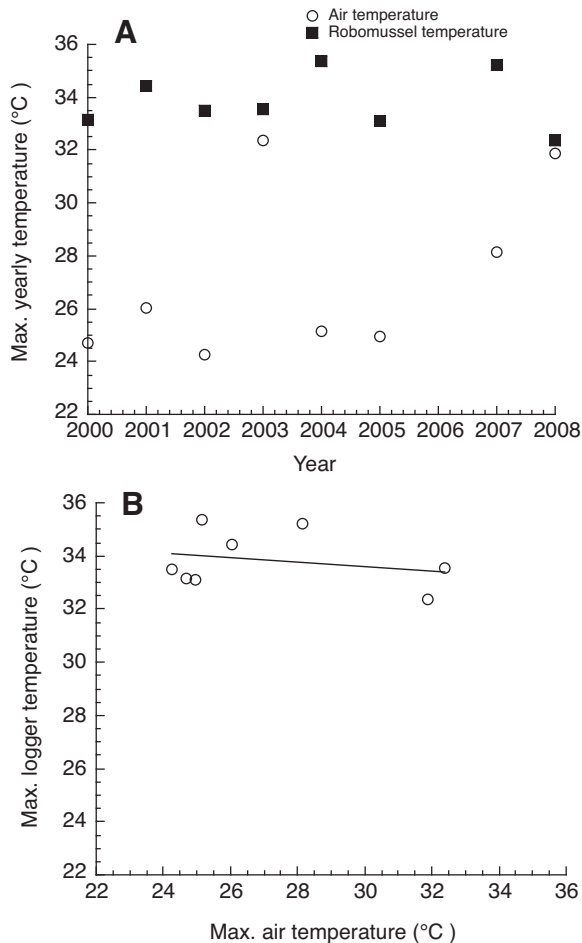
Fig. 1. Comparison of yearly maximum 'robomussel' (biomimetic sensor) temperatures *vs* yearly maximum air temperatures. For this analysis, only air temperature data during low tide were used, based on estimates of still tide height and wave splash. (A) Yearly patterns in maximal air temperature and maximal mussel temperature did not follow similar patterns. While maximum biomimetic sensor temperatures were highest in 2007, this year did not correspond to a year with extreme air temperatures. By contrast, years with extreme air temperatures (2003 and 2008) did not result in unusually high maximum mussel temperatures. (B) A regression of yearly maximum body temperature *vs* maximum air temperature shows that yearly extremes in mussel temperature are always hotter than records of air temperature, and that air temperature can explain very little of the variability in yearly maximum mussel temperature (R^2=0.08).
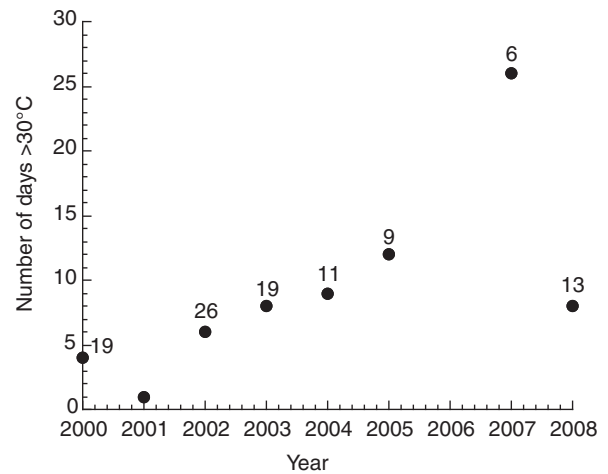

Fig. 2. The number of days per year where biomimetic sensor loggers exceeded 30°C for at least 30 min, along with (numbers above closed circles) the average return time (number of days between extreme events). Note that in 2007 there were 26 incidences where mussels experienced temperatures above 30°C, with an average timing of six days between each event (median value of one day).

these threshold-type responses, 2007 clearly emerges as one of the hottest years for mussels during the interval 2000–2008, both in terms of the number of events as well as in the mean time between events (with shorter times between events likely to be more stressful), followed by 2000.

Notably, estimates of interannual patterns based on seasonal averages (Fig. 3) are very different from those based on more acute thresholds (extreme daily maxima). Using a three-month (90 days) running mean 2004, followed closely by 2003 and 2007, emerges as the hottest year in this nine-year record for longer-term responses such as growth (all other factors such as food assumed to be equal). When this mean is extended to a five-month (150 days, e.g. May to September) running mean, the year 2007 appears to be a very average year but 2003 and 2004 continue to appear as hot years. In other words, while more extreme events occurred in 2007, they

occurred during a comparatively short period of time and thus longer temporal averaging quickly diminishes the influence of these acute events. By contrast, during 2003, a year when mean temperatures were high, relatively few extremes (days >30°C) occurred. This analysis thus points to an important connection to physiological studies. In this example, depending on the relative importance of elevated temperatures over different time scales (three *vs* five months), very different predictions of temporal patterns in stress emerge. It is presently unclear what time scale is most relevant to growth in *M. californianus*, and of how temperature interacts with other factors such as food (Blanchette et al., 2007). These issues need to be resolved using physiological experimentation, with guidance from field measurements of body temperatures (Denny and Helmuth, 2009).

In Fig. 4, we present a calculation of DHH for this site. We used 25°C as a threshold for peak monthly average daily maximum based on the long-term records from this site (Helmuth et al., 2006a), along with a 30-day running sum [an exposure duration where aerial temperatures have been shown to cause differences in survival and growth (Schneider, 2008)]. Using the DHH metric, 2004 followed by 2007 emerges as the physiologically most stressful year. Notably, in contrast to measurements of seasonal temperature, 2003 appears to be a very average year. Again, however, a major limitation is our understanding of (a) what threshold temperature should be used, and (b) the amount of time that degree hours should be summed.

It is likely that contrasts such as this – the annual maximum of a physiologically important factor cannot be predicted from the mean of any single environmental parameter or in this case from the seasonal mean of body temperature – are common in ecology. Denny et al. noted that many extreme events in ecology stem from the random coincidence of multiple 'normal' factors, and it seems likely that the extreme body temperatures (>30°C) recorded in 2007 were the result of such a chance coincidence (Denny et al., 2009). Although the stochastic nature of environmental coincidences makes it impossible to predict precisely when specific extreme events will occur, the same stochastic character makes it possible
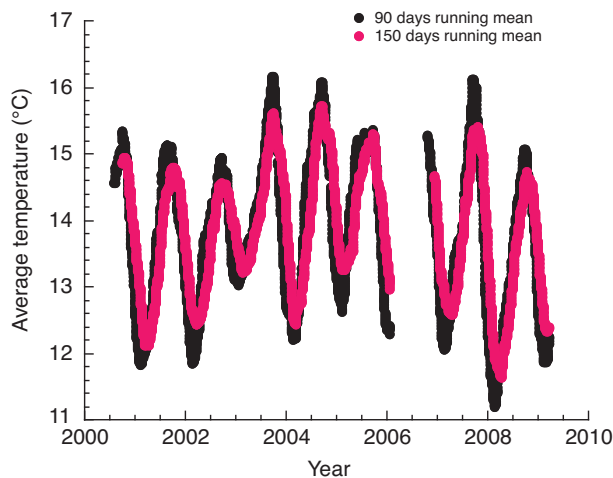
Fig. 3. Comparison of interannual variability in seasonal mussel temperature using three-month (90 days) and five-month (150 days) running means. For each time point, temperature thus represents the mean of all previous raw data for the preceding 90 or 150 days. Whereas 2007 was a hot year in terms of extreme events, it was a more or less average year in terms of seasonal temperature, especially over 150-day time periods. By contrast, seasonal averages peaked during 2004 but were coupled with a very moderate incidence of extreme events (shown in Fig. 2).
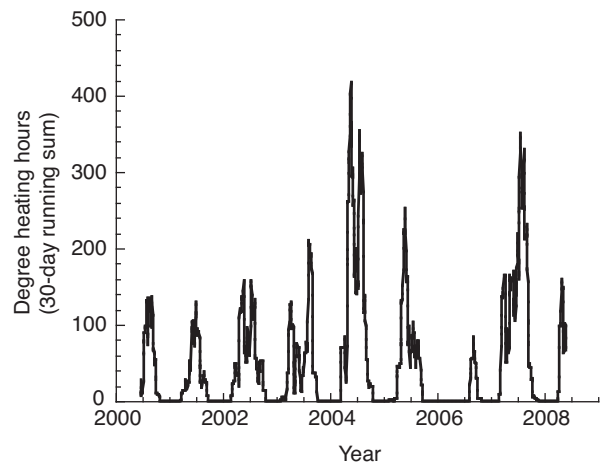

Fig. 4. Estimation of degree heating hours at the Hopkins Marine Station (Pacific Grove, CA, USA) intertidal site. Values were calculated by adding the degree hours above a threshold of 25°C (the observed peak mean daily temperature at this site) using a running sum of 30 days.

to accurately predict the average return times of such events, a valuable method for predicting the likelihood of threshold-type responses such as mortality and reproductive failure (Denny et al., 2009).

While we here primarily focus on temporal (interannual) variability in physiologically relevant signals, the ultimate goal of this method is to examine large-scale spatial variability in these temporal signals (Helmuth et al., 2006a) over long time periods, i.e. 'organismal' as opposed to 'habitat' climatology. As an example of this approach (Fig. 5), we show a comparable analysis of the peak seasonal (90-day running average) temperatures and number of days >30°C for mid-intertidal mussels at Boiler Bay, OR, USA (44.83°N, 124.05°W). Results show that both the mean seasonal temperature and the number of days over 30°C are higher at the Oregon site than at the California site, even though the latter site is ~1000 km closer to the equator. This pattern is likely to be due to a higher incidence of low tides in the middle of the day at the Oregon site as compared with Pacific Grove, combined with differences in wave splash, cloud cover and coastal fog (Helmuth et al., 2002). As before, temporal patterns in seasonal peaks and the incidence of extremes do not occur in phase with one another. It also should be noted that while 2001 was clearly a hot year for mussels at the Oregon site, this corresponds to a cool year in Pacific Grove.

Environmental drivers and the relative importance of multiple signals

Measuring aspects of the environment that are relevant to an organism's physiology can be difficult. In general, environmental signals such as air and water temperature are often measured at very coarse spatial or temporal scales *via* remote sensing (R/S) or else at point locations using buoys or weather stations. While these approaches are the only currently practical way of measuring environmental parameters on large temporal and spatial scales, it remains unclear how patterns measured at large scales correspond, even qualitatively, to those at the level of the organism, unless they

are first 'translated' using biophysical models (e.g. Gilman et al., 2006). Explorations of the relationship between R/S climatologies and niche-level measurements relevant to organismal performance are thus of prime importance.

If we hope to draw from results of physiological studies, forecasts of the impacts of climate change need to move away from simple predictions and measurements of environmental parameters alone and towards models and measurements that consider the factors that actually drive physiological stress and mortality, and include explicit quantification of the physiological performance curves underlying responses to changing environments (Denny and Helmuth, 2009). For example, IPCC projections (IPCC, 2007) focus on air temperature, land surface temperature and SST, as does public understanding of climate change. The results shown here suggest that without an understanding of how 'environmental signals' such as air temperature interact with other signals such as cloud cover, water temperature, solar radiation and wave height (splash) to drive body temperature we may be misled in our predictions of where and when impacts on organisms and ecosystems are most (or least) likely to occur (Kearney, 2006). Similarly, without understanding the role of 'sensitivity' and 'vulnerability' to those niche-level phenomena (Gilman et al., 2006), our predictive capacity may be severely curtailed.

The successful merger of these approaches thus depends on our ability to record physiologically relevant components of environmental parameters over large spatial and temporal scales. For example, instead of using metrics of monthly maximum air temperature as inputs to climate envelope models, environmental parameters can be first translated into estimates of body temperature. These results could then be used to derive metrics of the likelihood of occurrences of events over fixed physiological thresholds (e.g. Hsp production, lethal temperature, reproductive failure), or cumulative effects (seasonal means, return times) on reproduction and survival, and used in a hybrid statistical model. This type of pioneering approach has been used in terrestrial environments by Kearney and colleagues (e.g. Kearney et al., 2008; Kearney and
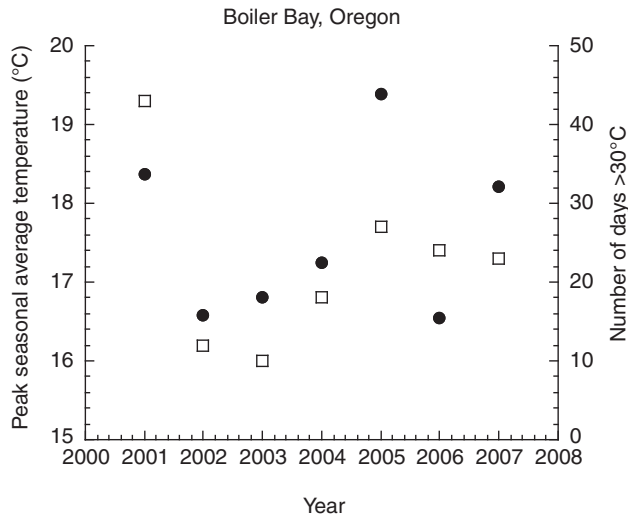
Fig. 5. Peak seasonal temperatures (90-day running mean), shown in solid circles, and number of days over 30°C, shown in open squares, for mid-intertidal mussels at a moderately wave-exposed site in central Oregon, Boiler Bay, OR, USA. Note that both of these metrics are higher at this site than at the California site.

Porter, 2009) but has yet to be fully tackled in marine environments (but see Wethey and Woodin, 2008).

Importantly, these estimates must be based on organismal climatologies rather than on simple metrics of habitat. While we use nine years of data measured empirically, these approaches are also amenable to techniques such as the reconstruction of body temperature using heat budget models combined with long-term weather and climate data. For example, Wethey and Woodin retrospectively predicted geographical shifts in intertidal barnacles using historical SST data and models of aerial temperature combined with an understanding of how temperature drives reproductive success (Wethey and Woodin, 2008). Denny et al. have shown that it is possible to statistically estimate the future probability of extreme events such as wave force and intertidal temperature using a combination of empirical and theoretical approaches (Denny et al., 2009). These 'mechanistic ecological forecasts' thus hold significant promise (Helmuth, 2009). Much work remains to be done but clearly significant progress is being made in bringing physiological knowledge to bear on questions of biogeography and climate change.

Conclusions

Forecasting the location, magnitude and timing of the impacts of climate change on ecosystems is a crucially important task. To date, our attempts to generalize how organisms respond to environmental changes have shown us that climatic factors are spatially and temporally heterogeneous, that organisms do not respond to overall changes in the 'climate' *per se* but rather to fluctuations in habitat conditions (Hallett et al., 2004; Stenseth et al., 2003), and that organismal responses to these changes in their local habitat can be complex and counterintuitive. Thus, to accurately predict the ecological impacts of climate change on organisms requires an ability to distill large-scale environmental signals into niche-level processes, and to decipher how these processes are translated into physiological responses. We have outlined an approach to characterize patterns in 'organismal climatology' that may be relevant to physiological performance and can be used to understand and predict the responses of organisms and populations. In doing

so, our intention is to provide a starting point for bridging large-scale models of weather and climate with physiological studies conducted in the field and under controlled laboratory conditions. Our analysis suggests that patterns of organismal stress probably cannot be easily predicted from single environmental parameters such as air temperature. Results also suggest that different indicators of 'stress' may not always march lockstep with one another. For example, mussels repeatedly reached the most extreme (hottest) temperatures during a year when 'average' conditions might suggest rather moderate exposures. Conversely, hot years (based on mean seasonal temperatures) did not always produce extremes. These results suggest that what defines a year as 'extreme' depends on the physiological metric in question, and almost certainly varies between species (Broitman et al., 2009). Using the methods described here, we can begin to tease apart patterns of organism response in the field, identifying the relative importance of different environmental signals to organism physiology. In turn, designing laboratory studies based on measured or anticipated frequency patterns of physiologically relevant events, such as specific return times, will allow us to explore the impacts of realistic field conditions in a controlled laboratory setting. By deciphering the physiological mechanisms underlying organism responses to physical conditions and quantifying resultant spatial and temporal patterns in these responses, we can better understand and more accurately forecast the ecological ramifications of a changing climate.

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