



Predator–prey interactions under climate change: the importance of habitat vs body temperature

B. R. Broitman, P. L. Szathmary, K. A. S. Mislán, C. A. Blanchette and B. Helmuth

B. R. Broitman (*broitman@nceas.ucsb.edu*), National Center for Ecological Analysis and Synthesis, State St. 735, Suite 300, Santa Barbara, CA 93101, USA, and Centro de Estudios Avanzados de Zonas Áridas (CEAZA), Facultad de Ciencias del Mar, Univ. Católica del Norte, Larrondo 1281, Coquimbo, Chile. – P. L. Szathmary, K. A. S. Mislán and B. Helmuth, Dept of Biological Sciences, Univ. of South Carolina, Columbia, SC 29208, USA. – C. A. Blanchette, Marine Science Inst., Univ. of California-Santa Barbara, Santa Barbara, CA 93106, USA.

Habitat temperature is often assumed to serve as an effective proxy for organism body temperature when making predictions of species distributions under future climate change. However, the determinants of body temperature are complex, and organisms in identical microhabitats can occupy radically different thermal niches. This can have major implications of our understanding of how thermal stress modulates predator–prey relationships under field conditions. Using body temperature data from four different sites on Santa Cruz Island, California, we show that at two sites the body temperatures of a keystone predator (the seastar *Pisaster ochraceus*) and its prey (the mussel *Mytilus californianus*) followed very different trajectories, even though both animals occupied identical microhabitats. At the other two sites, body temperatures of predator and prey were closely coupled across a range of scales. The dynamical differences between predator and prey body temperatures depended on the location of pairs of sites, at the extremes of a persistent landscape-scale weather pattern observed across the island. Thus, the well understood predator–prey interaction between *Pisaster* and *Mytilus* cannot be predicted based on habitat-level information alone, as is now commonly attempted with landscape-level ('climate envelope') models.

The temperature of a plant or animal's body can affect virtually all of its physiological processes (Buckley et al. 2001, Somero 2005). These cellular and subcellular-level processes in turn have cascading effects on the distribution and abundance of organisms and populations and the functioning of ecosystems, and have been the focus of ecological investigation for decades. Moreover, understanding the role of body temperature in driving patterns of organism distribution has taken on a new urgency in the face of global climate change (IPCC 2007) and a pressing need to forecast the impacts of climate change on natural ecosystems (Clark et al. 2001, Helmuth et al. 2006b). This need has given rise to a number of both mechanistic and statistically-based approaches, all with the common goal of explicitly hindcasting and/or forecasting the impacts of climate change on patterns of species distributions and organism abundances (Stockwell and Peters 1999, Porter et al. 2000, Hugall et al. 2002, Pearson and Dawson 2003, Kearney and Porter 2004, Pörtner and Knust 2007).

One of the most commonly used approaches (the 'climate envelope' method) relies on correlations between environmental variables (parameters such as air or water temperature) observed at the current edges of a species range boundary to estimate a species fundamental niche space (Hugall et al. 2002). By extrapolating to future climatic conditions, these approaches predict future range

boundaries by assuming that the current range edge is set by some aspect of climate. Even many individual-based approaches still rely on habitat temperature (usually surface or air temperature) as a starting point, and then predict operative body temperature based on correlation (Buckley et al. 2008, but see Kearney and Porter 2004 for a more mechanistic approach).

As emphasized by Kearney (2006), such 'climate envelope' methods generally assume that aspects of the habitat (such as air or surface temperature) are equivalent to axes of the organism's fundamental niche space (such as body temperature), thus ignoring any details of the organism's interaction with the surrounding environment. In other words, not only is the organism's realized niche space assumed to equal its fundamental niche space, but no consideration is given to the organism itself: estimates of organisms' fitness are based solely on the characteristics of current and future habitat conditions. It has long been known that the body temperatures of ectothermic organisms are driven by multiple, interacting climatic parameters and are often quite different from the temperature of the surrounding air or substrate (Porter and Gates 1969, Stevenson 1985, Huey et al. 1989). The flux of heat to and from an organism is affected by its size, color, morphology, and material properties, and two different ectothermic species exposed to identical climatic conditions

can experience markedly different body temperatures (Porter and Gates 1969, Helmuth 2002). As a result, not only are measurements of habitat temperature (e.g. air or surface temperature) insufficient proxies of a species thermal niche but they also are highly unlikely to serve as effective proxies for the current or future body temperature of more than one species (Helmuth 2002, Fitzhenry et al. 2004). While methods that estimate body temperature based on habitat temperature do allow different offsets for each species, they nevertheless assume that organism body temperature varies linearly with habitat temperature, and that this offset is constant from site to site. In other words, they are based on correlations with habitat temperature.

Recent studies have shown that predictions of the impacts of weather and climate on organismal distributions are fundamentally different when these predictions are based on body temperature rather than on environmental parameters (Hallett et al. 2004, Helmuth et al. 2006a, 2006b). Understanding the effects of weather and climate in driving body temperature is particularly important when examining predator–prey interactions (Durant et al. 2007, Pincebourde et al. 2008). While several recent studies have made significant advances to mechanistically model the effects of climate, and climate change, on the current and future distribution of species ranges by including the direct physiological effects of climate (Porter et al. 2000, Kearney and Porter 2004) we are just beginning to understand some of the indirect effects of climate on species interactions (Sanford 1999, 2002, Pincebourde et al. 2008). Specifically, most predictions of the effects of climate change on species distributions, and indeed most ecological studies, base estimates of climate-influenced predator–prey interactions on measurements of habitat temperature. Here we show that the relative difference in body temperature between a predator and its prey varies significantly – both quantitatively and qualitatively – between sites despite exposure to identical microhabitat conditions at each site. Importantly, these patterns are unlikely to be predictable in space and time without a mechanistic understanding that includes some prediction or direct measurement of their actual body temperatures in the field. Our results highlight the importance of considering the interaction of an organism’s morphology and thermal properties with its surrounding environment in determining body temperature, as well as an organism’s physiological response to temperature when forecasting ecological responses to environmental stress. Moreover, they uncover strong landscape-scale variability in the degree to which predators and their prey are coupled in their thermal responses to their ambient thermal environments.

Methods

Study site and organisms

The California mussel, *Mytilus californianus* (hereafter *Mytilus*) forms dense beds in the mid-intertidal zones of rocky shores from Alaska to Baja and is a primary prey species for the predatory seastar, *Pisaster ochraceus* (hereafter *Pisaster*) (Paine 1974, Menge et al. 1994). In the absence of predation or disturbances to control its population size,

Mytilus has been shown to expand its distribution and out-compete all plant and animal species from most of the intertidal zone (Paine 1974, Robles et al. 1995). Unlike *Mytilus*, which is sessile and cannot escape thermal stress, *Pisaster* is mobile. Many intertidal predators show little or no movement during low tide (Newell 1973), and *Pisaster* in particular are inactive during low tide (Robles et al. 1995). Robles et al. (1995) found that *Pisaster* move upshore with the incoming tide to feed and then move downshore before the tide recedes again. They also found that *Pisaster* can move >3 m vertically and >10 m along the rock surface during a single tide before returning to low intertidal levels to rest during low tide. The potential for behavioral thermoregulation in *Pisaster* could thus greatly impact the consumer–resource dynamics, a process that has recently been observed in the interaction between grazing limpets and seaweeds in other intertidal systems (Harley 2003).

We examined temporal and spatial patterns in the body temperature of *Pisaster* and *Mytilus* body temperatures at four sites around Santa Cruz Island, California. Santa Cruz Island is the largest of the Northern California Channel Islands and is located in a region of high oceanographic variability in the Santa Barbara Channel on the northern portion of the Southern California Bight (Fig. 1). A persistent thermal gradient exists along the channel where higher sea surface temperatures in the southeastern portion of the channel are associated with the influx of north-flowing warm subtropical water. On the northwestern part of the channel, equatorward, upwelling-favorable winds are topographically intensified around Point Conception, and much cooler ocean temperatures prevail due to the intense advection of cold water from the nearby Point Conception and Point Arguello upwelling centers (Winant et al. 2003). These oceanic characteristics produce persistent differences in ocean temperature ($\sim 2^{\circ}\text{C}$) and fog formation between the southeastern and northwestern sides of the island

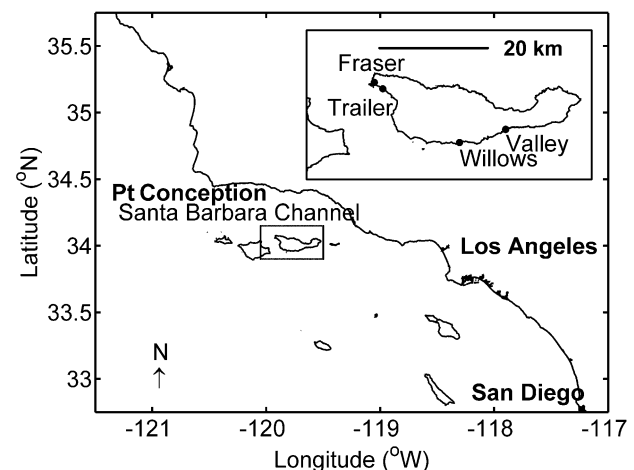


Figure 1. Location of the four study sites around Santa Cruz Island. The sites represent extremes along a steep gradient in oceanographic conditions observed along the island shores with sites located on the western end of the island (Fraser and Trailer) experiencing cooler ocean temperatures than the sites located on the southwestern side (Valley and Willows). Detailed sea surface temperature satellite imagery highlighting the thermal gradient can be found at Otero and Siegel (Otero and Siegel 2004).

(Broitman et al. 2005, Fischer and Still 2007). We selected four intertidal study sites that represent the extremes of this environmental gradient (Fig. 1, inset): two sites on the northwest shore of the island (Fraser and Trailer) and two on the southeastern shore (Willows and Valley). The number and locations of sites were limited by accessibility and other logistical constraints, and sites were selected to be as similar as possible in terms of geomorphology, wave exposure, and habitat type.

Instrumentation

We recorded temperatures corresponding to the body temperatures of *Mytilus* and *Pisaster* using pairs of biomimetic temperature loggers during the Boreal summer of 2006 (12 July to 10 October). As is true for the temperature of an organism's body, the temperature recorded by a sensor is significantly affected by the morphology, surface color, wetness and thermal properties (thermal inertia) of the instrument, and failure to match these characteristics to those of the intertidal animal of interest have been shown to lead to errors of 14°C or more (Fitzhenry et al. 2004). We thus used sensors designed to match the thermal characteristics of *Mytilus* and *Pisaster*. These instruments have previously been shown to record temperatures that are within 2–2.5 and 1°C of adjacent mussels and seastars, respectively (Fitzhenry et al. 2004, Szathmary et al. in press). Loggers were located in the mid intertidal zone, corresponding to the tidal elevations where maximal densities of each species are observed in the field (Blanchette et al. 2006). Loggers recorded temperature every 30 min and were serviced every ~40 days. In the case of seastar biomimetic loggers, the microhabitat location of sensors was intended to mimic the temperatures of animals aerially exposed while they are feeding on mussels rather than when they are concealed in crevices (Pincebourde et al. 2008). Thus, whenever possible, seastar loggers were deployed directly adjacent to biomimetic sensors mimicking mussel body temperatures so that each sensor was exposed to similar microhabitat conditions. In all, cases pairs of seastar and mussel loggers were deployed within ~20 cm vertical elevation of one another at each site. Biomimetic loggers were sometimes lost haphazardly across sites and were replaced during the next visit to the site.

Data analysis

The primary goal of our study was to determine if subtle variations in local weather affected body temperatures of predator and prey differently at each of four different sites on Santa Cruz Island. We were not able to perform a spectral analysis to establish the pattern of dynamical coupling between both records using the cross-coherence function because of repeated instrument loss and the short study period (Bendat and Piersol 1986). Alternatively, we examined the temporal cross-covariance between the body temperatures of *Mytilus* relative to the body temperatures of *Pisaster* at multiple temporal scales (i.e. frequencies). To remove serial correlation, we transformed all temperature

time series to anomalies through first-order differencing before calculating statistics (Helmuth et al. 2006a). We examined patterns of thermal covariance over different temporal scales filtering the time series from 0.5 to 24 h using a 30-min running-mean filter (48 scales) and calculating Kendall–Tau (R_τ) cross-correlations between seastar and mussel body temperatures lagging the filtered anomaly time series between ± 240 min (± 4 h or 8 lags back and forward in time plus lag-0, e.g. 17 lags). Negative lags in the cross-correlation correspond to the seastar temperature anomalies leading the correlation (e.g. the seastars heating or cooling before the mussels), while positive lags corresponded to the mussel temperature anomalies leading the correlation. We computed R_τ by sampling the time series at the frequencies prescribed by the filter lengths across all scales. Then, using Monte Carlo simulations, we calculated significant cross-correlations through the standard error distribution of R_τ (Sokal and Rohlf 1981). We used a Bonferroni correction for the multiple comparisons (48 time scales \times 17 lags) to adjust our significance levels accordingly ($\alpha < 0.05$). In this way, we are estimating concordance (Kruskal 1958) between the two signals at different lags and time scales, and using simulations to establish their significance and accommodate error in their measurement.

Results

The body temperature of both mussels and seastars (as recorded by biomimetic sensors) showed large amplitude fluctuations during the 40-day study period. However, the body temperatures of seastars were consistently lower than those of adjacent mussels, and their body temperature fluctuations were of smaller amplitude. As expected for intertidal ectotherms, temporal variation in body temperature was dominated by the daily cycle with ca 12 h fluctuations between daily thermal extremes. The periodicity in the detrended temperature time series was uncorrelated to the fortnightly tidal cycle at all sites (results not shown). For mussels, oscillations of approximately 8°C were observed at the beginning of the study period at the southeastern sites (Valley and Willows, Fig. 2A–B). The mean body temperature of both mussels and seastars followed a clear spatial gradient with the highest temperatures observed at the southeastern sites and the lowest at the northwestern sites. Both mean body temperature and variance in body temperature was higher for mussels than for seastars. For mussels, the largest variances were observed at the sites with the lowest means (Table 1). At the southeastern sites (Valley and Willows, Fig. 2A–B), daily fluctuations in seastar body temperature were smaller than those of their mussel prey. In contrast, at northwestern sites, where overall mean temperatures were lower (Trailer and Fraser, Fig. 2C–D), daily fluctuations were greater between the two species.

The dynamical association between temperature fluctuations showed that at the scale of sites, mussel and seastar body temperatures covary over a range of temporal scales (Fig. 3). Temporal decoupling was more pronounced at the

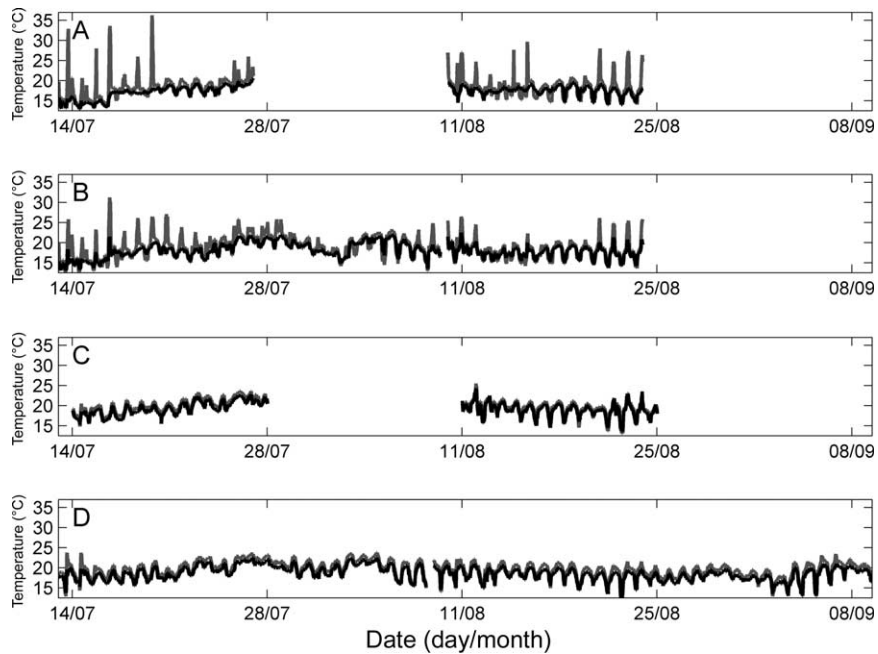


Figure 2. Temperature time series of the seastar *Pisaster ochraceus* (black lines) and the mussel *Mytilus californianus* (gray lines) during the study period (July–August 2006) at the four study sites around Santa Cruz Island in southern California. (A) Valley, (B) Willows, (C) Trailer and (D). Fraser. Note the larger amplitude of the body temperature fluctuations in the mussel. Gaps in the record are due to instrument loss.

northwestern sites, Trailer (Fig. 3C) and Fraser (Fig. 3D), where body temperatures of *Mytilus* and *Pisaster* were not correlated at scales smaller than about 6 h, and instead were restricted to the daily temperature cycle of ~ 12 h. Predator and prey body temperatures were more tightly coupled at the southeastern sites, with highly significant correlations between 1 and 24 h across a broad range of lags (Fig. 3A–B). At all sites, the body temperature of *Mytilus* led the correlations (i.e. *Mytilus* warmed or cooled before *Pisaster*), more notably at the 12-h scale. The rapid response of *Mytilus* body temperature was apparent through the prevalence of significant correlations at positive lags, particularly in the northwestern sites where temperatures were largely decoupled. The symmetrical pattern of lagged correlation at the 12-h scale observed at the northwestern sites suggested that body temperatures of *Mytilus* and *Pisaster* became coupled only during the extremes of the daily temperature cycle.

Table 1. Body temperature statistics of biomimetic sensors of (A) the seastar *Pisaster ochraceus* and (B) the mussel *Mytilus californianus*. Note that although the southeastern sites (Valley and Willows) are warmer, variances are generally larger at the cooler sites (Trailer and Fraser) for both seastars and mussels.

	Valley	Willows	Trailer	Fraser
(A) <i>Pisaster</i>				
Mean	19.053	18.444	18.007	17.209
Variance	2.964	2.948	3.462	2.208
Anomaly variance	0.156	0.132	0.125	0.082
(B) <i>Mytilus</i>				
Mean	19.752	19.411	18.726	18.289
Variance	3.230	3.831	7.198	7.139
Anomaly variance	0.167	0.174	0.529	1.210

Discussion

Our results showed that the body temperature of two ectotherms, a dominant intertidal mussel and its keystone seastar predator, can have very different temporal patterns of body temperature across sites, both in terms of maximum temperature and in level of dynamical coupling. Since we used standardized biomimetic sensors to monitor the body temperature of these two species, and controlled for microhabitat characteristics, we attribute the contrasting temperature dynamics to landscape-scale differences in climate and the interaction of climate with the thermal properties of *Mytilus* and *Pisaster* bodies. Importantly, it is highly unlikely that these impacts on predator and prey could be predicted by patterns in habitat alone, which appear to have a large impact on the prey species but only a very subtle impact on the predator.

Differences in climate between the southeast and northwest of the island are associated with the gradient in ocean temperature driven by the oceanographic transition zone around Point Conception (Winant et al. 2003). The gradient is particularly steep across Santa Cruz Island (Broitman et al. 2005), and the two extremes of the island experience different oceanic and atmospheric conditions, with the northwestern extreme being dominated by fog formation and much cooler temperatures, particularly during summer insolation maxima (Fischer and Still 2007). This landscape-level thermal and insolation gradient causes the body temperatures of both ectotherms to be tightly coupled at the warmer southeastern sites but not at the cooler northwestern sites.

Climate is a defining characteristic of these habitats, and it can be described without any reference to the organism. However, the niche space that an organism occupies has

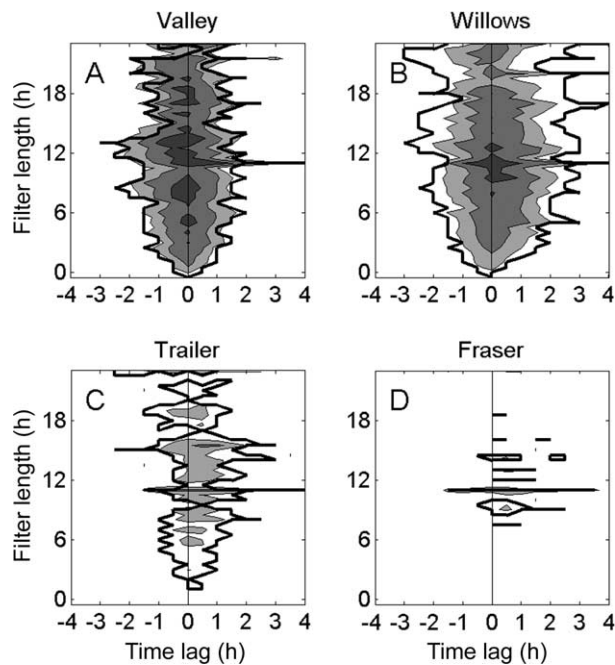


Figure 3. Kendall correlation coefficients showing the dynamical coupling between time series of body temperature anomalies of *Mytilus* and *Pisaster* at the four study sites. (A) Valley, (B) Willows, (C) Trailer and (D) Fraser. Correlations were calculated across a range of lags and filters representing scales of temporal integration. Correlations inside the black contour indicate significant correlations and the greyscale contours, from black to white, indicate the magnitude of significant correlations (0.95, 0.75, 0.65 and <0.65 , respectively). Positive lags correspond to *Mytilus* body temperature anomalies leading the correlation (*Mytilus* warming or cooling before), while negative lags indicate *Pisaster* leading. Significant correlations are always maximal around lag 0 and lag 1 showing that the *Mytilus* time series usually led the correlation. Highly significant correlations extend into positive and negative lags at the 12 h filter scale indicating that the body temperatures of both species are maximally coupled during the extremes of the daily thermal cycle. The largest degree of coupling is observed on temporal scales (filters) above one hour while in Fraser, the coolest site, temperatures are significantly coupled around the extremes of the daily cycle. Note the contrasting pattern of the overall dynamical coupling with the southeastern (warmer) sites showing greater coupling between predator and prey temperatures than the northwestern (cooler) sites.

more dimensions than climate. For example, the ‘environment’ cannot be described without reference to a particular organism (Kearney 2006). These two species occupy basically the same habitat as suggested by their overlapping biogeographic ranges and ecological characteristics, but *Pisaster* predation regulates the abundance and vertical distribution of *Mytilus* (Paine 1974, Menge et al. 1994). Also, it is necessary to understand how morphology, physiology, and especially behavior, determine the kind of environment an organism experiences when living in a particular habitat to define its niche space. *Pisaster* is mobile and has the ability to behaviorally thermoregulate, and its feeding activity can be modulated by both submerged and aerial body temperature (Szathmary et al. in press). Pincebourde et al. (2008) showed that while *Pisaster* was

unlikely to experience body temperatures close to its lethal limit (35°C) in the field (Fig. 2A), it regularly experienced temperatures that reduced feeding. Chronic exposures (>8 days) to body temperatures above 23°C resulted in a 30–40% reduction in feeding rate on mussels and concomitantly decreased rates of growth. In contrast acute exposure caused increased feeding rates. These laboratory results were supported by field measurements conducted at Bodega Bay, CA, and at Strawberry Hill, OR which showed that the number of exposures to physiologically damaging temperatures varied with tidal height (Petes et al. 2008). These results suggest that despite *Pisaster*’s ability to move, it nevertheless is exposed to varying conditions in the field, which may compromise its ability to feed (Pincebourde et al. 2008). When mussels collected from the mainland near Santa Cruz Island were exposed to a range of aerial body temperatures, mortality rates of 100% were observed for the following condition – body temperatures of 36°C for periods of 2 h or more for 3 days (Mislan unpubl.). Mussel biomimetic logger temperatures at Valley (Fig. 2A) approached 36°C once during this study suggesting that mussels can experience harmful body temperatures at some sites and not others on Santa Cruz Island which is in broad agreement with the mosaic structure of body temperature patterns of *Mytilus* along the coast of western north America (Helmuth et al. 2002, 2006a).

Habitat alone does not determine the distribution and abundance of these two species, and additional explicit mechanisms related to more than one dimension of the species’ niche may be required to understand the present and future distribution of *Mytilus* and *Pisaster*. If the predator–prey interaction is included in the calculation of the niche, one can obtain better approximation of the realized niche of either species (Hutchinson 1957, Kearney 2006). We have shown that the temporal dynamics of body temperatures of an ectothermic predator–prey pair can significantly depart under different climate scenarios. Vertical distribution of *Mytilus* may actually expand if atmospheric temperatures in the future are stressful enough to decrease *Pisaster* feeding rates but not high enough to kill *Mytilus* (Pincebourde et al. 2008). Alternatively, a milder atmospheric temperature increase can positively affect *Pisaster* feeding rates and contract *Mytilus* vertical distribution. Since the vertical distribution of *Mytilus* can have major community-level consequences (Paine 1974), a statistical model describing associations between the distributions of organisms across a landscape and bioclimatic features can be considered at best as a ‘habitat model’ (Kearney 2006). Only when interspecific interactions and their sensitivity to climate become part of the bioclimate models we may be approaching functional trait-based multispecies distribution models which are capable of reliable ecological forecasting (Kearney and Porter 2004, Kearney 2006, McGill et al. 2006).

Acknowledgements – BRB acknowledges support from the National Center for Ecological Analysis and Synthesis a Center funded by NSF (Grant no. DEB-0553768), the Univ. of California, Santa Barbara, and the State of California. BH, LS and KAS were

supported by funding from NASA NNG04GE43G and by NOAA NA04NOS4780264.

References

- Bendat, J. S. and Piersol, A. G. 1986. Random data: analysis and measurement procedures. – Wiley.
- Blanchette, C. A. et al. 2006. Intertidal community structure and oceanographic patterns around Santa Cruz Island, California, USA. – *Mar. Biol.* 149: 689–701.
- Broitman, B. R. et al. 2005. Recruitment of intertidal invertebrate and oceanographic variability at Santa Cruz Island, California. – *Limnol. Oceanogr.* 50: 1473–1479.
- Buckley, B. A. et al. 2001. Adjusting the thermostat: the threshold induction temperature for the heat-shock response in intertidal mussels (genus *Mytilus*) changes as a function of thermal history. – *J. Exp. Biol.* 204: 3571–3579.
- Buckley, L. B. et al. 2008. Thermal and energetic constraints on ectotherm abundance: a global test using lizards. – *Ecology* 89: 48–55.
- Clark, J. S. et al. 2001. Ecological forecasts: an emerging imperative. – *Science* 293: 657–660.
- Durant, J. M. et al. 2007. Climate and the match or mismatch between predator requirements and resource availability. – *Clim. Res.* 33: 271–238.
- Fischer, D. T. and Still, C. J. 2007. Evaluating patterns of fog water deposition and isotopic composition on the California Channel Islands. – *Water Resour. Res.* 43: doi:10.1029/2006WR005124.
- Fitzhenry, T. et al. 2004. Testing the effects of wave exposure, site, and behavior on intertidal mussel body temperatures: applications and limits of temperature logger design. – *Mar. Biol.* 145: 339–349.
- Hallett, T. B. et al. 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.
- Helmuth, B. 2002. How do we measure the environment? Linking intertidal thermal physiology and ecology through biophysics. – *Int. Comp. Biol.* 42: 837–845.
- Helmuth, B. S. et al. 2002. Climate change and latitudinal patterns of intertidal thermal stress. – *Science* 298: 1015–1017.
- Helmuth, B. et al. 2006a. Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. – *Ecol. Monogr.* 76: 461–479.
- Helmuth, B. et al. 2006b. Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. – *Annu. Rev. Ecol. Syst.* 37: 373–404.
- Huey, R. et al. 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. – *Ecology* 70: 931–944.
- Hugall, A. et al. 2002. Reconciling paleodistribution models and comparative phylogeography in the wet tropics rainforest land snail *Gnarosiphia bellendenkerensis* (Brazier 1875). – *Proc. Natl Acad. Sci. USA* 99: 6112–6117.
- Hutchinson, G. E. 1957. Concluding remarks. – *Cold Spring Harbour Symp. Quant. Biol.* 22: 415–427.
- IPCC 2007. Climate Change 2007: The physical science basis. Contribution of Working Group I to the 4th Assessment Rep. of the Intergovernmental Panel on Climate Change. – Camb. Univ. Press.
- Kearney, M. 2006. Habitat, environment and niche: what are we modelling? – *Oikos* 115: 186–191.
- Kearney, M. and Porter, W. P. 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. – *Ecology* 85: 3119–3131.
- Kruskal, W. H. 1958. Ordinal measures of association. – *J. Am. Stat. Assoc.* 53: 814–861.
- McGill, B. J. et al. 2006. Rebuilding community ecology from functional traits. – *Trends Ecol. Evol.* 21: 178–185.
- Menge, B. A. et al. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. – *Ecol. Monogr.* 64: 249–286.
- Newell, R. C. 1973. Factors affecting the respiration of intertidal invertebrates. – *Int. Comp. Biol.* 13: 513–528.
- Otero, M. P. and Siegel, D. A. 2004. Spatial and temporal characteristics of sediment and phytoplankton blooms in the Santa Barbara Channel. – *Deep Sea Res. II* 51: 1129–1149.
- Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. – *Oecologia* 15: 93–120.
- Pearson, R. G. and Dawson, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? – *Global Ecol. Biogeogr.* 12: 361–371.
- Petes, L. E. et al. 2008. Effects of environmental stress on intertidal mussels and their seastar predators. – *Oecologia* 156: 671–680.
- Pincebourde, S. et al. 2008. Body temperature during low tide alters the feeding performance of a top intertidal predator. – *Limnol. Oceanogr.* 23: 1562–1573.
- Porter, W. P. and Gates, D. M. 1969. Thermodynamic equilibria of animals with environment. – *Ecol. Monogr.* 39: 245–270.
- Porter, W. P. et al. 2000. Calculating climate effects on birds and mammals: impacts on biodiversity, conservation, population parameters, and global community structure. – *Am. Zool.* 40: 597–630.
- Pörtner, H. O. and Knust, R. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. – *Science* 315: 95–97.
- Robles, C. et al. 1995. Responses of a key intertidal predator to varying recruitment of its prey. – *Ecology* 76: 565–579.
- Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. – *Science* 283: 2095–2097.
- Sanford, E. 2002. Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. – *Int. Comp. Biol.* 42: 881–891.
- Sokal, R. R. and Rohlf, F. J. 1981. Biometry. – W. H. Freeman.
- Somero, G. N. 2005. Linking biogeography to physiology: evolutionary and acclimatory adjustments of thermal limits. – *Front. Zool.* 2: doi:10.1186/1742–9994–2–1.
- Stevenson, R. D. 1985. Body size and limits to the daily range of body temperature in terrestrial ectotherms. – *Am. Nat.* 125: 102–117.
- Stockwell, D. and Peters, D. 1999. The GARP modelling system: problems and solutions to automated spatial prediction. – *Int. J. Geogr. Inf. Sci.* 13: 143–158.
- Szathmari, P. L. et al. in press. Climate change in the rocky intertidal zone: predicting and measuring the body temperature of an intertidal keystone predator. – *Mar. Ecol. Prog. Ser.*
- Winant, C. D. et al. 2003. Characteristic patterns of shelf circulation at the boundary between central and southern California. – *J. Geophys. Res.* 108: doi: 10.1029/2001JC001302.