

Themed Issue Article: Biomechanics and Climate Change

Mapping physiology: biophysical mechanisms define scales of climate change impacts

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The rocky intertidal zone is a highly dynamic and thermally variable ecosystem, where the combined influences of solar radiation, air temperature and topography can lead to differences greater than 15°C over the scale of centimetres during aerial exposure at low tide. For most intertidal organisms this small-scale heterogeneity in microclimates can have enormous influences on survival and physiological performance. However, the potential ecological importance of environmental heterogeneity in determining ecological responses to climate change remains poorly understood. We present a novel framework for generating spatially explicit models of microclimate heterogeneity and patterns of thermal physiology among interacting organisms. We used drone photogrammetry to create a topographic map (digital elevation model) at a resolution of 2 × 2 cm from an intertidal site in Massachusetts, which was then fed into a model of incident solar radiation based on sky view factor and solar position. These data were in turn used to drive a heat budget model that estimated hourly surface temperatures over the course of a year (2017). Body temperature layers were then converted to thermal performance layers for organisms, using thermal performance curves, creating 'physiological landscapes' that display spatially and temporally explicit patterns of 'microrefugia'. Our framework shows how non-linear interactions between these layers lead to predictions about organismal performance and survivorship that are distinct from those made using any individual layer (e.g. topography, temperature) alone. We propose a new metric for quantifying the 'thermal roughness' of a site (RqT, the root mean square of spatial deviations in temperature), which can be used to quantify spatial and temporal variability in temperature and performance at the site level. These methods facilitate an exploration of the role of micro-topographic variability in driving organismal vulnerability to environmental change using both spatially explicit and frequency-based approaches.

Key words: Biomechanics, ecophysiology, environmental heterogeneity, intertidal zone, microclimate, microhabitat

Editor: Frank Seebacher

Received 2 March 2019; Revised 24 April 2019; Editorial Decision 5 May 2019; Accepted 7 May 2019

Cite as: Choi F, Gouhier T, Lima F, Rilov G, Seabra R, Helmuth B (2019) Mapping physiology: biophysical mechanisms define scales of climate change impacts. *Conserv Physiol* 7(1): cozo28; doi:10.1093/conphys/coz028.

Introduction

Ongoing climate change is having clear impacts on the abundance, health and distribution of organisms and subsequently on patterns of biodiversity and ecosystem function (Doney *et al.*, 2012; Bonebrake *et al.*, 2018). In an effort to forecast and potentially mitigate some of the worst impacts of these changes, conservation biologists are increasingly turning to forecasting approaches to predict which populations and species are most vulnerable to accelerating climate change (Dong *et al.*, 2017; Sará *et al.*, 2018; Rilov *et al.*, 2019), where environmental change is occurring most rapidly (Sunday *et al.*, 2015; Brito-Morales *et al.*, 2018) and what measures might be enacted to protect threatened species and ecosystems by either reducing the effects of non-climatic stressors such as development and overharvesting (Przeslawski *et al.*, 2005; Sará *et al.*, 2018) or by prioritizing the protection of refugia (Morelli *et al.*, 2017). Laboratory- and field-based physiological methods are playing an increasingly important role in our understanding of how climate change is affecting natural and managed systems and of the range of possible conservation interventions that can be enacted (Seebacher and Franklin, 2012; Chown and Gaston, 2016; Marn *et al.*, 2017; Teal *et al.*, 2018; Rilov *et al.*, 2019).

At the same time, our ability to quantify, model and forecast the physical parameters, such as temperature, nutrients, rainfall and ocean pH, that drive these observed and projected changes continues to improve (Shukla, 1998; Maclean *et al.*, 2019). For example, the thermal limits of key species can be measured under natural and controlled temperatures and then compared against contemporary and projected patterns of ‘environmental temperature’ to estimate ‘thermal safety margins’, the difference between what an organism experiences in the field relative to its tolerance (Kingsolver, 2009; Polgar *et al.*, 2015; Bruno *et al.*, 2018). Yet there remain frequent mismatches between what are often very careful and detailed measurements of physiological vulnerability and the scale at which environmental measurements and projections are made in the field (e.g. see discussions in Sears *et al.*, 2011; Boyd *et al.*, 2016; Torossian *et al.*, 2016; Garcia *et al.*, 2019). For example, projections of vulnerability based on climatic (or even annual) means have little hope of forecasting the effects of much higher frequency variability in environmental conditions such as heat waves and cold snaps (Wetthey *et al.*, 2011a; Roitberg and Mangel, 2016), which are themselves becoming more frequent under anthropogenic climate change. Comparably, remote sensing is frequently unable to capture environmental conditions at the level of microhabitats (Sears *et al.*, 2011; Faye *et al.*, 2016; Maclean *et al.*, 2019) that ultimately drive biotic responses (Scheffers *et al.*, 2014a; Storlie *et al.*, 2014).

This study explores this fundamental disconnect (Denny and Helmuth, 2009; Helmuth *et al.*, 2010) and describes how an understanding of the mechanisms by which plants and animals interact with their physical environment (i.e.

ecophysiology) can lend insight into how these scales can be better aligned (Helmuth *et al.*, 2005; Flynn *et al.*, 2012; Harley, 2013; Scheffers *et al.*, 2014b; Jurgens and Gaylord, 2017). Specifically, we examine how biophysical approaches (photogrammetry coupled with heat budget modelling and physiological measurements) can be used to address questions of scale (Sears *et al.*, 2011), both in terms of how we measure the physical environment (Potter *et al.*, 2013; Maclean *et al.*, 2019) and of how we measure physiological, behavioural and ecological responses to environmental conditions (Flynn *et al.*, 2012; Woods *et al.*, 2015; Rebaudo *et al.*, 2016).

Scale, environmental heterogeneity and physiological response

Questions about scale and especially about the importance of environmental heterogeneity (EH) have a rich history in ecology spanning many decades (Schneider, 2001). Relationships between EH in space and time and biological parameters such as distribution, abundance, biomass, biodiversity and resilience in the face of perturbations have been explored in habitats as diverse as coral reefs (Keith *et al.*, 2013), open ocean systems (Boyd *et al.*, 2016), terrestrial forests (van Rensburg *et al.*, 2002; Morelli *et al.*, 2018), deserts (Migliore *et al.*, 2013), deep sea benthos (Williams *et al.*, 2010), seamounts (Clark *et al.*, 2012) and rocky reefs (Matias *et al.*, 2011). Understanding the role of EH in these processes has taken on new significance in this era of ongoing rapid environmental change (Boyd *et al.*, 2016; Kelly, 2019), and a number of studies have begun to explore the role that microclimates may play in mediating larger-scale climatic drivers (Sears *et al.*, 2011, 2016; Potter *et al.*, 2013; Hannah *et al.*, 2014; Maclean *et al.*, 2015). For example, sites with high levels of EH (and thus presumably species richness) may represent priority areas for conservation or similarly serve as ‘rescue sites’ following extreme events (Hanski and Ovaskainen, 2000; Roberts *et al.*, 2017). EH driven by structuring species such as bivalves and macroalgae has been shown to override large-scale geographic trends in environmental conditions (Jurgens and Gaylord, 2017), with implications for predictions of range shifts and resilience to climate change. Increasing surface complexity has also been explored as a mechanism to increase biodiversity on seawalls (Chapman and Bulleri, 2003; Loke *et al.*, 2017).

Methods for measuring structural complexity have also expanded rapidly in recent years with the easy access of small unmanned aerial systems (sUAS), i.e. ‘drones’. sUAS are now frequently used to construct digital elevation models (DEMs) and other types of 3D virtual models, providing new tools for exploring different ecological descriptors of various ecosystems. These include structural complexity in coral reefs (Gonzalez-Rivero *et al.*, 2017), habitat categorization in rocky shores (Garza, 2016) and in freshwater fish habitats (Kalacska *et al.*, 2018), species distributions and biodiversity surveys in forest ecosystems (Torossian *et al.*, 2016) and

thermal distribution in agricultural landscapes (Faye *et al.*, 2016).

An increasing number of physiological studies are similarly beginning to consider the scales over which physiological responses can vary in time and space (Dowd *et al.*, 2013; Malishev *et al.*, 2017). Dong *et al.* (2017), for example, measured cardiac function in three species of intertidal snails and showed that intraspecific variation (physiological polymorphism) in flat-line temperatures exceeded interspecific differences. They also showed that, congruently, differences in habitat temperatures within sites far exceeded differences among sites along a 12° gradient in latitude on the coast of China. Denny *et al.* (2011) reported differences in within-site microhabitat temperatures that exceeded those reported over 14° of latitude on the west coast of North America, and Seabra *et al.* (2011) found similar differences on the Iberian coast. These combinations of heterogeneity in environmental conditions (microclimates) with inter-individual variability in physiological sensitivity have significant implications for how we envision selective regimes (Schmidt *et al.*, 2000; Lawson *et al.*, 2014; Denny, 2018; Kelly, 2019), notably in ways that cannot be predicted when physiological tolerance is considered as a species trait with no inter-individual variability (e.g. Diamond *et al.*, 2012) or when an environmental parameter such as temperature is measured in one specific location and then used to represent an entire site (e.g. Enquist *et al.*, 2017).

Despite the large number of studies exploring the role of microhabitats and EH, comparatively few have quantitatively measured how structural complexity actually mediates the local microenvironments (microclimates) of plants and animals (but see e.g. Sears *et al.*, 2011; Barton and Terblanche, 2014; Kearney *et al.*, 2014; Hayford *et al.*, 2015; Pincebourde *et al.*, 2016; Jurgens and Gaylord, 2017; Maclean *et al.*, 2019). A recent meta-analysis by Ortega *et al.* (2018) showed that a majority of studies over the last two decades exploring EH/structural complexity reported a positive relationship between EH and species richness (S). However, their analysis also showed that, somewhat surprisingly, very few experiments have quantitatively explored the underlying mechanisms driving the EH and S relationship, leading them to the conclusion that this area of research was still in its ‘infancy’. Other reviews have come to similar conclusions, again pointing to a dearth of studies focused on mechanism (Kovalenko *et al.*, 2012; Loke *et al.*, 2015). This paucity of research serves as a major impediment to our understanding of how microenvironments affect community resilience to climate change (Potter *et al.*, 2013; Woods *et al.*, 2015).

To a large extent, these gaps in our understanding exist for the simple reason that modelling and measuring environmental conditions at scales that are both relevant to organismal physiology (i.e. microclimates), but that can also be applied over scales sufficient to detect biogeographic shifts in response to environmental change, are usually impractical (Bates *et al.*, 2018). Fixed sensors can record time series at a single location with high accuracy but may not be reflective of the actual spa-

tial diversity in environmental conditions (Denny *et al.*, 2011; Miller and Dowd, 2017). Infrared cameras can survey large areas (e.g. with drones) but typically can only record environmental conditions at a single point in time, unless they are mounted in place for extended periods (Scherrer and Koerner, 2010). Satellites can accomplish both feats to limited degrees but with spatial (e.g. 1–100 km²) and temporal (e.g. 6 hr) resolutions that may be irrelevant to the organism in question (Potter *et al.*, 2013; Simó *et al.*, 2016; Geller *et al.*, 2017).

A case study: rocky intertidal zones

Perhaps nowhere are the challenges inherent in measuring microclimates as apparent as in rocky intertidal zones, areas with enormous spatial and temporal variation in factors such as wave force (Helmuth and Denny, 2003), oxygen (Frieder *et al.*, 2012), pH (Hofmann *et al.*, 2011; Baumann and Smith, 2018) and, especially, temperature during aerial exposure at low tide (Denny *et al.*, 2011). Body temperature is one of the most universal determinants of a plant or animal's physiological performance and survival (Somero, 2002, 2010; Sinclair *et al.*, 2016), and the rocky intertidal zone has long served as a model ecosystem for exploring the relationship between temperature and ecological responses over local and geographic scales (Connell, 1972; Sorte *et al.*, 2019). A number of recent studies have documented that many species of intertidal invertebrates—animals whose ancestors evolved in a fully aquatic environment—currently live very close to their thermal limits (Somero, 2002; Wetthey and Woodin, 2008; Mislán *et al.*, 2014). Large-scale mortality events in response to elevated low-tide temperatures have been reported (e.g. Harley, 2008), in some cases on a recurring basis (Williams and Morritt, 1995; Firth and Williams, 2009).

Notably, it is the temperature of an organism's body that ultimately drives physiological responses and not the temperature of its surrounding environment per se. Kearney (2006) defines this as the ‘niche’ temperature, as differentiated from aspects of the ‘environment’ such as local air temperature. This distinction is not trivial, as the body temperature of ectothermic plants and animals can be very different from local air temperature, especially when exposed to direct sunlight (Fitzhenry *et al.*, 2004; Chaperon *et al.*, 2016). In air at low tide, body temperatures are driven by multiple environmental factors including solar radiation, air temperature, humidity, wind speed and cloud cover (Denny *et al.*, 2006) and are affected by the characteristics of the organism such as colour, shape, mass and material properties (Helmuth, 2002). For organisms with large areas of their body adhered to the substratum (limpets, barnacles, some snails and small mussels) body temperature usually closely tracks the temperature of the rock surface (Wetthey, 2002), which on sunny days is much hotter than the air above it. For larger animals (e.g. large bivalves) or organisms with a wetted surface (e.g. seastars) body temperatures can be substantially different from either rock or air (Broitman *et al.*, 2009; Miller and Dowd, 2017).

In terrestrial and intertidal systems, by far the most significant driver of ectotherm temperature is exposure to direct solar radiation (Helmuth, 1998; Scheffers *et al.*, 2017; Maclean *et al.*, 2019). While mortality events are often associated with episodes of high air temperature (Mislán *et al.*, 2014; Sorte *et al.*, 2019) these only occur when both air temperature is elevated and solar radiation is at a maximum; both conditions are typically required in order for large-scale mortality to occur, and thus elevated air temperature alone is an effective indicator of mortality events *only* when it occurs on cloud free days with maximum solar radiation (Gilman *et al.*, 2006; Mislán *et al.*, 2014). Because of the importance of solar radiation (Marshall *et al.*, 2010; Chapperon *et al.*, 2016), the difference in temperature between an animal on a poleward-facing (shaded) microsite and one on a nearby equatorial-facing (sunny) microsite can easily exceed 15°C (Helmuth and Hofmann, 2001; Sears *et al.*, 2011). Such large differences in thermal environments among shaded and unshaded surfaces have been shown to lead to even larger differences in physiology (Jimenez *et al.*, 2015; Miller *et al.*, 2015), survival (Harley, 2008), abundance (Meager *et al.*, 2011) and selection for different species and genotypes (Schmidt *et al.*, 2000; Schneider and Helmuth, 2007; Seabra *et al.*, 2011). This non-linear translation between small changes in body temperature and large changes in physiological performance is best conceptualized using Jensen's inequality (Martin and Huey, 2008; Denny, 2019), which further highlights the dangers of using temporal or spatial averages to predict biological responses. Over geographic scales, the presence of shaded refugia has been proposed as a mechanism that allows species to extend their range boundaries beyond what they could survive if only sunny habitats were available (Sunday *et al.*, 2014; Lima *et al.*, 2016).

Aerial temperatures at low tide in intertidal zones can often be difficult to measure. Thermocouple sensors (often used in terrestrial studies) are easily broken by wave action, and drones equipped with infrared cameras can take snapshot measurements of intertidal rock and organism temperatures but only for limited amounts of time (Lathlean *et al.*, 2012; Seuront *et al.*, 2018). Biomimic sensors have provided significant insights into the temperature that intertidal invertebrates experience (reviewed in Judge, 2018), but measurements are typically restricted by the number of sensors that can be deployed at any given site (Helmuth *et al.*, 2016) or by the duration of deployment (Denny *et al.*, 2011). However, when combined with heat budget models that use environmental inputs from weather station data or gridded (reanalysed) meteorological data (Mislán and Wetthey, 2011; Dong *et al.*, 2017), intertidal animal temperatures can be estimated over a range of scales. Several mathematical (heat budget) models are now available to convert weather data into estimates of intertidal organism temperature (Bell, 1995; Helmuth, 1998, 1999; Denny and Harley, 2006; Szathmary *et al.*, 2009; Helmuth *et al.*, 2011; Iacarella and Helmuth, 2011; Sarà *et al.*, 2011; Wetthey *et al.*, 2011b; Mislán and Wetthey, 2015;

Marshall *et al.*, 2015; Kish *et al.*, 2016; Dong *et al.*, 2017). These models range in complexity from simple regression-based approaches (Elvin and Gonor, 1979; Kish *et al.*, 2016) to much more sophisticated land surface-based models (Wetthey *et al.*, 2011b; Mislán and Wetthey, 2015).

To date, however, most heat budget models (but see Sears *et al.*, 2011; Kearney *et al.*, 2014; Dong *et al.*, 2017; Kearney and Porter, 2017; Maclean *et al.*, 2019) have tended to ignore the role of small-scale microclimates and especially the role of incident solar radiation in driving within-site variation in microhabitat temperatures. Here we present an integrative framework that utilizes DEMs and heat budget models to quantify microhabitat temperatures (Fig. 1), using a $\sim 50\text{ m} \times 100\text{ m}$ intertidal site on the Northeast coast of the US (Fort Beach in Marblehead, MA; 42.508° N, 70.843° W; Fig. 2) as a case study. Using this approach we characterize the full suite of microenvironments at this rocky intertidal site as a function of structural complexity and discuss how this approach can be used to explore the role of microclimate in driving patterns of behaviour, physiological performance and mortality. This framework includes (i) capturing fine-scale topographic data using drone photography to produce 3D models and DEMs, (ii) transforming large-scale weather data to account for surface orientation to solar radiation, (iii) identifying microhabitat temperatures using a heat budget model and (iv) comparing predictions of body temperature against thermal performance models to make spatially and temporally explicit predictions of relative physiological performance.

Spatial model framework

DEMs

In the past, fine-scale topographic data have been difficult and expensive to obtain, and DEMs were produced using methods such as real-time kinetic (RTK) Global Positioning System (GPS) mapping (Morton *et al.*, 1999; Freeman *et al.*, 2004), Light Detection and Ranging (LiDAR) (Polat and Uysal, 2015) and radar interferometry or photogrammetry methods (Colomina *et al.*, 2008; Eisenbeiss, 2009). The advancement and accessibility of sUAS have allowed some of these methods, especially photogrammetry and LiDAR, to become more accessible to field biologists (Faye *et al.*, 2016). In this framework, fine-scale topographic data are mapped using an sUAS flown at low elevations (e.g. 5 m) above ground level, in a grid format and from various directions, to capture numerous high-resolution images from a camera angle of 45°. We used this approach to capture a total of 528 photos at Fort Beach. This high number of images is needed to capture all the topographic characteristics and to allow photogrammetric methods to estimate aspects, slopes and height of these topographies at a resolution of $2 \times 2\text{ cm}$. Agisoft Photoscan Pro photogrammetry software was used to convert footage from the sUAS to 3D virtual models, which were exported as DEMs (Fig. 3). A detailed workflow

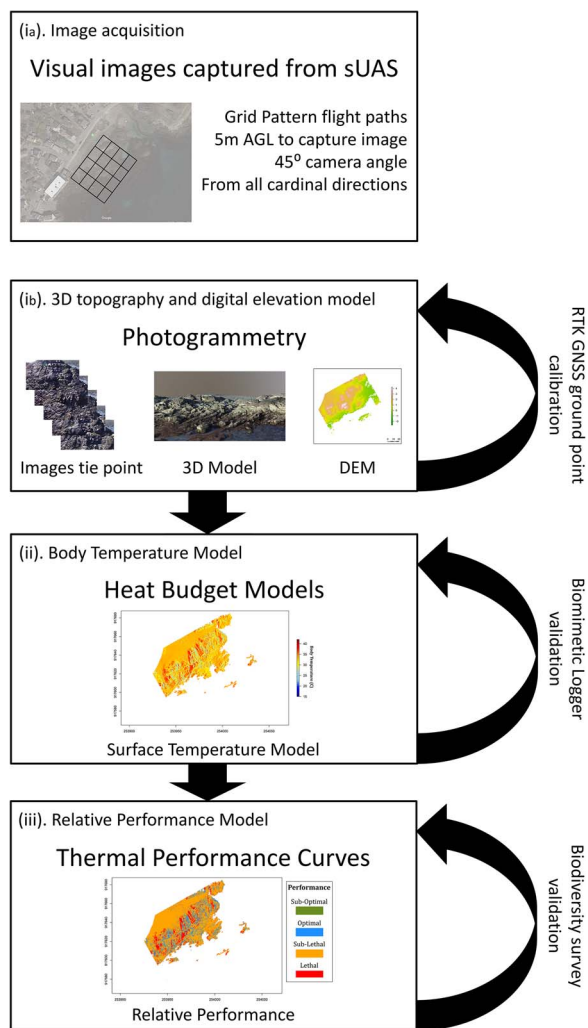


Figure 1: Systematic workflow of the integrative framework to analyse thermal landscapes. Following the framework steps: (i) create DEM through (ia) image acquisition with sUAS and (ib) image processing through photogrammetry. (ii) Estimate surface temperatures with heat budget model. Finally, (iii) estimate relative performance with thermal performance curve.

of photogrammetric methods, such as matching image tie points and generating dense point clouds, can be found in James and Robson (2012) and Faye *et al.* (2016). To provide reference points for the photogrammetry software, multiple precise (sub-centimetre accuracy) GPS coordinates, including elevation, of topographic features were recorded using a Trimble RTK global navigation satellite system. Figure 3 shows a DEM produced through photogrammetry of the Fort Beach site.

Surface temperature model

To date, most heat budget models for ecological forecasting have failed to incorporate complex topography on a



Figure 2: Fort Beach in Marblehead, MA USA (42.508° N, 70.843° W).

spatially explicit basis (but see Sears *et al.*, 2011, who used complex simulated surfaces, and Maclean *et al.*, 2019, who calculated topographic complexity at scales of ~ 10 m). The major advancement in the framework presented here is to use DEMs from actual sites to estimate direct and reflected solar radiation on each surface element at very fine spatial scales, which can then be used as inputs to a heat budget model. This approach is accomplished by downscaling total solar radiation measurements recorded from a local weather station or from (reanalysed) gridded meteorological data (Mislan and Wethey, 2011; Dong *et al.*, 2017; Maclean *et al.*, 2019) to estimate spatial and temporal distribution of solar radiation at a local level. Downscaling is a multi-step process that involves (i) generating solar geometry: plotting the locations of the sun relative to each pixel throughout the day (via latitude, azimuth and motion of the sun) and adjusting the intensity of direct solar radiation through calculations of the solar azimuth and solar zenith (Braun and Mitchell, 1983); (ii) calculating albedo effects and the atmosphere diffusion factor (Bindi *et al.*, 1992) to describe the effect of direct solar radiation entering through the atmosphere and hitting the surface; and (iii) measuring and incorporating DEM topographic variables [elevation, slope, aspect and sky view factor (SVF)] that define the distribution of solar radiation on complex topography (Tovar-Pescador *et al.*, 2006). The most complex of these parameters, the SVF, is widely used to measure shading in urban environments, by hillsides, and in forest canopies (Holmer *et al.*, 2001; Zakšek *et al.*, 2011; Polo López *et al.*, 2016; Hoylman *et al.*, 2018), but it is relatively under-utilized in heat budget modelling and ecological forecasting. Calculated by using vectors and their distances on a hemisphere per pixel, SVF represents the amount of sky each pixel is exposed to, an index from 0 to 1, where 0 is completely shaded and 1 is completely exposed to the sky (Fig. 4). Hence, this metric helps create a shade/exposed solar radiation relationship between each pixel and its neighbors (Zhang *et al.*, 2017). Incorporating SVF local shadowing

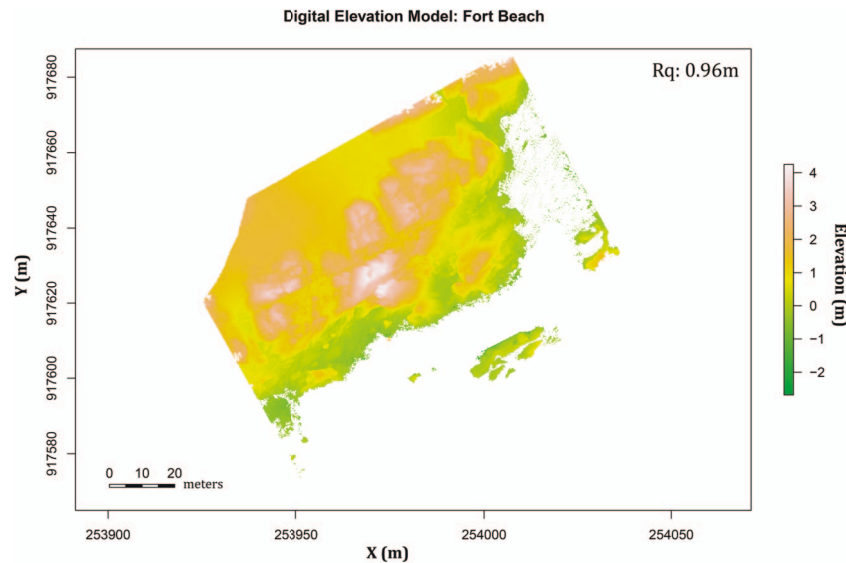


Figure 3: DEM of Fort Beach. Colours represent elevation across the model, with max elevation at 4.3 m above mean lower low water. Rq, the surface roughness, is calculated to be 0.96 m at Fort Beach. Note that blank spaces represent coverage by water at low tide.

effects into downscaling can provide a more robust model for solar radiation on complex topography (Matzarakis *et al.*, 2007; Zakšek *et al.*, 2011; Polo López *et al.*, 2016).

We downsampled solar radiation data obtained from the Climate Forecast System Reanalysis (CFSR) meteorological database (Mislán and Wethey, 2011). These downsampled data were used as inputs with other weather data from CFSR (air temperature, wind speed and water temperature) to a heat budget model (described in Dong *et al.*, 2017) to estimate surface temperature distribution spatially (sub-centimetre) and temporally (hourly) across all the microhabitats within the site. Still tidal elevation predictions (XTide; <http://www.flaterco.com/xtide/>) were used to estimate when microsites were submerged and when they were aerially exposed. This modified heat flux model (Helmuth, 1998; Dong *et al.*, 2017) was used to estimate surface temperatures across the entire rocky shore of Fort Beach (Fig. 5). We ran hourly simulations for an entire year (2017, shown in Supplement A) but here focus on the 2 days of the year with the highest surface temperature estimations, 22 June and 23 June. While these predictions were not fully validated—an exercise that would require high-resolution sampling over time using sensors and/or repeated images using infrared thermography—the results are consistent with the range of temperatures reported in past studies for other sites (Denny *et al.*, 2011; Seabra *et al.*, 2011; Dong *et al.*, 2017). During the hottest surface day in 2017 at Fort Beach (22 June), where the peak global solar radiation reached 883 Wm^{-2} , modeled surface temperatures ranged from 25.7°C to 41.4°C , consistent with the temperature range measured with *in situ* loggers from this site in sunny and shaded microhabitats (unpublished data). Notably, maximum air temperature on this day was only 27.8°C , pointing to

the importance of solar radiation. Conversely, the highest air temperature of the year occurred on 12 June (34.7°C), but surface temperature at Fort Beach remained low because most of the beach was submerged during peak solar periods (Helmuth *et al.*, 2002).

It should be noted that we used the model to estimate only rock surface temperature, which has been used as a direct proxy for the body temperature of animals with a high proportion of their body in contact with the rock, for example limpets (Seabra *et al.*, 2011) and barnacles (Wethey, 2002). For some animals, especially larger animals such as mussels (Helmuth, 1998) and seastars (Szathmary *et al.*, 2009), rock temperature is not equivalent to animal temperature, but the same approach used here can be applied on an organism-specific level by modifying model parameters (e.g. Szathmary *et al.*, 2009; Dong *et al.*, 2017). For simplicity we also assume that animals are sessile during low tide, a reasonable assumption for many organisms that ‘hunker in place’ during aerial exposure, but less realistic for other, more mobile organisms (Williams and Morritt, 1995; Monaco *et al.*, 2015). Notably, the model presented here does not include the role of water retention in tidepools or other small features of the rock surface, which could provide additional refugia through cooling from evaporation of saltwater, albeit at the potential cost of physiological stress from high salinity.

Relative performance model

The ultimate goal of the approach described here is to provide a method of mapping physiological performance and survival over space and time using DEMs. The simplest approach to doing so is to convert body temperature to some

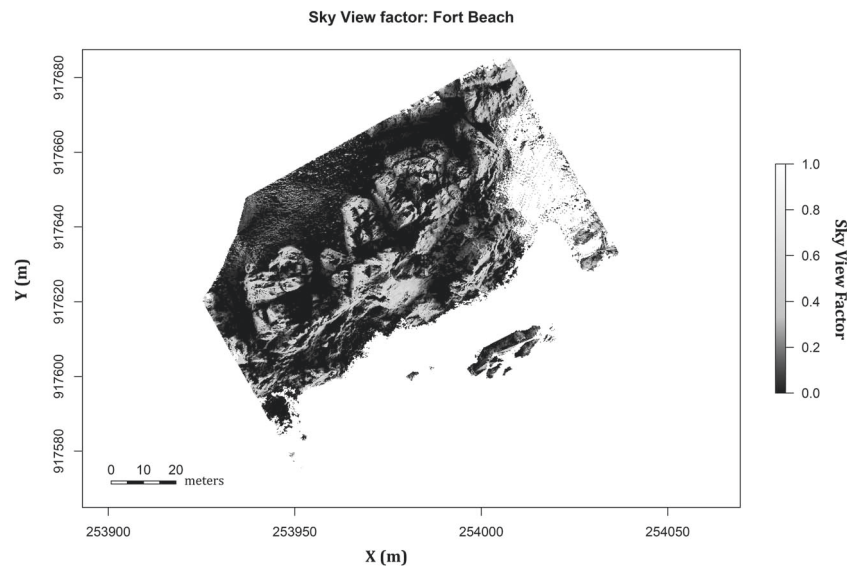


Figure 4: SVF of Fort Beach. SVF is calculated by using 32 search vectors per pixel and a maximum search radius of 5 m per vector. SVF ranges from 0 to 1 for each pixel of the map, 0 being 100% shaded and 1 being 100% exposed to the sky. Note that blank spaces represent coverage by water at low tide.

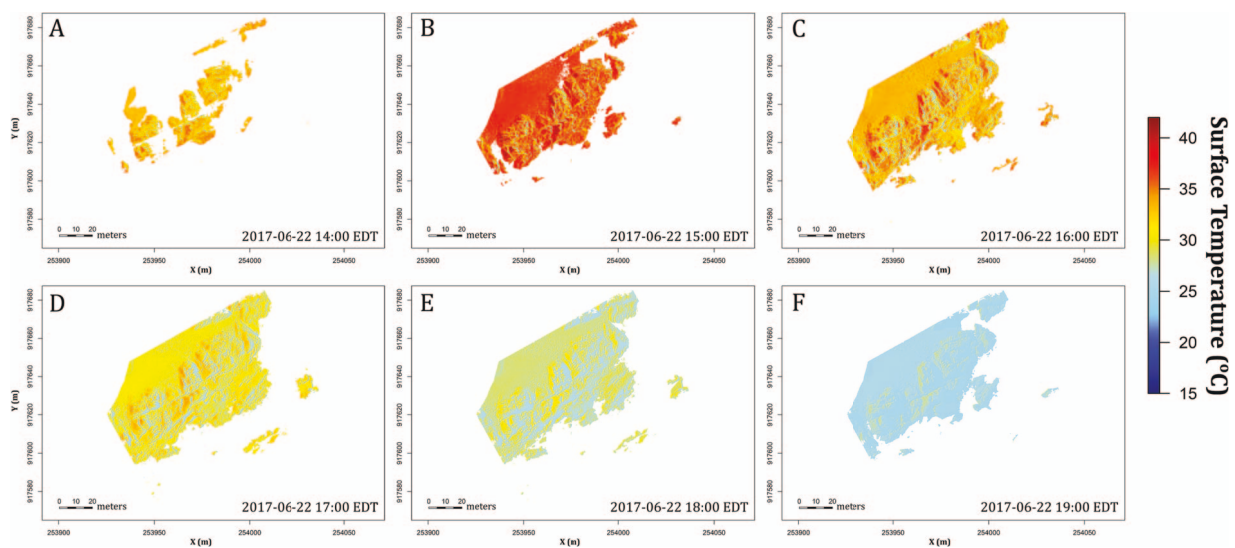


Figure 5: Surface temperature models at Fort Beach. Figure presents the low-tide period during the hottest day of 2017 (22 June) from (A) 14:00 EDT to (F) 19:00 EDT (solar noon at this location is at 13:00 EDT). Surface temperature distribution is highly variable through space and time. Note that blank spaces represent coverage by water at high tide.

metric of relative performance using a thermal performance curve (TPC), which in turn is based on indirect metrics of fitness such as respiration, movement or heart rate (Huey and Slatkin, 1976; Huey and Stevenson, 1979; Sinclair *et al.*, 2016). TPCs describe the non-linear relationship (Martin and Huey, 2008; Denny, 2017) between temperature and these physiological rates, most typically as a curve in which performance rises slowly with temperature up to an optimal level, T_{opt} , and then drops rapidly (Angilletta, 2006,

2009; Kish *et al.*, 2016) (Fig. 6). The assumption that TPCs remain constant over time (i.e. no capacity for acclimatization) or that they can be based on a single performance metric such as heart beat rate or behaviour is problematic and has been discussed by several authors (Kingsolver and Woods, 2016; Sinclair *et al.*, 2016; Stoffels *et al.*, 2016; Monaco *et al.*, 2017). However, they provide an easy first-cut approach in estimating performance based on body temperature. More sophisticated approaches could, for example, alter the spatial

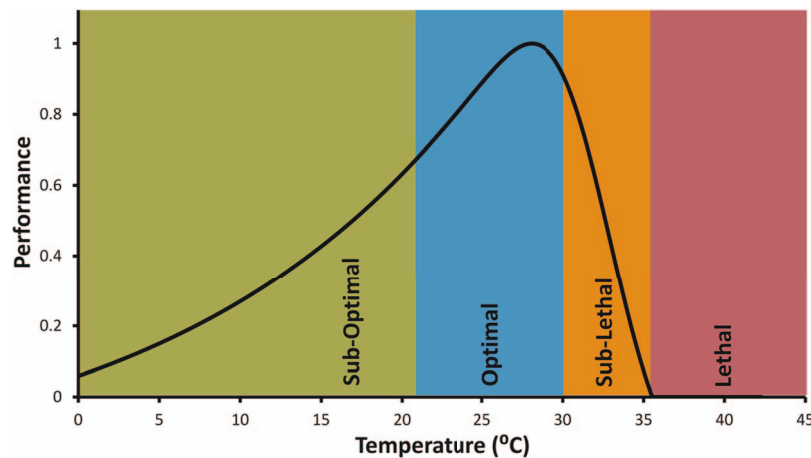


Figure 6: A typical TPC for intertidal organisms. TPC is divided into different performance categories to identify the levels of thermal stress. This TPC has its sub-optimal range from 0°C to 21.2°C; optimal range is from 21.2°C to 30.1°C with optimal temperature (T_{opt}) at 28°C; sub-lethal range from 30.1°C to 35°C and finally high lethal temperature is >35°C.

distribution of individual TPCs of animals based on their thermal history (Kingsolver and Woods, 2016) or could use physiological approaches such as Dynamic Energy Budget models that explicitly account for thermal history (Augustine and Kooijman, 2019).

TPCs for intertidal species can be estimated through physiological experiments measuring movement speed (Tepler *et al.*, 2011), respiration rate (Marshall *et al.*, 2010) and heart rate (Dong *et al.*, 2017), and there is a growing body of data for various intertidal species. Figure 7 is an example of a spatially explicit relative performance model that combines a generic TPC with a T_{opt} of 28°C and a lethal temperature of 35°C (Fig. 6), with a DEM from the Fort Beach site over the course of 6 h. Here, a performance is divided into categories of suboptimal, optimal, sublethal and lethal (after Kish *et al.*, 2016).

Applications of the approach

The model layers presented here—structural (microhabitat), thermal (microclimate) and physiological—provide an example of the non-linear way in which EH affects the performance and survival of organisms (Martin and Huey, 2008; Denny, 2017) and argues that knowledge of one metric (e.g. structure) does not necessarily provide a full understanding of the mechanisms by which microhabitats drive thermal ecology. As described by Stein and Kreft (2014) it has been commonly assumed that habitat (structural) complexity can serve as a direct proxy for EH and microclimate diversity (but see Angilletta, 2009; Armstrong *et al.*, 2013; Scheffers *et al.*, 2017 for counter examples). Certainly, physical structures such as forests, coral reefs, bivalve beds and algal canopies can drive EH through their influence on processes such as shading

(Reed and Foster, 1984) and reductions in wind or water flow (Guichard *et al.*, 2001; Lenihan *et al.*, 2008; Gaylord *et al.*, 2012), but these relationships can be far more complex and non-linear than is generally appreciated (Layton *et al.*, 2019). All of this points to the issue that the many approaches that have been adopted for quantifying habitat structural complexity (Frost *et al.*, 2005; Dibble and Thomaz, 2009), while likely correlated to varying degrees with microclimate diversity (Ehbrecht *et al.*, 2017), cannot be assumed to serve as a direct proxy for environmental conditions at the level of the organism (Meager and Schlacher, 2013; Stein and Kreft, 2014). In other words, the knowledge of structural complexity alone does not automatically translate into an understanding of the heterogeneity of environmental conditions that ultimately drive physiological performance, survival and biodiversity nor does it account for the non-linear relationship between body temperature and physiological performance, i.e. Jensen's inequality (Martin and Huey, 2008; Denny, 2017). These issues are highlighted in Figs 8 and 9, which show frequency distributions of surface temperature (Fig. 8) and relative performance (Fig. 9) over the course of a 6-hour low-tide exposure. Such frequency distributions provide considerably more information than simply bracketing the range of temperatures using the coolest (full shade) and hottest (full sun) microsites, an approach that has been used in previous studies (e.g. Marshall *et al.*, 2015; Dong *et al.*, 2017).

As a first attempt at rectifying the potential disconnect between the different data layers (structural, thermal and physiological) we calculated a common metric of surface roughness, R_q , the root mean square (RMS) of deviations in surface elevation above the mean plane (Thomas, 1999). For the Fort Beach site, the estimate for R_q was calculated as 0.96 (Fig. 3). Here we propose an analogous metric of 'thermal roughness' (R_qT) that comparably calculates the

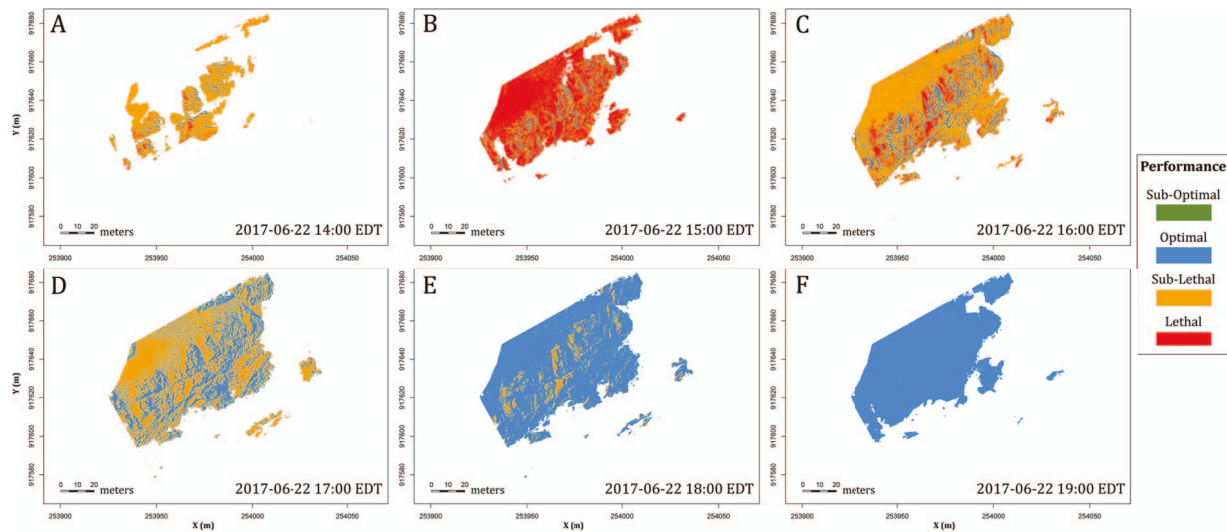


Figure 7: Relative performance models at Fort Beach. The figure describes variation in performance distribution spatially as well as throughout a low-tide period. Performances are categorized into sections for sub-optimal (green), optimal (blue), sub-lethal (orange) and lethal (red). Colours correspond to the categories in Fig. 6, and blank spaces correspond to water at high tide.

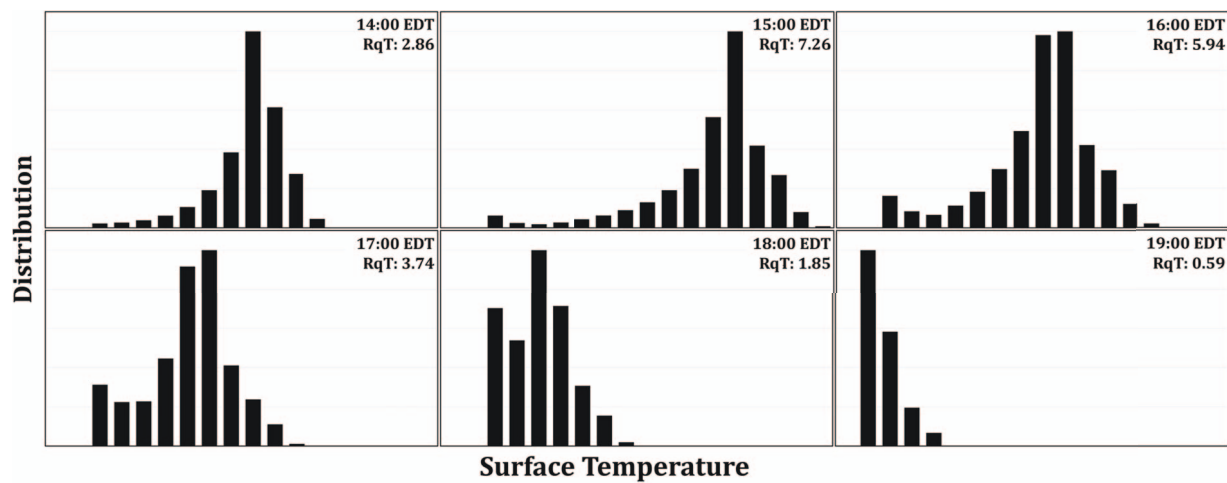


Figure 8: Frequency distribution of surface temperature across the six timestamps on 22 June 2017 shown in Fig. 5. Surface temperature distribution range from 22°C to 41°C (from left to right at each panel). Panels describe variations in the peaks and shape at each timestamp. The patterns of surface temperature distribution can be quantify through thermal roughness (RqT), where the higher RqT means higher distribution of temperatures across the site.

RMS of deviations in temperature within a site (Fig. 8). These will change over time, ranging from very low values (Fig. 8A) when the sun is low, or immediately after emersion, to peak values when thermal heterogeneity at the site is the highest (Fig. 8). In the example shown in Fig. 8, RqT ranges from 0.59 to 7.26 over the course of 6 h. Similar approaches can be used to estimate performance variability (RqP; Fig. 9). Both of these approaches could be used to quantify, for example, variability in selective regimes at a site over the course of a day, season, year or over longer climatic scales.

Spatially explicit body temperature and physiological performance modelling can further be used to quantify areas of micro-refugia (Monaco *et al.*, 2015) by applying a series of threshold temperatures. For example, using a definition of ‘refugia’ as any temperature under 28°C, the area calculated from the Fort Beach site at 16:00 Eastern Daylight Time (EDT) (20:00 Greenwich Mean Time (GMT)) is 255 m², less than 7% of the total aerially exposed site area (3931 m²; Fig. 10). Simulations of relative performance provide the opportunity for an even more in-depth examination

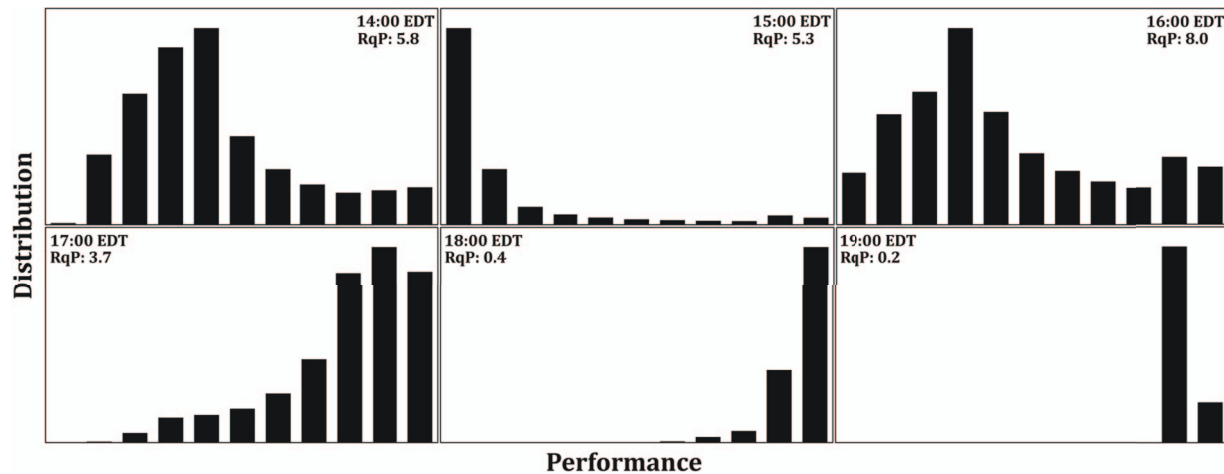


Figure 9: Frequency distribution of relative performance across the six timestamps on 22 June 2017 shown in Fig. 7. Relative performance distribution range from 0 to 1 (from left to right at each panel). Panels describe variations in the peaks and shape at each timestamp. The patterns of performance distribution can be quantified through performance roughness (RqP), where the higher RqP means higher distribution of performances across the site.

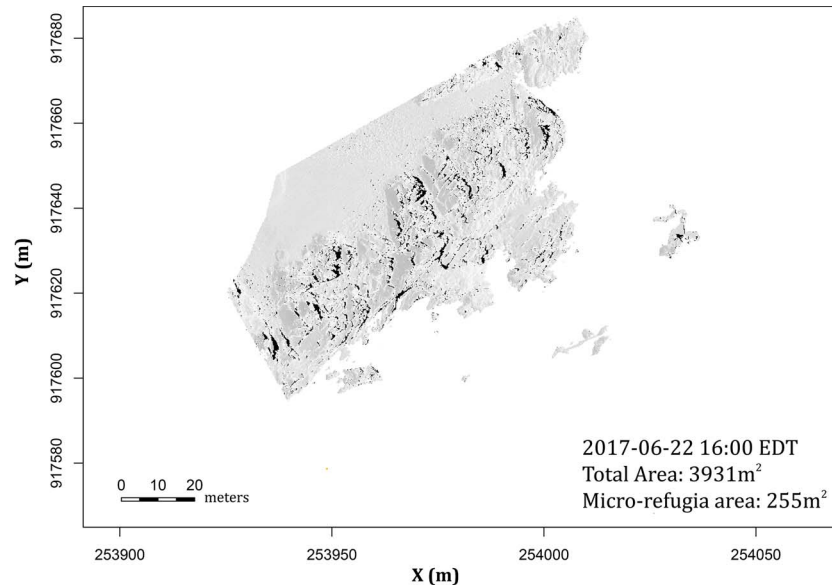


Figure 10: Surface temperature distribution on 22 June 2017 at 16:00 EDT. This figure compares the total area (greyscale) during low tide to micro-refugia area shown in black (in this scenario, micro-refugia are defined as sites where surface temperature < 28°C). This figure shows how spatial models can reveal the scarcity of micro-refugia at the rocky shores during a heat event.

of the ecological consequences of temperature variability, by identifying areas of lethal, sub-optimal temperature, optimal temperature, sub-lethal temperature and lethal temperature (Fig. 7).

While these calculations ignore the role that body size can play in defining micro-refugia (Meager and Schlacher, 2013), this aspect could be included by considering only sites larger than a minimum area related to body size

or, conversely, by spatially averaging surface temperatures to account for large organisms that themselves shade the substrate (such as seastars; Monaco *et al.*, 2015). This approach also offers the opportunity to explore the role of behavioural thermoregulation (Williams *et al.*, 2005; Sunday *et al.*, 2014), for example by identifying thermally protected ‘corridors’ and ‘barriers’ in the landscape (Fig. 11). For highly mobile species, movement to protected microhabitats during extreme conditions at low tide can serve as an

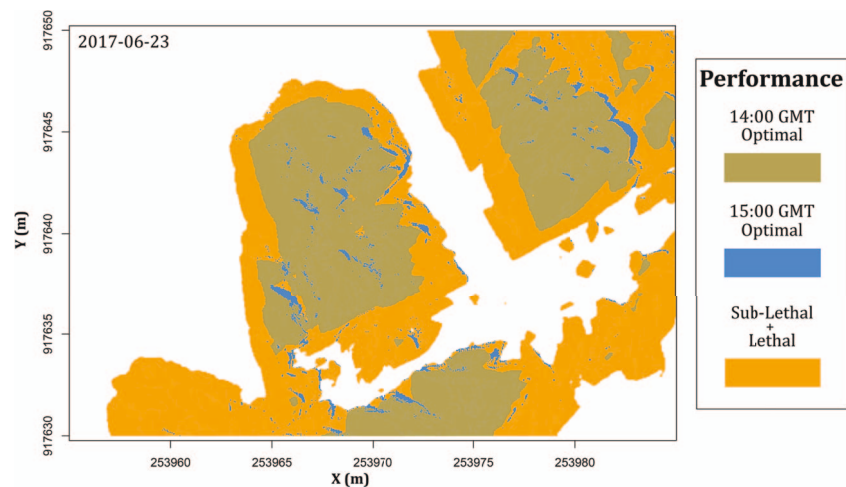


Figure 11: Changes in optimal performance areas within 1 h on 23 June 2017. Blue–brown represents optimal performance areas at 14:00 EDT, while blue represents optimal performance areas at 15:00 EDT. Orange represents areas of sub-lethal or lethal performance. Relative performance is based on an intertidal organism TPC with a T_{opt} of 28°C. Temporal comparisons of relative performance can be an opportunity to describe thermal behaviour for mobile species. The difference of optimal performance area between timestamps represents potential thermal corridors for mobile species.

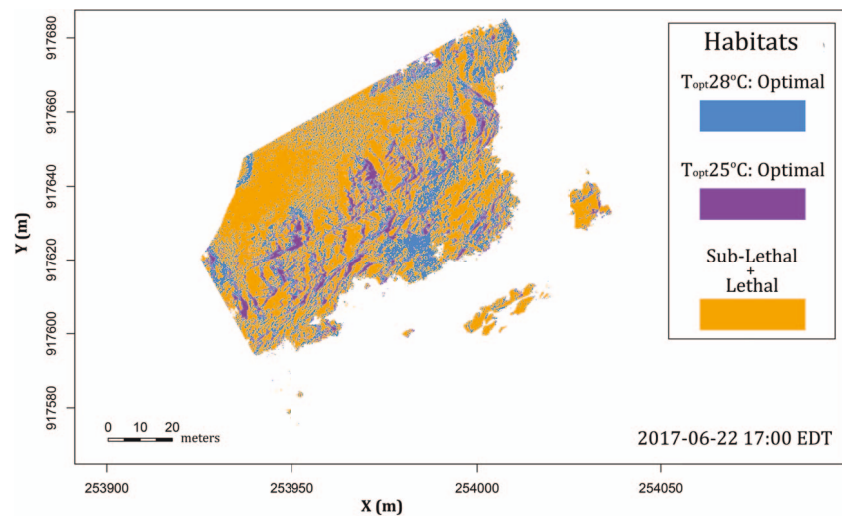


Figure 12: Habitat structure based on the relative performance of interacting species. Blue represents a prey species with a TPC of 28°C; purple represents a predator or dominant species with a TPC of 25°C. Species blue is bounded by not only the habitat of the predator but also its own upper thermal limits, shown in orange.

effective form of behavioural thermoregulation (Iacarella and Helmuth, 2011; Darnell *et al.*, 2015; Sears *et al.*, 2016). For other, more slow-moving species, the decision of whether or not to shelter in a shaded microhabitat occurs during the preceding high tide so that at low tide they may move very little or not at all. For example, many snail species pre-emptively move to crevices and other shaded areas during high tide to avoid extreme temperatures during the following low tide (Marshall *et al.*, 2010; Cartwright and

Williams, 2012; Ng *et al.*, 2017). Corridors for pre-emptive movement based on thermoregulation have been studied in the field using infrared cameras (Chappon and Seuront, 2011), with radio-frequency identification tags (Hayford *et al.*, 2015, 2018) and survey classification (Monaco *et al.*, 2015).

The approach shown here also allows an opportunity to explore the potential for competition for refugia sites among

interacting organisms (as has been done much more extensively for lizards and snakes, e.g. Goller *et al.*, 2014; Sears *et al.*, 2016; Lopez-Alcaide *et al.*, 2017). For example, Fig. 12 shows the location of refugia available to an organism—for example a predator or dominant competitor—with a lower thermal optimum (here, $T_{\text{opt}} = 25^{\circ}\text{C}$) and lethal limit, vs. one by an organism with a higher thermal limit ($T_{\text{opt}} = 28^{\circ}\text{C}$), its prey. In this example, as in Fig. 12, the predator/dominant competitor dominates in cooler microhabitats, and the prey/subordinate competitor can only persist in microrefugia that are unfavourable to the predator/competitive dominant (Wethey, 1983, 1984). Using a spatially explicit model for multiple species can be useful to predict patterns of vertical zonation that results from the interaction between the physical environment experienced by an organism and its physiological limits and biotic interactions (Lewis, 1964; Connell, 1972; Wethey, 1983, 1984; Somero, 2002; Garza and Robles, 2010). For example in the Pacific coast of North America, the thermal limit of the seastar *Pisaster* may prevent its excursion into the mid intertidal zone, where its prey (such as the mussel *Mytilus californianus*) can then survive (Fly *et al.*, 2012; Monaco *et al.*, 2015).

Conclusions

The development of fine-scale, spatially explicit models of physical structure, temperature and ultimately physiological performance can provide critical insights into the impacts of climate change and the potential role of small-scale refugia in driving much larger-scale, geographic patterns. Specifically, the modelling framework we present shows why the relationships between these different data layers can be highly non-linear and therefore urges extreme caution when extrapolating from structural complexity (EH) and microclimate diversity. While the case study shown here has direct relevance to rocky intertidal systems, it also has applicability to other ecosystems, especially those where temperature is largely driven by patterns of solar radiation (Pincebourde *et al.*, 2007; Sears *et al.*, 2016). Moreover, conceptually these same principles apply to other biophysical processes such as water or air flow, which are comparably influenced by physical structure (Lenihan *et al.*, 2008; Denny and Gaylord, 2010; Hurd, 2015). With an increasing emphasis on the potential importance of within-site variability in selective regimes and physiological sensitivity (Dong *et al.*, 2017), quantitative methods for evaluating small-scale microclimates will continue to play a crucial role in forecasting ecological impacts of climate change and in informing conservation efforts to contend with these challenges (Rilov *et al.*, 2019).

Acknowledgements

This is publication 391 of the Northeastern University Marine Science Center.

Funding

F.C., T.G. and B.H. were supported by a grant from the National Science Foundation (OCE-1635989). G.R. was funded by the Israeli Binational Science Foundation. F.L. and R.S. were supported by FEDER - European Regional Development Fund (Fonds Européen de Développement Économique et Régional) through COMPETE - Operational Programme Factors of Competitiveness ("Programa Operacional Factores de Competitividade") and by the Portuguese Foundation for Science and Technology (FCT - Fundação para a Ciência e a Tecnologia).

Supplementary material

Supplementary material is available at *Conservation Physiology* online.

References

- Angilletta MJ (2006) Estimating and comparing thermal performance curves. *J Therm Biol* 31: 541–545.
- Angilletta MJ (2009) *Thermal Adaptation: A Theoretical and Empirical synthesis*. Oxford University Press, New York
- Armstrong JB, Schindler DE, Ruff CP, Brooks GT, Bentley KE, Torgersen CE (2013) Diel horizontal migration in streams: juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology* 94: 2066–2075.
- Augustine S, Kooijman S (2019) A new phase in DEB research. *J Sea Res* 143: 1–7.
- Barton MG, Terblanche JS (2014) Predicting performance and survival across topographically heterogeneous landscapes: the global pest insect *Helicoverpa armigera* (Hubner, 1808) (Lepidoptera: Noctuidae). *Austral Entomol* 53: 249–258.
- Bates AE *et al.* (2018) Biologists ignore ocean weather at their peril. *Nature* 560: 299–301.
- Baumann H, Smith EM (2018) Quantifying metabolically driven pH and oxygen fluctuations in us nearshore habitats at diel to interannual time scales. *Estuaries Coast* 41: 1102–1117.
- Bell EC (1995) Environmental and morphological influences on thallus temperature and desiccation of the intertidal alga *Mastocarpus papillatus* Kützling. *J Exp Mar Biol Ecol* 191: 29–55.
- Bindi M, Miglietta F, Zipoli G (1992) Different methods for separating diffuse and direct components of solar radiation and their application in crop growth models. *Climate Res* 2: 47–54.
- Bonebrake TC *et al.* (2018) Managing consequences of climate-driven species redistribution requires integration of ecology, conservation and social science. *Biol Rev* 93: 284–305.
- Boyd PW, Cornwall CE, Davison A, Doney SC, Fourquez M, Hurd CL, Lima ID, McMinn A (2016) Biological responses to environmental

- heterogeneity under future ocean conditions. *Glob Chang Biol* 22: 2633–2650.
- Braun JE, Mitchell JC (1983) Solar geometry for fixed and tracking surfaces. *Sol Energy* 31: 439–444.
- Brito-Morales I *et al.* (2018) Climate velocity can inform conservation in a warming world. *Trends Ecol Evol* 33: 441–457.
- Broitman BR, Szathmari PL, Mislan KAS, Blanchette CA, Helmuth B (2009) Predator–prey interactions under climate change: the importance of habitat vs body temperature. *Oikos* 118: 219–224.
- Bruno JF, Bates AE, Cacciapaglia C, Pike EP, Amstrup SC, van Hooi donk R, Henson SA, Aronson RB (2018) Climate change threatens the world's marine protected areas. *Nat Clim Chang* 8: 499–503.
- Cartwright SR, Williams GA (2012) Seasonal variation in utilization of biogenic microhabitats by littorinid snails on tropical rocky shores. *Mar Biol* 159: 2323–2332.
- Chapman MG, Bulleri F (2003) Intertidal seawalls—new features of landscape in intertidal environments. *Landsc Urban Plan* 62: 159–172.
- Chappon C, Seuront L (2011) Behavioral thermoregulation in a tropical gastropod: links to climate change scenarios. *Glob Chang Biol* 17: 1740–1749.
- Chappon C, Volkenborn N, Clavier J, Seite S, Seabra R, Lima FP (2016) Exposure to solar radiation drives organismal vulnerability to climate: evidence from an intertidal limpet. *J Therm Biol* 57: 92–100.
- Chown SL, Gaston KJ (2016) Macrophysiology—progress and prospects. *Funct Ecol* 30: 330–334.
- Clark MR, Schlacher TA, Rowden AA, Stocks KI, Consalvey M (2012) Science priorities for seamounts: research links to conservation and management. *PLoS One* 7: e29232.
- Colomina I, Blázquez M, Molina P, Parés M, Wis M (2008) Towards a new paradigm for high-resolution low-cost photogrammetry and remote sensing. *ISPRS, The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences*, Vol XXXVIII-B1, pp 1201–1206
- Connell JH (1972) Community interactions on marine rocky intertidal shores. *Ann Rev Ecol Syst* 3: 169–192.
- Darnell MZ, Nicholson HS, Munguia P (2015) Thermal ecology of the fiddler crab *Uca panacea*: thermal constraints and organismal responses. *J Therm Biol* 52: 157–165.
- Denny MW (2015) The fallacy of the average: on the ubiquity, utility and continuing novelty of Jensen's inequality. *J Exp Biol* 220: 139–146.
- Denny MW (2018) Survival in spatially variable thermal environments: consequences of induced thermal defense. *Integr Zool* 13: 392–410.
- Denny MW (2019) Performance in a variable world: using Jensen's inequality to scale up from individuals to populations. *Conserv Physiol* (in press).
- Denny MW, Dowd WW, Bilir L, Mach KJ (2011) Spreading the risk: small-scale body temperature variation among intertidal organisms and its implications for species persistence. *J Exp Mar Biol Ecol* 400: 175–190.
- Denny MW, Gaylord B (2010) Marine ecomechanics. *Annu Rev Mar Sci* 2: 1–26.
- Denny MW, Harley CDG (2006) Hot limpets: predicting body temperature in a conductance-mediated thermal system. *J Exp Biol* 209: 2409–2419.
- Denny MW, Helmuth B (2009) Confronting the physiological bottleneck: a challenge from ecomechanics. *Integr Comp Biol* 49: 197–201.
- Denny MW, Miller LP, Harley CDG (2006) Thermal stress on intertidal limpets: long-term hindcasts and lethal limits. *J Exp Biol* 209: 2420–2431.
- Diamond SE, Nichols LM, McCoy N, Hirsch C, Pelini SL, Sanders NJ, Ellison AM, Gotelli NJ, Dunn RR (2012) A physiological trait-based approach to predicting the responses of species to experimental climate warming. *Ecology* 93: 2305–2312.
- Dibble ED, Thomaz SM (2009) Use of fractal dimension to assess habitat complexity and its influence on dominant invertebrates inhabiting tropical and temperate macrophytes. *J Freshwater Ecol* 24: 93–102.
- Doney SC *et al.* (2012) Climate change impacts on marine ecosystems. *Annu Rev Mar Sci* 4: 11–37.
- Dong Y-w, Li X-x, Choi FMP, Williams GA, Somero GN, Helmuth B (2017) Untangling the roles of microclimate, behaviour and physiological polymorphism in governing vulnerability of intertidal snails to heat stress. *Proc R Soc Lond B Biol Sci* 284: 20162367.
- Dowd WW, Felton CA, Heymann HM, Kost LE, Somero GN (2013) Food availability, more than body temperature, drives correlated shifts in ATP-generating and antioxidant enzyme capacities in a population of intertidal mussels (*Mytilus californianus*). *J Exp Mar Biol Ecol* 449: 171–185.
- Ehbrecht M, Schall P, Ammer C, Seidel D (2017) Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. *Agric For Meteorol* 242: 1–9.
- Eisenbeiss H (2009) UAV photogrammetry. *PhD dissertation*. ETH-Zürich, Switzerland
- Elvin DW, Gonor JJ (1979) The thermal regime of an intertidal *Mytilus californianus* Conrad population on the Central Oregon coast. *J Exp Mar Biol Ecol* 39: 265–279.
- Enquist BJ *et al.* (2017) Assessing trait-based scaling theory in tropical forests spanning a broad temperature gradient. *Glob Ecol Biogeogr* 26: 1357–1373.
- Faye E, Rebaudo F, Yáñez-Cajo D, Cauvy-Fraunié S, Dangles O (2016) A toolbox for studying thermal heterogeneity across spatial scales: from unmanned aerial vehicle imagery to landscape metrics. *Methods Ecol Evol* 7: 437–446.
- Firth LB, Williams GA (2009) The influence of multiple environmental stressors on the limpet cellana toreuma during the summer

- monsoon season in Hong Kong. *J Exp Mar Biol Ecol* 375: 70–75.
- Fitzhenry T, Halpin PM, Helmuth B (2004) Testing the effects of wave exposure, site, and behavior on intertidal mussel body temperatures: applications and limits of temperature logger design. *Mar Biol* 145: 339–349.
- Fly EK, Monaco CJ, Pincebourde S, Tullis A (2012) The influence of intertidal location and temperature on the metabolic cost of emersion in *Pisaster ochraceus*. *J Exp Mar Biol Ecol* 422–423: 20–28.
- Flynn KJ, Blackford JC, Baird ME, Raven JA, Clark DR, Beardall J, Brownlee C, Fabian H, Wheeler GL (2012) Changes in pH at the exterior surface of plankton with ocean acidification. *Nat Clim Chang* 2: 510–513.
- Freeman CW, Bernstein DJ, Mitasova H (2004) Rapid response 3D survey techniques for seamless topo/bathy modeling: 2003 Hatteras Beach, North Carolina. *Shore and Beach* 72: 25–29.
- Frieder CA, Nam SH, Martz TR, Levin LA (2012) High temporal and spatial variability of dissolved oxygen and pH in a nearshore California kelp forest. *Biogeosciences* 9: 3917–3930.
- Frost NJ, Burrows MT, Johnson MP, Hanley ME, Hawkins SJ (2005) Measuring surface complexity in ecological studies. *Limnol Oceanogr Methods* 3: 203–210.
- Garcia RA, Allen JL, Clusella-Trullas S (2019) Rethinking the scale and formulation of indices assessing organism vulnerability to warmer habitats. *Ecography* 42: 1–13.
- Garza C (2016) Landscape complexity effects on fisheries: insights from marine landscape ecology. *Current Landscape Ecology Reports* 1: 1–9.
- Garza C, Robles C (2010) Effects of brackish water incursions and diel phasing of tides on vertical excursions of the keystone predator *Pisaster ochraceus*. *Mar Biol* 157: 673–682.
- Gaylord B, Nickols KJ, Jurgens L (2012) Roles of transport and mixing processes in kelp forest ecology. *J Exp Biol* 215: 997–1007.
- Geller GN *et al.* (2017) Remote sensing for biodiversity. In M Walters, RJ Scholes, eds, *The GEO Handbook on Biodiversity Observation Networks*. Springer, pp. 187–210
- Gilman SE, Wetthey DS, Helmuth B (2006) Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. *Proc Natl Acad Sci U S A* 103: 9560–9565.
- Goller M, Goller F, French SS (2014) A heterogeneous thermal environment enables remarkable behavioral thermoregulation in *Uta stansburiana*. *Ecol Evol* 4: 3319–3329.
- González-Rivero M, Harborne AR, Herrera-Reveles A, Bozec Y-M, Rogers A, Friedman A, Ganase A, Hoegh-Guldberg O (2017) Linking fishes to multiple metrics of coral reef structural complexity using three-dimensional technology. *Scientific Reports* 7: 13965.
- Hannah L, Flint L, Syphard AD, Moritz MA, Buckley LB, McCullough IM (2014) Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. *Trends Ecol Evol* 29: 390–397.
- Hanski I, Ovaskainen O (2000) The metapopulation capacity of a fragmented landscape. *Nature* 404: 755–758.
- Harley CDG (2008) Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. *Mar Ecol Prog Ser* 371: 37–46.
- Harley CDG (2013) Linking ecomechanics and ecophysiology to interspecific interactions and community dynamics. In AL Angert, SL LaDeau, RS Ostfeld, eds, *Climate Change and Species Interactions: Ways Forward* Vol 1297, pp. 73–82
- Hayford HA, Gilman SE, Carrington E (2015) Foraging behavior minimizes heat exposure in a complex thermal landscape. *Mar Ecol Prog Ser* 518: 165–175.
- Hayford HA, O'Donnell MJ, Carrington E (2018) Radio tracking detects behavioral thermoregulation at a snail's pace. *J Exp Mar Biol Ecol* 499: 17–25.
- 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, Broitman BR, Yamane L, Gilman SE, Mach K, Mislan KAS, Denny MW (2010) Organismal climatology: analyzing environmental variability at scales relevant to physiological stress. *J Exp Biol* 213: 995–1003.
- Helmuth B, Carrington E, Kingsolver JG (2005) Biophysics, physiological ecology, and climate change: does mechanism matter? *Annu Rev Physiol* 67: 177–201.
- Helmuth B *et al.* (2016) Long-term, high frequency in situ measurements of intertidal mussel bed temperatures using biomimetic sensors. *Sci Data* 3: 160087.
- Helmuth B, Denny MW (2003) Predicting wave exposure in the rocky intertidal zone: do bigger waves always lead to larger forces? *Limnol Oceanogr* 48: 1338–1345.
- Helmuth BS, Harley CDG, Halpin P, O'Donnell M, Hofmann GE, Blanchette C (2002) Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298: 1015–1017.
- Helmuth B, Yamane L, Lalwani S, Matzelle A, Tockstein A, Gao N (2011) Hidden signals of climate change in intertidal ecosystems: what (not) to expect when you are expecting. *J Exp Mar Biol Ecol* 400: 191–199.
- Helmuth BST (1998) Intertidal mussel microclimates: predicting the body temperature of a sessile invertebrate. *Ecol Monogr* 68: 51–74.
- Helmuth BST (1999) Thermal biology of rocky intertidal mussels: quantifying body temperatures using climatological data. *Ecology* 80: 15–34.
- Helmuth BST, Hofmann GE (2001) Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. *Biol Bull* 201: 374–384.

- Hofmann GE *et al.* (2011) High-frequency dynamics of ocean pH: a multi-ecosystem approach. *PLoS One* 6: e28983.
- Holmer B, Postgard U, Ericksson M (2001) Sky view factors in forest canopies calculated with IDRISI. *Theor Appl Climatol* 68: 33–40.
- Hoylman ZH, Jencso KG, Hu J, Martin JT, Holden ZA, Seielstad CA, Rowell EM (2018) Hillslope topography mediates spatial patterns of ecosystem sensitivity to climate. *J Geophys Res Biogeosci* 123: 353–371.
- Huey RB, Slatkin M (1976) Cost and benefits of lizard thermoregulation. *Q Rev Biol* 51: 363–384.
- Huey RB, Stevenson RD (1979) Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am Zool* 19: 357–366.
- Hurd C (2015) Slow-flow habitats as refugia for coastal calcifiers from ocean acidification. *J Phycol* 51: 599–605.
- Iacarella JC, Helmuth B (2011) Experiencing the salt marsh environment through the foot of *Littoraria irrorata*: behavioral responses to thermal and desiccation stresses. *J Exp Mar Biol Ecol* 409: 143–153.
- James MR, Robson S (2012) Straightforward reconstruction of 3D surfaces and topography with a camera: accuracy and geoscience application. *J Geophys Res* 117: F03017.
- Jimenez AG, Jayawardene S, Alves S, Dallmer J, Dowd WW (2015) Micro-scale environmental variation amplifies physiological variation among individual mussels. *Proc R Soc Lond B Biol Sci* 282: 20152273.
- Judge R (2018) Recent advances in data logging for intertidal ecology. *Front Ecol Evol* 6: 213. doi: [10.3389/fevo.2018.00213](https://doi.org/10.3389/fevo.2018.00213).
- Jurgens LJ, Gaylord B (2017) Physical effects of habitat-forming species override latitudinal trends in temperature. *Ecol Lett* 21: 190–196.
- Kalacska M, Lucanus O, Sousa L, Vieira T, Arroyo-Mora JP (2018) Freshwater fish habitat complexity mapping using above and underwater structure-from-motion photogrammetry. *Remote Sens (Basel)* 10: 28.
- Kearney M (2006) Habitat, environment and niche: what are we modelling? *Oikos* 115: 186–191.
- Kearney MR, Isaac AP, Porter WP (2014) Microclim: global estimates of hourly microclimate based on long-term monthly climate averages. *Sci Data* 1: 140006.
- Kearney MR, Porter WP (2017) Nichemapr—an R package for biophysical modelling: the microclimate model. *Ecography* 40: 664–674.
- Keith SA, Baird AH, Hughes TP, Madin JS, Connolly SR (2013) Faunal breaks and species composition of Indo-Pacific corals: the role of plate tectonics, environment and habitat distribution. *Proc R Soc B Biol Sci* 280: 20130818. doi: [10.1098/rspb.2013.0818](https://doi.org/10.1098/rspb.2013.0818).
- Kelly MW (2019) Adaptation to climate change through genetic accommodation and assimilation of plastic phenotypes. *Philos Trans R Soc Lond B Biol Sci* 374: 20180176.
- Kingsolver JG (2009) The well-tempered biologist. *Am Nat* 174: 755–768.
- Kingsolver JG, Woods HA (2016) Beyond thermal performance curves: modeling time-dependent effects of thermal stress on ectotherm growth rates. *Am Nat* 187: 283–294.
- Kish NE, Helmuth B, Wetthey DS (2016) Physiologically grounded metrics of model skill: a case study estimating heat stress in intertidal populations. *Conserv Physiol* 4: doi:[10.1093/conphys/cow038](https://doi.org/10.1093/conphys/cow038).
- Kovalenko KE, Thomaz SM, Warfe DM (2012) Habitat complexity: approaches and future directions. *Hydrobiologia* 685: 1–17.
- Lathlean JA, Ayre DJ, Minchinton TE (2012) Using infrared imagery to test for quadrat-level temperature variation and effects on the early life history of a rocky-shore barnacle. *Limnol Oceanogr* 57: 1279–1291.
- Lawson CR, Bennie J, Hodgson JA, Thomas CD, Wilson RJ (2014) Topographic microclimates drive microhabitat associations at the range margin of a butterfly. *Ecography* 37: 732–740.
- Layton C, Shelamoff V, Cameron MJ, Tatsumi M, Wright JT, Johnson CR (2019) Resilience and stability of kelp forests: the importance of patch dynamics and environment-engineer feedbacks. *PLoS One* 14: e0210220.
- Lenihan HS, Adjeroud M, Kotchen MJ, Hench JL, Nakamura T (2008) Reef structure regulates small-scale spatial variation in coral bleaching. *Mar Ecol Prog Ser* 370: 127–141.
- Lewis JR (1964) *The Ecology of Rocky Shores*. English University Press, London
- Lima FP, Gomes F, Seabra R, Wetthey DS, Seabra MI, Cruz T (2016) Loss of thermal refugia near equatorial range limits. *Glob Chang Biol* 22: 254–263.
- Loke LHL, Bouma TJ, Todd PA (2017) The effects of manipulating microhabitat size and variability on tropical seawall biodiversity: field and flume experiments. *J Exp Mar Biol Ecol* 492: 113–120.
- Loke LHL, Ladle RJ, Bouma TJ, Todd PA (2015) Creating complex habitats for restoration and reconciliation. *Ecol Eng* 77: 307–313.
- Lopez-Alcaide S, Gonzalez-Salazar C, Macip-Rios R, Martinez-Meyer E (2017) Using microhabitat thermal heterogeneity to avoid lethal overheating: an empirical approximation in reproductive oviparous and viviparous lizards. *Revista Mexicana De Biodiversidad* 88: 683–690.
- Maclean IMD, Hopkins JJ, Bennie J, Lawson CR, Wilson RJ (2015) Microclimates buffer the responses of plant communities to climate change. *Glob Ecol Biogeogr* 24: 1340–1350.
- Maclean IMD, Mosedale JR, Bennie JJ (2019) Microclima: an R package for modelling meso- and microclimate. *Methods Ecol Evol* 10: 280–290.
- Malishev M, Bull CM, Kearney MR (2017) An individual-based model of ectotherm movement integrating metabolic and microclimatic constraints. *Methods Ecol Evol* 9: 472–489. doi: [10.1111/2041-210X.12909](https://doi.org/10.1111/2041-210X.12909)

- Marn N, Kooijman S, Jusup M, Legovic T, Klanjscek T (2017) Inferring physiological energetics of loggerhead turtle (*Caretta caretta*) from existing data using a general metabolic theory. *Mar Environ Res* 126: 14–25.
- Marshall DJ, McQuaid CD, Williams GA (2010) Non-climatic thermal adaptation: implications for species' responses to climate warming. *Biol Lett* 6: 669–673.
- Marshall DJ, Rezende EL, Baharuddin N, Choi F, Helmuth B (2015) Thermal tolerance and climate warming sensitivity in tropical snails. *Ecol Evol* 5: 5905–5919.
- Martin TL, Huey RB (2008) Why 'suboptimal' is optimal: Jensen's inequality and ectotherm thermal preferences. *Am Nat* 171: E102–E118.
- Matias MG, Underwood AJ, Hochuli DF, Coleman RA (2011) Habitat identity influences species-area relationships in heterogeneous habitats. *Mar Ecol Prog Ser* 437: 135–145.
- Matzarakis A, Rutz F, Mayer H (2007) Modelling radiation fluxes in simple and complex environments—application of the Rayman model. *Int J Biometeorol* 51: 323–334.
- Meager JJ, Schlacher TA (2013) New metric of microhabitat complexity predicts species richness on a rocky shore. *Mar Ecol* 34: 434–491.
- Meager JJ, Schlacher TA, Green M (2011) Topographic complexity and landscape temperature patterns create a dynamic habitat structure on a rocky intertidal shore. *Mar Ecol Prog Ser* 428: 1–12.
- Migliore J, Baumel A, Juin M, Fady B, Roig A, Duong N, Médail F (2013) Surviving in mountain climate refugia: new insights from the genetic diversity and structure of the relict shrub *Myrtus nivellei* (Myrtaceae) in the Sahara desert. *PLoS One* 8: e73795.
- Miller LP, Allen BJ, King FA, Chilin DR, Reynoso VM, Denny MW (2015) Warm microhabitats drive both increased respiration and growth rates of intertidal consumers. *Mar Ecol Prog Ser* 522: 127–143.
- Miller LP, Dowd WW (2017) Multimodal *in situ* datalogging quantifies inter-individual variation in thermal experience and persistent origin effects on gaping behavior among intertidal mussels (*Mytilus californianus*). *J Exp Biol* 220: 4305–4319.
- Mislan KAS, Helmuth B, Wetthey DS (2014) Geographical variation in climatic sensitivity of intertidal mussel zonation. *Glob Ecol Biogeogr* 23: 744–756.
- Mislan KAS, Wetthey DS (2011) Gridded meteorological data as a resource for mechanistic macroecology in coastal environments. *Ecol Appl* 21: 2678–2690.
- Mislan KAS, Wetthey DS (2015) A biophysical basis for patchy mortality during heat waves. *Ecology* 96: 902–907.
- Monaco CJ, McQuaid CD, Marshall DJ (2017) Decoupling of behavioural and physiological thermal performance curves in ectothermic animals: a critical adaptive trait. *Oecologia* 185: 583–593.
- Monaco CJ, Wetthey DS, Gullede S, Helmuth B (2015) Shore-level size gradients and thermal refuge use in the predatory sea star *Pisaster ochraceus*: the role of environmental stressors. *Mar Ecol Prog Ser* 539: 191–205.
- Morelli F, Benedetti Y, Simova P (2018) Landscape metrics as indicators of avian diversity and community measures. *Ecol Indic* 90: 132–141.
- Morelli TL, Maher SP, Lim MCW, Kastely C, Eastman LM, Flint LE, Flint AL, Beissinger SR, Moritz C (2017) Climate change refugia and habitat connectivity promote species persistence. *Climate Change Responses* 4: 8.
- Morton RA, Leach MP, Paine JG, Cardoza MA (1999) Monitoring beach changes using GPS surveying techniques. *J Coast Res* 9: 702–720.
- Ng TPT, Lau SLY, Seuront L, Davies MS, Stafford R, Marshall DJ, Williams GA (2017) Linking behaviour and climate change in intertidal ectotherms: insights from littorinid snails. *J Exp Mar Biol Ecol* 492: 121–131.
- Ortega JCG, Thomaz SM, Bini LM (2018) Experiments reveal that environmental heterogeneity increases species richness, but they are rarely designed to detect the underlying mechanisms. *Oecologia* 188: 11–22.
- Pincebourde S, Murdock CC, Vickers M, Sears MW (2016) Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments. *Integr Comp Biol* 56: 45–61.
- Pincebourde S, Sinoquet H, Combes D, Casas J (2007) Regional climate modulates the canopy mosaic of favourable and risky microclimates for insects. *J Anim Ecol* 76: 424–438.
- Polat N, Uysal M (2015) Investigating performance of airborne LiDAR data filtering algorithms for dtm generation. *Measurement* 63: 61–68.
- Polgar G, Khang TF, Chua T, Marshall DJ (2015) Gross mismatch between thermal tolerances and environmental temperatures in a tropical freshwater snail: climate warming and evolutionary implications. *J Therm Biol* 47: 99–108.
- Polo López CS, Sala M, Tagliabue LC, Frontini F, Bouziri S (2016) Solar radiation and daylighting assessment using the sky-view factor (SVF) analysis as method to evaluate urban planning densification policies impacts. *Energy Procedia* 91: 989–996.
- Potter KA, Woods HA, Pincebourde S (2013) Microclimatic challenges in global change biology. *Glob Chang Biol* 19: 2932–2939.
- Przeslawski R, Davis AR, Benkendorff K (2005) Synergistic effects associated with climate change and the development of rocky shore molluscs. *Glob Chang Biol* 11: 515–522.
- Rebaudo F, Faye E, Dangles O (2016) Microclimate data improve predictions of insect abundance models based on calibrated spatiotemporal temperatures. *Front Physiol* 7: 139. doi: 10.3389/fphys.2016.00139
- Reed DC, Foster MS (1984) The effects of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* 65: 937–948.
- Rilov G, Mazaris AD, Stelzenmüller V, Helmuth B, Wahl M, Guy-Haim T, Mieszkowska N, Ledoux J-B, Stelios K (2019) Adaptive marine conservation planning in the face of climate change: what can we learn from

- physiological, genetic and ecological studies? *Glob Environ Change* 17: e00566. doi: doi.org/10.1016/j.gecco.2019.e00566
- Roberts CM *et al.* (2017) Marine reserves can mitigate and promote adaptation to climate change. *Proc Natl Acad Sci USA* 114: 6167–6175.
- Roitberg BD, Mangel M (2016) Cold snaps, heatwaves, and arthropod growth. *Ecol Entomol* 41: 653–659. doi: [10.1111/een.12324](https://doi.org/10.1111/een.12324).
- Sarà G, Kearney M, Helmuth B (2011) Combining heat-transfer and energy budget models to predict thermal stress in mediterranean intertidal mussels. *Chem Ecol* 27: 135–145.
- Sarà G, Mangano MC, Johnson M, Mazzola A (2018) Integrating multiple stressors in aquaculture to build the blue growth in a changing sea. *Hydrobiologia* 809: 5–17.
- Scheffers BR, Edwards DP, Macdonald SL, Senior RA, Andriamahohatra LR, Roslan N, Rogers AM, Haugaasen T, Wright P, Williams SE (2017) Extreme thermal heterogeneity in structurally complex tropical rain forests. *Biotropica* 49: 35–44.
- Scheffers BR, Evans TA, Williams SE, Edwards DP (2014a) Microhabitats in the tropics buffer temperature in a globally coherent manner. *Biol Lett* 10. doi: [10.1098/rsbl.2014.0819](https://doi.org/10.1098/rsbl.2014.0819).
- Scheffers BR, Edwards DP, Diesmos A, Williams SE, Evans TA (2014b) Microhabitats reduce animal's exposure to climate extremes. *Glob Chang Biol* 20: 495–503.
- Scherrer D, Koerner C (2010) Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Glob Chang Biol* 16: 2602–2613.
- Schmidt PS, Bertness MD, Rand DM (2000) Environmental heterogeneity and balancing selection in the acorn barnacle *Semibalanus balanoides*. *Proc R Soc Lond B Biol Sci* 267: 379–384.
- Schneider DC (2001) The rise of the concept of scale in ecology. *Bio-science* 51: 545–553.
- Schneider KR, Helmuth B (2007) Spatial variability in habitat temperature may drive patterns of selection between an invasive and native mussel species. *Mar Ecol Prog Ser* 339: 157–167.
- Seabra R, Wetthey DS, Santos AM, Lima FP (2011) Side matters: micro-habitat influence on intertidal heat stress over a large geographical scale. *J Exp Mar Biol Ecol* 400: 200–208.
- Sears MW, Angilletta MJ, S. SM, Borchert J, Dilliplane KF, Stegman M, Rusch TW, Mitchell WA (2016) Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proc Natl Acad Sci USA*: 113(38): 10595–10600. doi: [10.1073/pnas.1604824113](https://doi.org/10.1073/pnas.1604824113).
- Sears MW, Raskin E, Angilletta MJ (2011) The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integr Comp Biol* 51: 666–675.
- Seebacher F, Franklin CE (2012) Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology. *Philos Trans R Soc B Biol Sci* 367: 1607–1614.
- Seuront L, Ng TPT, Lathlean JA (2018) A review of the thermal biology and ecology of molluscs, and of the use of infrared thermography in molluscan research. *J Moll Stud* 84: 203–232.
- Shukla J (1998) Predictability in the midst of chaos: a scientific basis for climate forecasting. *Science* 282: 728–731.
- Simó G, García-Santos V, Jiménez MA, Martínez-Villagrasa PR, Caselles V, Cuxart J (2016) Landsat and local land surface temperatures in a heterogeneous terrain compared to modis values. *Remote Sens (Basel)* 8: 849.
- Sinclair BJ *et al.* (2016) Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecol Lett* 19: 1372–1385.
- Somero GN (2002) Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integr Comp Biol* 42: 780–789.
- Somero GN (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *J Exp Biol* 213: 912–920.
- Sorte CJB, Bernatchez G, Mislan KAS, Pandori LLM, Silbiger NJ, Wallingford PD (2019) Thermal tolerance limits as indicators of current and future intertidal zonation patterns in a diverse mussel guild. *Mar Biol* 166: 6. doi: doi.org/10.1007/s00227-018-3452-6.
- Stein A, Kreft H (2014) Terminology and quantification of environmental heterogeneity in species-richness research. *Biol Rev Camb Philos Soc* 90: 815–836.
- Stoffels RJ, Richardson AJ, Vogel MT, Coates SP, Müller WJ (2016) What do metabolic rates tell us about thermal niches? Mechanisms driving crayfish distributions along an altitudinal gradient. *Oecologia* 180: 45–54.
- Storlie C, Merino-Viteri A, Phillips B, VanDerWal J, Welbergen J, Williams S (2014) Stepping inside the niche: microclimate data are critical for accurate assessment of species' vulnerability to climate change. *Biol Lett* 10(9): 20140576. doi: [10.1098/rsbl.2014.0576](https://doi.org/10.1098/rsbl.2014.0576).
- Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, Huey RB (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc Natl Acad Sci USA* 111: 5610–5615.
- Sunday JM *et al.* (2015) Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecol Lett* 18: 944–953.
- Szathmary PL, Helmuth B, Wetthey DS (2009) Climate change in the rocky intertidal zone: predicting and measuring the body temperature of a keystone predator. *Mar Ecol Prog Ser* 374: 43–56.
- Teal LR, Marras S, Peck MA, Domenici P (2018) Physiology-based modelling approaches to characterize fish habitat suitability: their usefulness and limitations. *Estuar Coast Shelf Sci* 201: 56–63.
- Tepler S, Mach K, Denny M (2011) Preference versus performance: body temperature of the intertidal snail *Chlorostoma funebris*. *Biol Bull* 220: 107–117.

- Thomas TR (1999) *Rough Surfaces*, Ed2nd. Imperial College Press, London
- Torossian JL, Kordas RL, Helmuth B (2016) Cross-scale approaches to forecasting biogeographic responses to climate change. *Adv Ecol Res* 55: 371–433.
- Tovar-Pescador J, Pozo-Vázquez D, Ruiz-Arias JA, Batlles J, López G, Bosch JL (2006) On the use of the digital elevation model to estimate the solar radiation in areas of complex topography. *Meteorol Appl* 13: 279–287.
- van Rensburg BJ, Chown SL, Gaston KJ (2002) Species richness, environmental correlates, and spatial scale: a test using South African birds. *Am Nat* 159: 566–577.
- Wetthey DS (1983) Geographic limits and local zonation: the barnacles *Semibalanus* (*Balanus*) and *Chthamalus* in New England. *Biol Bull* 165: 330–341.
- Wetthey DS (1984) Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus*: a field experiment. *Biol Bull* 167: 176–185.
- Wetthey DS (2002) Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. *Integr Comp Biol* 42: 872–880.
- Wetthey DS, Brin LD, Helmuth B, Mislan KAS (2011b) Predicting intertidal organism temperatures with modified land surface models. *Ecol Model* 222: 3568–3576.
- Wetthey DS, Woodin SA (2008) Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. *Hydrobiologia* 606: 139–151.
- Wetthey DS, Woodin SA, Hilbish TJ, Jones SJ, Lima FP, Brannock PM (2011a) Response of intertidal populations to climate: effects of extreme events versus long term change. *J Exp Mar Biol Ecol* 400: 132–144.
- Williams A, Althaus F, Dunstan PK, Poore GCB, Bax NJ, Kloser RJ, McEnulty FR (2010) Scales of habitat heterogeneity and megabenthos biodiversity on an extensive Australian continental margin (100–1100 m depths). *Marine Ecology—An Evolutionary Perspective* 31: 222–236.
- Williams GA, De Pirro M, Leung KMY, Morritt D (2005) Physiological responses to heat stress on a tropical shore: the benefits of mushrooming behaviour in the limpet *Cellana grata*. *Mar Ecol Prog Ser* 292: 213–224.
- Williams GA, Morritt D (1995) Habitat partitioning and thermal tolerance in a tropical limpet, *Cellana grata*. *Mar Ecol Prog Ser* 124: 89–103.
- Woods HA, Dillon ME, Pincebourde S (2015) The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. *J Therm Biol* 54: 86–97.
- Zakšek K, Oštir K, Kokalj Ž (2011) Sky-view factor as a relief visualization technique. *Remote Sens (Basel)* 3: 398–415.
- Zhang YL, Chang XL, Liang J (2017) Comparison of different algorithms for calculating the shading effects of topography on solar irradiance in a mountainous area. *Environ Earth Sci* 76: 295.