Commentary

From cells to coastlines: how can we use physiology to forecast the impacts of climate change?

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Summary

The interdisciplinary fields of conservation physiology, macrophysiology, and mechanistic ecological forecasting have recently emerged as means of integrating detailed physiological responses to the broader questions of ecological and evolutionary responses to global climate change. Bridging the gap between large-scale records of weather and climate (as measured by remote sensing platforms, buoys and ground-based weather stations) and the physical world as experienced by organisms (niche-level measurements) requires a mechanistic understanding of how 'environmental signals' (parameters such as air, surface and water temperature, food availability, water flow) are translated into signals at the scale of the organism or cell (e.g. body temperature, food capture, hydrodynamic force, aerobic capacity). Predicting the impacts of how changing environments affect populations and ecosystems further mandates an understanding of how organisms 'filter' these signals *via* their physiological response (e.g. whether they respond to high or low frequencies, whether there is a time lag in response, etc.) and must be placed within the context of adult movement and the dispersal of larvae and gametes. Recent studies have shown that patterns of physiological stress in nature are far more complex in space and time than previously assumed and challenge the long-held paradigm that patterns of biogeographic distribution can be based on simple environmental gradients. An integrative, systems-based approach can provide an understanding of the roles of environmental and physiological variability in driving ecological responses and can offer considerable insight and predictive capacity to researchers, resource managers and policy makers involved in planning for the current and future effects of climate change.

Key words: biogeography, climate change, conservation physiology, ecological forecasting, biophysical modeling.

Introduction

A fundamental tenet of physiological ecology is that processes that occur at the level of the organism, cell and genome can have cascading effects on the distribution, abundance and fitness of organisms at scales ranging from microhabitats to continents and oceans (Magnuson, 1991; Pörtner, 2002; Somero, 2005). In recent years, the linkages between physiological mechanism and the evolution and biogeography of organisms ha
 received new impetus because of the observed effects of climate change and variability on ecosystems (Helmuth et al., 2006b; Kearney et al., 2008; Pörtner and Farrell, 2008). As society faces the consequences of rapid changes in the Earth's climate resulting from human activity (IPCC, 2007), a major challenge before the scientific community is not only to understand how natural and managed ecosystems have responded historically to changes in climate (CCSP, 2008; Parmesan et al., 2005; US Environmental Protection Agency (EPA), 2008) but also to develop methods that measure and predict ongoing and future impacts of these factors (Clark et al., 2001; Gilman et al., 2006; Helmuth et al., 2006b; Kearney et al., 2008).

Physiologists and ecologists have long been interested in the effects of physical parameters (e.g. temperature, salinity, rainfall) on organisms and their interactions. New techniques in the areas of genomics, gene expression and transcriptomics (Gracey and Cossins, 2003; Hofmann and Gaines, 2008; Hofmann and Place, 2007; Place et al., 2008) and biochemical indicators of stress (Dahlhoff, 2004; Sagarin and Somero, 2006) have opened new

doors for measuring the responses of organisms to their physical environment in both the laboratory and field (Costa and Sinervo, 2004). With the application of remote sensing coupled with extensive ground-based measurements of weather and climate (Hofmann and Gaines, 2008; Richardson and Poloczanska, 2008), physiology is now being explored on a landscape scale by integrating information on physiological function with knowledge of temporal and spatial patterns in the physical environment (Chown et al., 2004; Porter et al., 2002; Somero, 2005). These tools and theories thus set the stage for explorations of 'macrophysiology' (Chown et al., 2004; Somero, 2005) and play a significant role in preparing for ongoing and future ecological responses to climate change (Helmuth et al., 2005; Kearney et al., 2008).

Here I explore some of the remaining challenges facing the application of physiological approaches to ecology and biogeography, focusing on studies related to climate change. Specifically, I explore the question of why such approaches may be much more complex than have been previously appreciated and how integrative methods can be used to reveal 'hidden' patterns that may otherwise go unnoticed (Gilman et al., 2006; Helmuth et al., 2006a; Place et al., 2008) but which may be crucial for predicting ecological responses. In doing so, I advocate for the generation of data and predictions at scales that are useful to 'boots on the ground' resource managers and policy makers (Baskett et al., 2007; CCSP, 2008; Hoffman, 2003; Magnuson, 1991; US Environmental Protection Agency (EPA), 2008; Wikelski and

Cooke, 2006); while basic science remains vital, observed and projected rates of climate change mandate that we, as scientists, find ways to address issues related to societal needs as quickly as possible (Hofmann and Gaines, 2008; Richardson and Poloczanska, 2008; Wikelski and Cooke, 2006).

Challenges and hidden signals

In the simplest terms, an organism experiences only its immediate microhabitat. As an organism samples its surrounding environment *via* its behavior, it is exposed to a range of microhabitats that determine the environmental conditions to which the organism is exposed. Depending on their physiological optima and thresholds, organisms then respond to these signals in different ways. Physiological responses are translated into patterns of survival, growth and reproductive output, which determine fitness. Taken in the aggregate, the responses and interactions of individuals drive population dynamics, and the species-dependent responses of organisms drive rates of interspecific competition (Petes et al., 2007; Wethey, 1983) and predation (Aronson et al., 2007; Pincebourde et al., 2008). Rates of exchange of adults, juveniles, larvae and gametes determine the level of connectivity between populations as well as larval supply and drive both local processes and metapopulation dynamics (Erlandsson and McQuaid, 2004; Kinlan et al., 2005). Over large spatial scales, these nested interactions serve to determine biogeographic range boundaries and patterns of species invasions (Aronson et al., 2007; US Environmental Protection Agency (EPA), 2008). In theory, therefore, it should be a relatively direct (albeit detailed) exercise to analyze the relationship between environmental signals [air and water temperature, photosynthetically active radiation (PAR), rainfall, etc.] and the responses of populations and ecosystems over a range of spatial and temporal scales, given sufficient information of mechanism and detailed measurements of environmental parameters.

Indeed, correlations between environmental variables and range boundaries are often made using multiple regression techniques, typically lumped under the rubric of 'climate envelope modeling' (e.g. Pearson and Dawson, 2003). Similarly, correlations are often made between fluctuations in large-scale indices of climate, such as the North Atlantic Oscillation (NAO), the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO), and patterns of abundance, distribution and physiological condition (Stenseth et al., 2003). Such correlative studies generally recognize that the underlying driver of these relationships is some aspect of local weather acting on organismal physiological response and that essentially treating climatic indices as 'black boxes' provides little mechanistic insight (Forchhammer and Post, 2004). Moreover, they acknowledge that the scale of prediction is important: while correlative climate envelope models appear to have good predictive power over broad spatial scales, they are not always effective at small temporal and spatial scales (Pearson and Dawson, 2003).

Because they do not include some aspect of physiological mechanism, purely correlative approaches also run the danger of being ineffective for predicting future biogeographic patterns because they are based on observations of realized rather than fundamental niche spaces and because projected environmental conditions can exceed those used to develop the model (Helmuth et al., 2005; Kearney, 2006; Phillips et al., 2008). Paradoxically, however, climatic indices have frequently been shown to serve as better indicators of ecological responses than patterns of local weather (Hallett et al., 2004). To a large extent, this disconnection may be a failure to account for physiological mechanism.

Specifically, in cases where mechanistic details have been examined, studies have shown that the comparatively poor association between local weather and organismal response is due to an incorrect focus on which aspect of weather matters (Hallett et al., 2004; Helmuth et al., 2005) and, potentially, on the scale at which it is measured (Broitman et al., 2009; Kearney, 2006). For example, Hallett et al. report that multiple environmental factors (high rainfall, high winds and low temperatures) cause mortality in Soay sheep (*Ovis ares*) (Hallett et al., 2004). However, long-term trends in any one of these parameters, when measured locally, are a less effective predictor of mortality than the NAO (a large scale index that alternates between 'phases' of different strength). Hallett et al. developed a physiologically based model that recognizes that extremes in any one of these parameters can cause mortality and that these environmental factors often alternate in their impacts (Hallett et al., 2004). In other words, while extremes in rainfall may kill animals during one period of time, low temperatures may be responsible at another time. Thus, long-term trends in mortality are not well correlated with either one of these parameters. In contrast to simple relationships based on sequential correlations between weather parameters and mortality, however, model results that include knowledge of physiological limits showed that local climate and weather actually had strong predictive power, but only when both direct effects (on sheep) and indirect effects (on their food supply) were accounted for (Hallett et al., 2004).

This example raises the specter of why we cannot always simply take large-scale measurements of environmental data at face value, combine them with measurements of physiological response made under controlled conditions and extrapolate to ongoing and future impacts of climate change in nature. First, while it is axiomatic that natural habitats are heterogeneous in space and variable in time, we often have a very poor understanding of the scales over which this variability, as perceived by organisms, occurs in nature (e.g. Weins and Milne, 1989). Second, even when we have good descriptors of physiologically relevant environmental conditions, we do not always have a detailed understanding of which aspects of environmental signals most affect performance and survival: what is 'signal' and what is 'noise'? Importantly, we cannot hope to address the first question (how do environmental signals relevant to organisms vary in space and time) until we have some understanding of the second (to what frequencies of environmental signals do organisms respond?). In other words, when do the temporal and spatial structure of environmental and physiological heterogeneity matter (Baskett et al., 2007; Denny et al., 2006; Gracey et al., 2008; Nathan et al., 2005; Weins and Milne, 1989)? As we will see, radically different patterns can emerge when we examine the world through the lens of the organism as compared to signals measured at scales with which we humans are most familiar.

Organisms as filters: viewing the world as a nonhuman organism

We are in an unprecedented era in terms of measuring and recording environmental information, although even more capacity is needed if we are to face the challenges of climate change (Richardson and Poloczanska, 2008). Satellites, weather stations and buoys are able to record multiple environmental parameters over many portions of the globe, and a wealth of historical information can be tapped for use in studies (e.g. Denny et al., 2006; Gilman et al., 2006; Wethey and Woodin, 2008). Importantly, however, the information recorded by these instruments is often very different from that actually experienced by organisms. To any plant or animal, the world at any given time

does not extend beyond its immediate environment (Helmuth, 2002; Kearney, 2006; Wiens and Milne, 1989), even though we may measure the environment at a large spatial or temporal scale. For example, Pfister et al. have shown that offshore water temperatures (as recorded by a buoy) can be very different from onshore water temperatures (Pfister et al., 2007). Thus, even though events such as ENSO and NAO may drive large-scale changes in offshore sea surface temperature (SST), these fluctuations in SST will only affect onshore (intertidal and shallow subtidal) organisms if that 'signal' is translated to those habitats. Similarly, Leichter et al. reported significant differences among water temperatures at different depths (0–40 m) on coral reefs and showed that geographic patterns predicted from SST were very different from those predicted from *in situ* measurements of water temperature at varying depths (Leichter et al., 2006).

One of the most extreme examples of spatial and temporal heterogeneity in temperature occurs in rocky intertidal systems, where the body temperatures of invertebrates and algae are driven primarily by solar radiation (Denny and Harley, 2006; Helmuth, 1998). In this habitat, animals living on horizontally oriented surfaces regularly experience body temperatures 6–13°C higher than nearby organisms living on adjacent north-facing surfaces (Helmuth and Hofmann, 2001). These differences (observed over the scale of centimeters) can be as great or greater than those observed over the scale of thousands of km and, depending on local tidal dynamics, can exceed differences between animals living in the high and low intertidal zones (Helmuth et al., 2006a). Comparable results have been shown for patterns of hydrodynamic force, where variation in small-scale topography can have a much more important role in determining drag and dislodgement than does variability in wave height (Denny et al., 2004).

Importantly, the morphology (Koehl and Wolcott, 2004) and behavior (Schneider et al., 2005; Williams and Morritt, 1995) of organisms also significantly modify their interactions with their surrounding environment, often in counterintuitive ways. For example, the shape of a sessile suspension feeder strongly modifies its ability to capture suspended food, and two organisms exposed to identical flow conditions can have markedly different rates of prey interception (Sebens et al., 1998). Similarly, dissolved oxygen and nutrient concentrations can be a poor indicator of gas and nutrient uptake because of interactions of morphology with flow (Patterson, 1992). The morphology, behavior and surface properties of organisms can also have major effects on their body temperature. Recent evidence suggests that both the shape (Jimenez et al., 2008) and color (Fabricius, 2006) of corals can lead to differences of several degrees between coral body temperature and the temperature of the surrounding water due to the competing influences of heat gain from solar radiation and heat loss through convection. Differences between ambient (air and surface) temperature and the body temperature of ectotherms are even more extreme in terrestrial environments (and intertidal environments at low tide) where daily fluctuations of 20°C or more are common (Helmuth, 2002).

These studies all point to a very important concept: parameters such as body temperature and gas exchange are metrics of niche parameters and are therefore signals that drive physiological response (Kearney, 2006; Kearney et al., 2008). However, because of the influence of an organism's physical properties such as morphology, niche-level measurements are not always well-correlated with habitat-level measurements (Gilman et al., 2006; Helmuth, 1998) [but see Denny et al. (Denny et al., 2006) and Wethey (Wethey, 2002)], and two organisms exposed to identical

microenvironments can experience very different levels of mass (gas and nutrient) flux, body temperature and mechanical force (Fig. 1).

As a result, spatial and temporal patterns of niche-level measurements (such as body temperature) can show very different patterns in space and/or time compared with patterns based on habitat-level parameters (such as air temperature or SST) (Fig. 2). Even though the importance of the interaction of organisms with their local microhabitat in driving exchanges of heat, mass and momentum has long been recognized (e.g. Koehl and Wolcott, 2004; Patterson, 1992), we still frequently base patterns of physiological stress on large-scale, habitat-level measurements. Specifically, when looking at biogeographic patterns, it is usually assumed that organisms live along environmental gradients of stress that reflect measurements of factors such as air and water temperature. When we actually measure patterns at the level of the niche, however, fundamentally different patterns, and thus qualitatively different predictions of the impacts of climate change, can emerge (Fig. 2).

For example, geographic patterns in the body temperature of intertidal mussels along the west coast of the USA display a pattern that can be at variance with water and air temperature measurements (Helmuth et al., 2002). Instead of showing a smooth
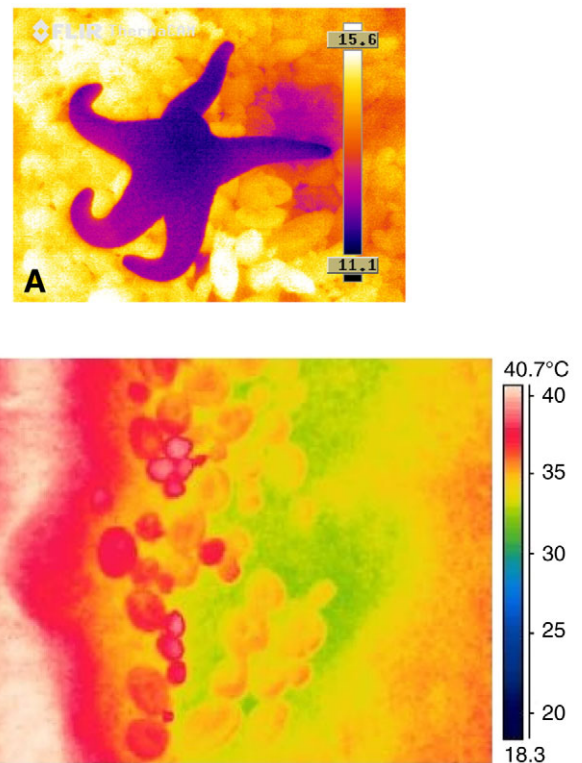

Fig. 1. Images of intertidal invertebrates taken using a FLIR Infrared Camera (FLIR systems, Boston, MA, USA). This instrument shows surface temperature as a false color image (scale bar on right of each image) with an accuracy of approximately 2°C. (A) Because of the effects of factors such as morphology, color and surface water content, two organisms (here, a predatory seastar, *Pisaster ochraceus*, feeding on prey, *Mytilus californianus*, in Oregon, USA) can have very different body temperatures, even though they are exposed to identical microclimates. (B) The effect of substrate orientation and aspect can also have a large effect on surface and organism temperature, as demonstrated by limpets living on rock surfaces with slightly different orientations to the sun (Botany Bay, Australia).
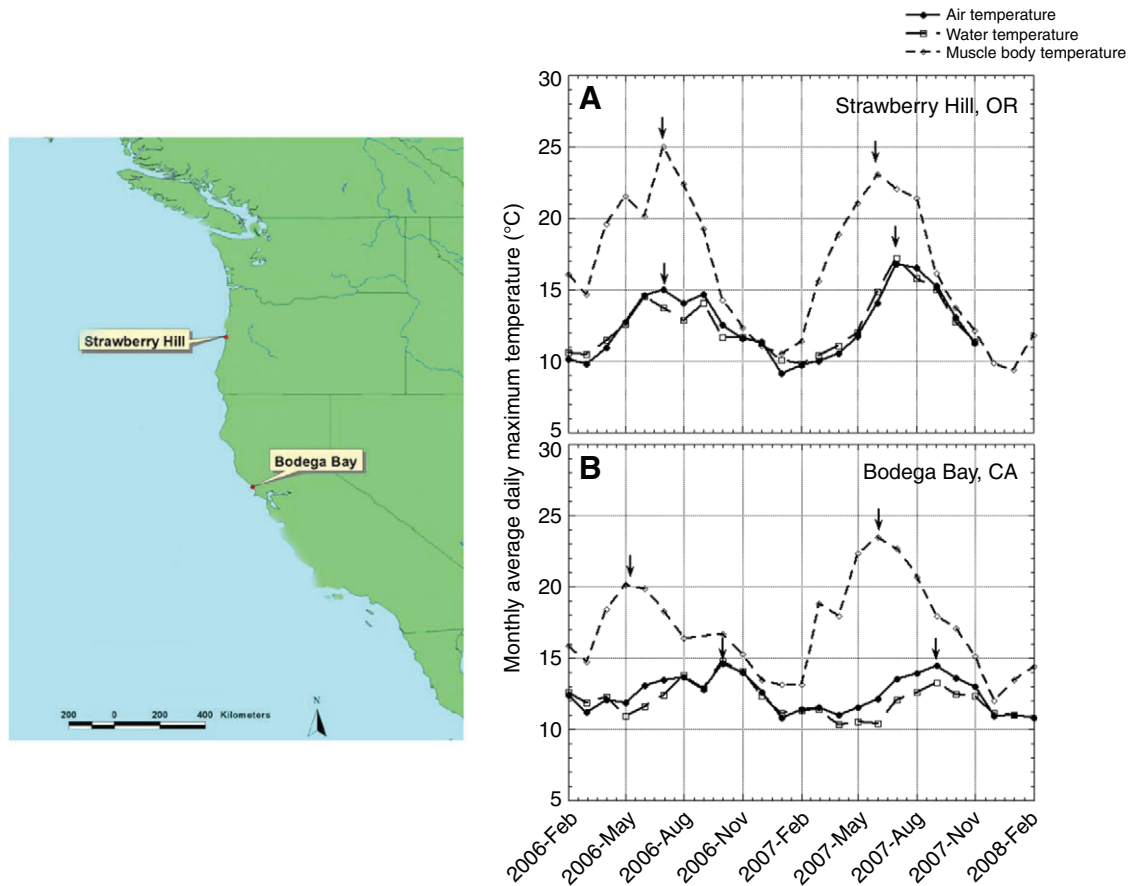
Fig. 2. Air and water temperature (measured by offshore buoys) and mussel body temperature in the mid intertidal zones of (A) Strawberry Hill, Oregon, USA and (B) Bodega Bay, California, USA from February 2006 to February 2008. At the Oregon site, annual peaks (indicated by arrows) in body temperature are in phase with air and water temperature and occur in late June/early July. By contrast, at the central Californian site, peaks in body temperature (in late May/early June) are out of phase with annual peaks in air and water temperature (which occur in September). Moreover, a comparison of the magnitude of the peaks at the two sites shows that mussels at the two sites experienced similar peak annual temperatures in 2007, but animals experienced substantially higher temperatures at the Oregon (more pole ward) site in 2006. These data show that habitat-level measurements (air and water temperature) cannot always be used as indicators of temporal patterns in organism temperature and that temperatures do not always decrease with increasing latitude. While air and water temperature are important drivers of intertidal temperature, the effects of wave splash, fog and, most importantly, the timing of low tides modify these factors. Air temperatures were recorded by NOAA (National Buoy Data Center) buoys 46050 (Stonewall Banks, 20 nautical miles offshore) and 46013 (Bodega Bay, 30 nautical miles offshore). Biomimetic sensors, instruments that mimic the thermal characteristics of organisms recorded mussel body temperatures.

cline in temperatures along a latitudinal gradient, these animals experience a thermal mosaic manifested as a series of 'hot' and 'cold' spots, where local conditions of tide, cloud cover and wave splash override the effect of the large-scale gradient in climate (Helmuth et al., 2006a). Measurements of gene expression further show that patterns of physiological stress match predictions based on body temperature (Place et al., 2008), and measurements of heat-shock protein expression also display nonlinear patterns with latitude (Sagarin and Somero, 2006). Leslie et al. have shown comparable levels of heterogeneity in upwelling regimes that correspond to major changes in reproductive output in barnacles (Leslie et al., 2005). And, as described before, geographic patterns of water temperature measured adjacent to corals can be substantially different from concomitant patterns of SST (Leichter et al., 2006).

Broitman et al. showed not only that temporal patterns in the body temperatures of predators and their prey cannot be predicted based on habitat-level parameters but also that relative patterns of body temperature vary from one site to the next (Broitman et al.,

2009). Specifically, Broitman et al. found that at some sites, seastar (*Pisaster ochraceus*) body temperatures were tightly coupled with the body temperatures of their prey (the mussel *Mytilus californianus*) (Broitman et al., 2009). At other sites, however, predator and prey temperatures were decoupled at higher frequencies (shorter than 6 h). Moreover, at some sites, predators and prey experienced similar body temperatures; at others, prey were markedly hotter than their predators. Because both aerial and aquatic body temperature can have significant effects on *P. ochraceus* foraging (Pincebourde et al., 2008; Sanford, 2002), these patterns are likely to have a cascading effect on the intertidal ecosystem, where *P. ochraceus* is a keystone predator (Paine, 1974). These studies thus strongly suggest that our predictions of the effects of climate, and climate change, must be based on niche-level, rather than habitat-level, measurements and predictions of environmental parameters (Kearney, 2006) and that relative levels of environmental stress between predator and prey need to incorporate aspects of the animal's physiological niche space (Menge et al., 2002; Petes et al., 2008).

Deciphering signal from noise

Just as we need to consider the spatial and temporal scales of heterogeneity in nature, we also need to estimate the potential roles of acclimation and adaptation in driving physiological responses to those environmental signals. For example, Stillman (Stillman, 2003) and Stillman and Somero (Stillman and Somero, 2000) explored the interspecific variability in thermal tolerance of porcelain crabs (genus *Petrolisthes*). They found that species with the greatest tolerance to high temperatures displayed the smallest acclimation capacity and were therefore the most susceptible to the small increases in body temperature (Stillman, 2003). In other words, the ability to acclimate to increased temperatures was least in the most heat-tolerant species. Hilbish examined tolerance of intertidal gastropods (*Melampus bidentatus*) to cold temperatures and discovered the existence of physiological races along the east coast of the USA that differed in their cold tolerance (Hilbish, 1981).

Temporal variability and time history likewise play a central role in driving the physiological responses of organisms but are often not considered when making projections of range shifts. Bleaching in corals is most commonly associated with anomalies in temperature rather than absolute thresholds in SST and usually involves a measurement of degree heating weeks (Gleeson and Strong, 1995). Other studies, however, have suggested that higher frequency fluctuations may be important to coral and zooxanthellae physiology (e.g. Winter et al., 1998).

Pincebourde et al. studied the effects of both short-term (acute, 1–2 days) and long-term (chronic, 8 days) exposure to elevated body temperatures (≥23°C) during aerial exposure on rates of feeding by the intertidal seastar *Pisaster ochraceus* on mussels *Mytilus californianus* (Pincebourde et al., 2008). They found that while acute exposures to elevated aerial body temperature led to a significant *increase* in feeding rate (~60%), chronic exposures caused a ~30–44% *decrease* in feeding rate. Tomanek and Somero studied the time course of heat-shock expression by congeners of an intertidal gastropod (genus *Tegula*) and report that the magnitude and time lag before expression varied between species adapted to different tidal heights (Tomanek and Somero, 2000), again suggesting that thermal history over both ecological and evolutionary time scales may be important in setting patterns of physiological stress.

Gracey et al. studied gene expression changes in mussels (*M. californianus*) living in high and low intertidal environments and identified at least four distinct physiological states, corresponding to a metabolism and respiration phase, a cell division phase and two stress-response signatures (Gracey et al., 2008). Importantly, they showed that the magnitude and timing of each of these states varied by microhabitat and between the upper and lower intertidal zones (Gracey et al., 2008). In other words, environmental signals, as translated *via* the organism to the cell, were manifested as different responses by each of the four physiological states identified.

The role of physiology in climate change research

Many of the concepts presented here appear at first glance to be 'common sense' or have been discussed for several decades. For example, physiologists have long recognized that ectotherms have body temperatures that differ significantly from their ambient environment (e.g. Southward, 1958), and the role of habitat heterogeneity in driving ecosystem function has been at the core of many empirical and theoretical studies (Deutschman et al., 1999; Wiens and Milne, 1989). Many modern approaches to studying the

biogeography of organisms and the impacts of climate change on these distributions (largely owing their origin to the work of Warren Porter and colleagues) are based on detailed models and measurements of niche-level parameters combined with physiological information (e.g. Denny et al., 2006; Kearney et al., 2008; Mitchell et al., 2008; Porter et al., 2002; Wethey, 2002). Nevertheless, many studies still correlate large-scale measurements of environmental parameters to the response of species and populations, and plans for future monitoring platforms seldom consider the concepts discussed here. While such approaches are likely excellent 'first cut' methods for predicting patterns of abundance and distribution (Pearson and Dawson, 2003), they may not always serve as an effective means of predicting future patterns in the face of climate change, and thus may be insufficient for management and policy purposes. Specifically, we often have a very poor understanding of the spatial and temporal scales over which the physical environment varies and the means by which dispersal (or isolation) between groups of individuals living at a nested range of scales drives the ecology, physiology, genetic structure and biogeography of populations and species (e.g. Baskett et al., 2007; Benedetti-Cecchi et al., 2005; Guichard et al., 2001; Schmidt et al., 2000). Likewise, we are just beginning to explore how temporal and spatial variability in environmental signals is translated into physiological responses (Gracey et al., 2008; Stillman, 2003). Thus, while large-scale correlative approaches may provide a means of 'drawing rough edges', they may hide detail that may be crucial for forecasts needed for decision-making.

Forecasting the direct and indirect effects of climate change (i.e. ecological forecasting) mandates that we understand the roles of (a) habitat heterogeneity in driving local microhabitat conditions, (b) the effect of organism characteristics (morphology, color, etc) on the translation of environmental signals at the level of the microhabitat to signals relevant to physiological performance; (c) the impacts of those signals on physiological response (and ultimately fitness); (d) the capacity for organisms to acclimate to (or the ability of populations to evolve in response to) those signals at varying temporal scales; (e) the indirect effects of physiological responses on interspecific and intraspecific interactions and (f) the role of dispersal in maintaining connectivity between organisms living at nested spatial scales.

Obviously this is a very tall order. It is exceedingly difficult to measure or model on a spatially explicit basis variability and heterogeneity at small scales over large geographic gradients. Moreover, not only is each component listed above difficult to measure, but errors or unaccounted-for variability and linkages at any level of inquiry can potentially be propagated to the next level (Deutschman et al., 1999). Nevertheless, several related avenues appear potentially fruitful.

Sensitivity analyses

First, mechanistic approaches can be used to conduct a sensitivity analysis of the roles of environmental signals, their translation, and physiological and genetic responses (Deutschman et al., 1999). For example, simple measurements of SST, when combined with physiological information on reproduction, have been successfully used to predict geographic range shifts in barnacles and polychaetes (Wethey and Woodin, 2008). By contrast, Hummel et al. suggested that even though the southern geographic range of bivalves was correlated with temperature, the species' range was more strongly driven by the interactive effects of other factors such as food availability and possibly pollutants (Hummel et al., 2000). Other studies have shown that the interactions of aerobic scope (anoxia)

with temperature can set geographic limits (Pörtner, 2002). Similarly, Harley and Helmuth found that temperature and exposure duration (likely related to food or oxygen demand) alternated in setting the upper distribution of barnacles (Harley and Helmuth, 2003). By exploring sensitivity of organisms to climate-related factors, we can better understand which of these parameters (or combinations thereof) are most likely to affect species in the future, guiding more detailed studies of mechanism at specific locations.

From deterministic to probabilistic predictions

Second, we use deterministic approaches to better understand the role of heterogeneity (both in habitat and physiological response) in driving population dynamics and species distributions (Denny et al., 2004; Guichard et al., 2001). However, in order to be practicable, these deterministic approaches will likely need to be placed within a probabilistic framework. Much of ecology has been based on the concept of gradients in stress, the most common being a latitudinal gradient in temperature (reviewed by Harley, 2003). In fact, much of biogeography is built on the idea that latitudinal gradients in air and water temperature drive species range boundaries (Hutchins, 1947). A recent example of this is presented by Harley, who examined the upper and lower zonation limits of an intertidal alga along a well-established gradient in stress along the north coast of the Olympic Peninsula in Washington State (USA) (Harley, 2003). Harley experimentally showed that the upper zonation limit of the algae was set by stressors related to some aspect of aerial exposure, so that as one moved from west to east (along a gradient of increasing stress) the upper zonation limit of this species shifted closer to the subtidal zone. By contrast, the lower limit, set by herbivory, did not shift along this gradient. As a result, the algae were 'squeezed' at its upper end by weather, and at the point where the upper limit met the lower limit, the species met a local geographic range edge (Harley, 2003).

While gradients such as that described by Harley along the Olympic Peninsula certainly exist, they also mask considerable variability within sites, which can drive ecological processes over a range of scales (Denny et al., 2004; Erlandsson et al., 2005; Guichard et al., 2001). For sessile organisms, much of this heterogeneity in environmental stress is due to the angle and aspect of the substrate, which drives solar radiation and patterns of water and air flow (Denny et al., 2004; Guichard et al., 2001; Helmuth and Hofmann, 2001). For example, at the sites Harley examined, algae were restricted to shaded surfaces and were effectively excluded on south-facing slopes, where the upper limit again converged on the lower limit.

Whether or not this type of intrasite variability matters to organisms has still yet to be determined for most ecosystems. Schmidt et al. have shown that the variable selective regimes created by habitat heterogeneity (shaded/unshaded surfaces) maintain genetic variation in populations of barnacles (Schmidt et al., 2000). Wethey has shown that both local and geographic range limits of barnacles in New England appear to be set by both high summer and low winter temperatures, which in turn were influenced by substratum angle and orientation (Wethey, 1983). Harley found that mortality in mussels and limpets corresponded significantly to substrate orientation and the timing of low tide in summer (Harley, 2008). Using biophysical approaches and ecological forecasting models, we can predict the relative importance of heterogeneity over a nested range of spatial scales (e.g. microhabitat *vs* latitudinal). Even though a spatially explicit approach across a large scale may be unrealistic, we can

nevertheless examine frequency distributions of different habitats (such as north- *vs* south-facing slopes), or detailed measurements over smaller sections of sites, as means of predicting frequencies of different selective regimes (Benedetti-Cecchi et al., 2005; Denny et al., 2006; Guichard et al., 2001). When combined with information on physiological responses to environmental heterogeneity, probabilities of mortality, growth and reproductive failure can then be estimated over larger spatial scales. Previous studies have shown that, while detailed measurements of small-scale heterogeneity may not always be necessary for predicting higher order ecological responses, the roles of multiple scales of variability must be quantified before they can be dismissed (Deutschman et al., 1999).

The role of dispersal

Much of the importance of heterogeneity at varying scales will depend on the ability of organisms to disperse and exchange genetic material. As described previously, many geographic patterns do not occur over smooth latitudinal gradients, as previously assumed (Fig. 2). The importance of these thermal 'mosaics', which occur over the scale of tens to hundreds of kilometers, needs to be assessed within the context of larval dispersal and recruitment (Baskett et al., 2007; Kinlan et al., 2005). Evidence based on body temperature (Helmuth et al., 2006a), gene expression (Place et al., 2008) and heat-shock protein production (Sagarin and Somero, 2006) suggests that further climate change could potentially lead to disjunct populations with multiple range edges rather than smooth transitions from north to south. Importantly, levels of connectivity will likely vary not only as a function of dispersal capability but also as a function of species-specific responses to environmental conditions (Fig. 1).

Forecasting hot spots for management

While it may be difficult to assess all of the relevant parameters in detail across broad biogeographic scales, the approach described here can be used at specific sites of interest. For example, physiological information combined with predictions of climate can be used to identify potential protected areas (Hoffman, 2003; Mitchell et al., 2008). Likewise, if we predict the ideal location for crops, livestock and managed systems such as seafood, we can inform resource managers as to how best to plan for a changing world (US Environmental Protection Agency (EPA), 2008; CCSP, 2008).

Conclusion

No biologist doubts that nature is complex, and the fact that patterns of environmental signals and physiological responses vary at a range of temporal frequencies and spatial scales will surprise few. However, we are beginning to develop methods for quantifying and predicting precisely how these factors vary in space and time, and these studies have shown that variability within larger-scale gradients can play a large role in driving the physiological ecology and biogeography of species. Small-scale changes in habitat structure, for example, can lead to differences in climate-related parameters such as temperature that can exceed those observed over thousands of kilometers. The effect of organism morphology is so large that two organisms exposed to precisely the same microhabitats can experience wildly different conditions at the niche level. Similarly, meso-scale differences in environmental parameters can also lead to complex mosaics. Importantly, the effects of these processes are likely to be amplified by climate change as organisms exceed their physiological thresholds. Species

vary in their physiological responses to these environmental signals, as do individuals within populations, and rates of survival will be driven not only by absolute levels of niche-level parameters but also by the time history of exposure. While tackling this list of challenges is difficult, results suggest that if we do not account for each of these variables, we may make not only quantitatively but also qualitatively incorrect predictions of the effects of climate change on natural ecosystems. The question to ask is not just how we can possibly accomplish the challenges ahead but also what is likely to happen if we fail to include them.

Glossary

Climate
Prevailing (long-term) meteorological conditions. Averages of weather conditions of periods of approximately 30 years are used to calculate climatic conditions at a site.

Climate index
A large-scale descriptor of climate that encompasses many parameters such as rainfall, wind and air temperature. Examples include the North Atlantic Oscillation, the Southern Oscillation, and the Pacific Decadal Oscillation (see Stenseth et al., 2003).

Climate envelope model
A method that correlates observed species distributions with climate variables. While some approaches include some aspect of species' physiological responses to climate change, many assume that environmental conditions at the observed range boundary (i.e. the realized niche) are equivalent to the species' fundamental niche space (physiological tolerance) (see Pearson and Dawson, 2003).

Ecological forecasting
A deterministic approach for quantitatively predicting future patterns of abundance and distribution of organisms, and the ecological and economic consequences of these changes. The method can be validated using hindcasts of past changes in these parameters and often uses a deterministic understanding of physiological tolerances coupled with forecasted changes in climate. The approach generates the likelihood, with appropriate levels of uncertainty, of responses to climate change on a temporally and spatially explicit basis (see Clark et al., 2001).

El Niño Southern Oscillation (ENSO)
Ocean–atmosphere interactions that lead to an increase in SST along the west coast of South America. Exchanges of air between the eastern and western hemispheres (the Southern Oscillation, or SO) are closely linked to El Niño events, although changes in SST may occur without changes in the SO (see Stenseth et al., 2003).

Environmental signal analysis
A method for searching for quantitative associations between fluctuations in large-scale environmental parameters (signals), signals at the level of the niche, and responses at the physiological scale. For example, a time-series analysis (cross-correlation or cross-covariance) of environmental signals *vs* physiological responses might indicate that an organism 'filters out' some frequency components of the signal but responds to changes over longer time scales. Conversely, response to high-frequency changes indicates that organisms respond rapidly to environmental change. These relationships can then be used to generate hypotheses regarding the transfer of signals across scales.

Macrophysiology
Measured variation in physiological traits over large temporal and spatial scales (see Chown et al., 2004).

North Atlantic Oscillation (NAO)
A north–south (meridional) oscillation in atmospheric mass alternating between a high-pressure center over the Azores and a sub-polar low-pressure center over Iceland. During positive NAO conditions, westerly winds track further to the north, causing milder conditions in northern Europe and colder conditions in Southern Europe (see Stenseth et al., 2003).

Pacific Decadal Oscillation (PDO)
Pattern of ocean–atmosphere climate variability that occurs in the mid-latitude Pacific Ocean, generally over time scales of 20–30 years. During a warm (positive) phase, the western Pacific becomes cooler and parts of the Eastern Pacific become warmer. The opposite pattern occurs during a cool (negative) phase (see Mantua et al., 1997).

Sea surface temperature (SST)
Measurements of water temperature at the upper skin of the ocean's surface; when measured by remote sensing instruments, SST measurements reflect the temperature of the upper few millimeters of the ocean; when measured by buoy, surface temperature is an indication of the water temperature of the depth of the sensor, usually at 1–2 m.

Weather
Short-term (real-time) fluctuations in parameters such as wind, rainfall, air temperature and water temperature.

References

Aronson, R. B., Thatje, S., Clarke, A., Peck, L. S., Blake, D. B., Wilga, C. D. and Seibel, B. A. (2007). Climate change and invasibility of the Antarctic benthos. *Annu. Rev. Ecol. Evol. Syst.* **38**, 129-154.

Baskett, M. L., Weitz, J. S. and Levin, S. A. (2007). The evolution of dispersal in reserve networks. *Am. Nat.* **170**, 59-78.

Benedetti-Cecchi, L., Bertocci, I., Vaselli, S. and 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., Szathmary, P. L., Mislan, K. A. S., Blanchette, C. A. and Helmuth, B. (2009). Predator-prey interactions under climate change: the importance of habitat vs body temperature. *Oikos* **118**, 219-224.

CCSP (2008). The effects of climate change on agriculture, land resources, water resources, and biodiversity. A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research. Washington, DC: U.S. Environmental Protection Agency.

Chown, S. L., Gaston, K. J. and Robinson, D. (2004). Macrophysiology: large-scale patterns in physiological traits and their ecological implications. *Funct. Ecol.* **18**, 159-167.

Clark, J. S., Carpenter, S. R., Barber, M., Collins, S., Dobson, A., Foley, J. A., Lodge, D. M., Pascual, M., Pielke, R., Pizer, W. et al. (2001). Ecological forecasts: an emerging imperative. *Science* **293**, 657-660.

Costa, D. P. and Sinervo, B. (2004). Field physiology: physiological insights from animals in nature. *Annu. Rev. Physiol.* **66**, 209-238.

Dahlhoff, E. P. (2004). Biochemical indicators of stress and metabolism: applications for marine ecological studies. *Annu. Rev. Physiol.* **66**, 183-207.

Denny, M. W. and 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., Helmuth, B., Leonard, G. H., Harley, C. D. G., Hunt, L. J. H. and 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. and Harley, C. D. G. (2006). Thermal stress on intertidal limpets: long-term hindcasts and lethal limits. *J. Exp. Biol.* **209**, 2420-2431.

Deutschman, D. H., Levin, S. A. and Pacala, S. W. (1999). Propagation in a forest succession model: the role of fine-scale heterogeneity in light. *Ecology* **80**, 1927-1943.

Erlandsson, J. and McQuaid, C. D. (2004). Spatial structure of recruitment in the mussel *Perna perna* at local scales: effects of adults, algae and recruit size. *Mar. Ecol. Prog. Ser.* **267**, 173-185.

Erlandsson, J., McQuaid, C. D. and Kostylev, V. E. (2005). Contrasting spatial heterogeneity of sessile organisms within mussel (*Perna perna* L.) beds in relation to topographic variability. *J. Exp. Mar. Biol. Ecol.* **314**, 79-97.

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.

Forchhammer, M. C. and Post, E. (2004). Using large-scale climate indices in climate change ecology studies. *Popul. Ecol.* **46**, 1-12.

Gilman, S. E., Wethey, D. S. and Helmuth, B. (2006). Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. *Proc. Natl. Acad. Sci. USA* **103**, 9560-9565.

Gleeson, M. W. and Strong, A. E. (1995). Applying MCSST to coral reef bleaching. *Adv. Space Res.* **16**, 151-154.

Gracey, A. Y. and Cossins, A. R. (2003). Application of microarray technology in environmental and comparative physiology. *Annu. Rev. Physiol.* **65**, 231-259.

Gracey, A. Y., Chaney, M. L., Boomhower, J. P., Tyburczy, W. R., Connor, K. and Somero, G. N. (2008). Rhythms in gene expression in a fluctuating intertidal environment. *Curr. Biol.* **18**, 1-7.

Guichard, F., Bourget, E. and Robert, J. L. (2001). Scaling the influence of topographic heterogeneity on intertidal benthic communities: alternate trajectories mediated by hydrodynamics and shading. *Mar. Ecol. Prog. Ser.* **217**, 27-41.

Hallett, T. B., Coulson, T., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M. and Grenfell, B. T. (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* **430**, 71-75.

Harley, C. D. G. (2003). Abiotic stress and herbivory interact to set range limits across a two-dimensional stress gradient. *Ecology* **84**, 1477-1488.

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. and 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.

Helmuth, B. S. T. (1998). Intertidal mussel microclimates: predicting the body temperature of a sessile invertebrate. *Ecol. Monogr.* **68**, 51-74.

Helmuth, B. (2002). How do we measure the environment? Linking intertidal thermal physiology and ecology through biophysics. *Integr. Comp. Biol.* **42**, 837-845.

Helmuth, B. S. T. and 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. and Blanchette, C. (2002). Climate change and latitudinal patterns of intertidal thermal stress. *Science* **298**, 1015-1017.

Helmuth, B., Carrington, E. and Kingsolver, J. G. (2005). Biophysics, physiological ecology, and climate change: does mechanism matter? *Annu. Rev. Physiol.* **67**, 177-201.

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. and Strickland, D. (2006a). Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. *Ecol. Monogr.* **76**, 461-479.

Helmuth, B., Mieszkowska, N., Moore, P. and Hawkins, S. J. (2006b). Living on the edge of two changing worlds: forecasting the response of rocky intertidal ecosystems to climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 373-404.

Hilbish, T. J. (1981). Latitudinal variation in freezing tolerance of *Melampus bidentatus* (Say) (Gastropoda: Pulmonata). *J. Exp. Mar. Biol. Ecol.* **52**, 283-297.

Hoffman, J. (2003). Temperate marine. In *Buying Time: A User's Manual For Building Resistance and Resilience to Climate Change in Natural Systems* (ed. L. J. Hansen, J. L. Biringer and J. R. Hoffman), pp. 123-155. Switzerland: WWF.

Hofmann, G. E. and Gaines, S. D. (2008). New tools to met new challenges: emerging technologies for managing marine ecosystems for resilience. *Bioscience* **58**, 43-52.

Hofmann, G. E. and Place, S. P. (2007). Genomics-enables research in marine ecology: challenges, risks and pay-offs. *Mar. Ecol. Prog. Ser.* **332**, 249-255.

Hummel, H., Bogaards, R. H., Bachelet, G., Caron, F., Sola, J. C. and Amiard-Triquet, C. (2000). The respiratory performance and survival of the bivalve *Macoma balthica* (L.) at the southern limit of its distribution area: a translocation experiment. *J. Exp. Mar. Biol. Ecol.* **251**, 85-102.

Hutchins, L. W. (1947). The bases for temperature zonation in geographical distribution. *Ecol. Monogr.* **17**, 325-335.

IPCC (2007). Climate change 2007: the physical science basis. Contribution of Working Group 1 to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK and New York, NY, USA: Cambridge University Press.

Jimenez, I. M., Kühl, M., Larkum, A. W. D. and 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.

Kearney, M. (2006). Habitat, environment and niche: what are we modelling? *Oikos* **115**, 186-191.

Kearney, M., Phillips, B. L., Tracy, C. R., Christian, K. A., Betts, G. and Porter, W. P. (2008). Modelling species distributions without using species distributions: the cane toad in Australia under current and future climates. *Ecography* **31**, 423-434.

Kinlan, B. P., Gaines, S. D. and Lester, S. E. (2005). Propagule dispersal and the scales of marine community process. *Divers. Distrib.* **11**, 139-148.

Koehl, M. A. R. and Wolcott, B. D. (2004). Can function at the organism level explain ecological patterns? *Ecology* **85**, 1808-1810.

Leichter, J. J., Helmuth, B. and 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.

Leslie, H. M., Breck, E. N., Chan, F., Lubchenco, J. and Menge, B. A. (2005). Reproductive hotspots linked to nearshore ocean condtions. *Proc. Natl. Acad. Sci. USA* **102**, 10534-10539.

Magnuson, J. J. (1991). Fish and fisheries ecology. *Ecol. Appl.* **1**, 13-26.

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M. and Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteor. Soc.* **78**, 1069-1079.

Menge, B. A., Olson, A. M. and Dahlhoff, E. P. (2002). Environmental stress, bottom-up effects, and community dynamics: Integrating molecular-physiological with ecological approaches. *Integr. Comp. Biol.* **42**, 892-908.

Mitchell, N. J., Kearney, M. R., Nelson, N. J. and Porter, W. P. (2008). Predicting the fate of a living fossil: how will global warming affect sex determination and hatching phenology in tuatara? *Proc. Biol. Sci.* **275**, 2185-2193.

Nathan, R., Sapir, N., Trakhtenbrot, A., Katul, G. G., Bohrer, G., Otte, M., Avissar, R., Soons, M. B., Horn, H., Wikelski, M. et al. (2005). Long-distance biological transport processes through the air: can nature's complexity be unfolded *in silico*? *Divers. Distrib.* **11**, 131-137.

Paine, R. T. (1974). Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* **15**, 93-120.

Parmesan, C., Gaines, S., Gonzalez, L., Kaufman, D. M., Kingsolver, J., Peterson, A. T. and Sagarin, R. (2005). Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos* **108**, 58-75.

Patterson, M. R. (1992). A chemical engineering view of cnidarian symbioses. *Am. Zool.* **32**, 566-582.

Pearson, R. G. and Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* **12**, 361-371.

Petes, L. E., Menge, B. A. and Murphy, G. D. (2007). Environmental stress decreases survival, growth, and reproduction in New Zealand mussels. *J. Exp. Mar. Biol. Ecol.* **351**, 83-91.

Petes, L. E., Mouchka, M. E., Milston-Clements, R. H., Momoda, T. S. and Menge, B. A. (2008). Effects of environmental stress on intertidal mussels and their sea star predators. *Oecologia* **156**, 671-680.

Pfister, C. A., Wootton, J. T. and Neufield, C. J. (2007). Relative roles of coastal and oceanic processes in determining physical and chemical characteristics of an intensively sampled nearshore system. *Limnol. Oceanogr.* **52**, 1767-1775.

Phillips, B., Chipperfield, J. D. and Kearney, M. R. (2008). The toad ahead: challenges of modelling the range and spread of an invasive species. *Wildl. Res.* **35**, 222-234.

Pincebourde, S., Sanford, E. and Helmuth, B. (2008). Body temperature during low tide alters the feeding performance of a top intertidal predator. *Limnol. Oceanogr.* **53**, 1562-1573.

Place, S. P., O'Donnell, M. J. and 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., Sabo, J. L., Tracy, C. R., Reichman, O. J. and Ramankutty, N. (2002). Physiology on a landscape scale: plant-animal interactions. *Integr. Comp. Biol.* **42**, 431-453.

Pörtner, H. O. (2002). Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comp. Biochem. Physiol.* **132A**, 739-761.

Pörtner, H. O. and Farrell, A. P. (2008). Physiology and climate change. *Nature* **322**, 690-692.

Richardson, A. J. and Poloczanska, E. S. (2008). Under-resourced, under threat. *Science* **320**, 1294-1295.

Sagarin, R. D. and Somero, G. N. (2006). Complex patterns of expression of heat-shock protein 70 across the southern biogeographical ranges of the intertidal mussel *Mytilus californianus* and snail *Nucella ostrina*. *J. Biogeogr.* **33**, 622-630.

Sanford, E. (2002). Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. *Integr. Comp. Biol.* **42**, 881-891.

Schmidt, P. S., Bertness, M. D. and Rand, D. M. (2000). Environmental heterogeneity and balancing selection in the acorn barnacle Semibalanus balanoides. *Proc. Biol. Sci.* **267**, 379-384.

Schneider, K. R., Wethey, D. S., Helmuth, B. S. T. and Hilbish, T. J. (2005). Implications of movement behavior on mussel dislodgement: exogenous selection in a *Mytilus* spp. hybrid zone. *Mar. Biol.* **146**, 333-343.

Sebens, K. P., Grace, S. P., Helmuth, B., Maney, E. J., Jr and Miles, J. S. (1998). Water flow and prey capture by three scleractinian corals, *Madracis mirabilis, Montastrea cavernosa* and *Porites porites*, in a field enclosure. *Mar. Biol.* **131**, 347-360.

Somero, G. N. (2005). Linking biogeography to physiology: evolutionary and acclimatory adjustments of thermal limits. *Front. Zool.* **2**, 1.

Southward, A. J. (1958). Note on the temperature tolerances of some intertidal animals in relation to environmental temperatures and geographical distribution. *J. Mar. Biol. Assoc. UK* **37**, 49-66.

Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K.-S., Yoccoz, N. G. and Adlandsvik, B. (2003). Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc. Biol. Sci.* **270**, 2087-2096.

Stillman, J. (2003). Acclimation capacity underlies susceptibility to climate change. *Science* **301**, 65.

Stillman, J. and Somero, G. N. (2000). A comparative analysis of the upper thermal tolerance limits of eastern Pacific porcelain crabs, genus *Petrolisthes*: influences of latitude, vertical zonation, acclimation, and phylogeny. *Physiol. Biochem. Zool.* **73**, 200-208.

Tomanek, L. and Somero, G. N. (2000). Time course and magnitude of synthesis of heat-shock proteins in congeneric marine snails (Genus *Tegula*) from different tidal heights. *Physiol. Biochem. Zool.* **73**, 249-256.

US Environmental Protection Agency (EPA) (2008). Effects of climate change for aquatic invasive species and implications for management and research, 337pp. Washington, DC: National Center for Environmental Assessment.

Wethey, D. S. (1983). Geographic limits and local zonation: the barnacles *Semibalanus (Balanus)* and *Chthamalus* in New England. *Biol. Bull.* **165**, 330-341.

Wethey, D. S. (2002). Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. *Integr. Comp. Biol.* **42**, 872-880.

Wethey, D. S. and Woodin, S. A. (2008). Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. *Hydrobiologia* **606**, 139-151.

Wiens, J. A., Milne, B. T. (1989). Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landsc. Ecol.* **3**, 87-96.

Wikelski, M. and Cooke, S. J. (2006). Conservation physiology. *Trends Ecol. Evol.* **21**, 38-46.

Williams, G. A. and Morritt, D. (1995). Habitat partitioning and thermal tolerance in a tropical limpet, *Cellana grata*. *Mar. Ecol. Prog. Ser.* **124**, 89-103.

Winter, A., Appeldoorn, R. S., Bruckner, A., Williams, E. H. J. and Goenaga, C. (1998). Sea surface temperatures and coral reef bleaching off La Parguera, Puerto Rico (northeastern Caribbean Sea). *Coral Reefs* **17**, 377-382.