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REVIEW ARTICLE

A review of the thermal biology and ecology of molluscs, and of the use of infrared thermography in molluscan research

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ABSTRACT

In an era of global change, thermal biology and ecology are becoming increasingly popular topics in invertebrate research, including molluscs. However, this area of research is still very limited, essentially due to the intrinsic spatial limitations of traditional single-point temperature measurements (e.g. thermocouples, iButtons and infrared thermometers). This is not the case, however, with infrared thermography, which has the desirable attribute of producing images that allow for simultaneous measurements of multiple molluscan individuals, species and communities. Infrared thermography allows for spatial and temporal monitoring of microclimates at scales relevant to individual organisms and hence may represent a first step to bridge the gap between field-based approaches (typically spanning from centimetres to tens of metres) to climatic scenarios (typically coarse-grained, i.e. 10 × 10 km). This review first provides a brief history of infrared thermography, followed by a description of the fundamental physical properties and quantities that bridge the gap between the physics of heat transfer and the physics of infrared thermography. We then thoroughly review the thermal biology and ecology of molluscs, and the previous biological and ecological applications of infrared thermography—including the very few in molluscan research. We provide detailed recommendations related to the proper use of infrared thermography. Finally, we discuss the potential applications of infrared thermography in molluscan research, based on case studies involving both terrestrial and intertidal molluscs, with emphasis on its use as a tool for monitoring impacts of climate change.

THERMAL BIOLOGY AND ECOLOGY IN A CHANGING WORLD

As stated by Angilletta (2013: 1) in his seminal book "unlike many other variables that concern biologists, temperature is not just a property of life; it is a property of matter. Nothing escapes its control." Temperature indeed controls the individual metabolism and performance that ultimately determine fitness of organisms, structure of populations and function of ecosystems (Huey & Berrigan, 2001; Deutsch *et al*., 2008; Angilletta, 2013). The effect of temperature on temporal patterns of growth, survival and reproduction has been widely demonstrated in almost all phyla (Kingsolver, 2009; Kingsolver, Diamond & Buckley, 2013). Yet temperature does not affect different organisms equally (Somero, 2010) and does not affect the same organism equally at all stages of its life cycle (Pörtner & Farrell, 2008). Furthermore, organisms do not experience the same level of exposure to temperature at niche and ecosystem levels (Helmuth *et al*., 2010). In an era where ecosystems are increasingly threatened by anthropogenic climate change, through the increase in both mean temperature and its variability (Walther *et al*., 2002; Parmesan, 2006), Angilletta's statement becomes increasingly pertinent in research fields associated with thermal biology and ecology.

Shifts in phenology and geographic ranges of species, disruptions of ecological interactions, and changes in biodiversity and productivity driven by climate change have now been widely reported in both terrestrial and marine systems (see Beaugrand, 2015, for a recent review on marine ecosystems). However, the mechanistic links between environmental variables and body temperatures of ectotherms that control local (Miller, Harley & Denny, 2009) and global distribution patterns of organisms (Helmuth *et al*., 2002) seem to be much more complex than previously anticipated (Helmuth *et al*., 2011, 2014). The body temperatures of both terrestrial and marine ectotherms are determined by heat fluxes from and towards the organisms (Gates, 1980; Harley *et al*., 2009). These fluxes are controlled by the interactions between climatic factors such as air and water temperatures (Helmuth, 2002; Vidal *et al.*, 2010), nonclimatic heat sources such as solar irradiance and geothermal heating (Marshall, McQuaid & Williams, 2010), and biotic factors such as morphological and behavioural traits (Miller & Denny, 2011). Thermal conditions experienced by ectothermic organisms are thus determined by a multitude of factors, which often vary at fine spatial (metres) and temporal (minutes) scales, resulting in complex patterns in body temperatures (Helmuth *et al.*, 2002; Woods, Dillon & Pincebourde, 2014). In fact, fine-scale thermal variations in body temperatures of ectotherms often exceed those observed between latitudes in both terrestrial (Deutsch *et al.*, 2008; Angilletta, 2013; Potter, Woods & Pincebourde, 2013) and marine systems (Helmuth *et al.*, 2006; Denny *et al.*, 2011; Meager, Schlacher & Green, 2011). In a warming climate, ectothermic organisms, therefore, face the challenge to maintain their body temperatures at preferred ranges within their thermal tolerance windows by responding to heat stress over a range of (1) temporal scales spanning from minutes to generations (Barnes *et al.*, 2006; Bradshaw & Holzapfel, 2006) and (2) spatial scales ranging from small-scale habitats to large-scale geographic distances (Osovitz & Hofmann, 2007; Denny *et al.*, 2011; Stafford *et al.*, 2015).

In this context, measuring temperature, *a priori* an apparently simple task, is in fact particularly challenging as the understanding of the effect of both hydroclimatic variations and climate change on ectothermic organisms *de facto* requires information on the temperatures of both the environment and the organisms at temporal scales ranging from minutes to decades and spatial scales ranging from centimetres to thousands of kilometres. This complexity is emphasized by recent evidence that latitudinal patterns of both acute and chronic heat stress may be decoupled from average temperatures, which are typically assumed to decline with increasing latitude (Lathlean, Ayre & Minchinton, 2014). Traditionally, environmental and organismal temperatures have been measured using a range of data loggers (e.g. TidBit, iButton; Angilletta & Krochmal, 2003; Davis, Taylor & Denardo, 2008; Janisch, Wondzell & Ehinger, 2012), thermocouples (Iacarella & Helmuth, 2011) and biomimetic loggers (Lima & Wethey, 2009; Lathlean *et al.*, 2014; Helmuth *et al.*, 2016). All these devices, however, share intrinsic limitations that prevent them from providing synoptic information on both environmental and organismal temperatures at the high spatial resolutions needed to capture small and broad-scale patterns of heat stress (Osovitz & Hofmann, 2007; Denny *et al.*, 2011; Lathlean, Ayre & Minchinton, 2014). Data loggers allow single-point measurements that are limited by their battery life and the very high costs that would be associated with any attempt to cover large distances or surfaces at a spatial resolution compatible with the biology and ecology of individual organisms. Both wired thermocouples (contact or tissue-penetrating) and infrared thermocouples are essentially point measurements of body surfaces, and hence only appropriate for organisms with a limited mobility (Etter, 1988; Helmuth, 1999). Biomimetic loggers, even if they have been developed to match the thermal properties of a range of target organisms (Lima & Wethey, 2009; Szathmary, Helmuth & Wethey, 2009; Lima *et al.*, 2011; Seabra *et al.*, 2011; Lathlean *et al.*, 2014), cannot take into account behavioural thermoregulation (Muñoz *et al.*, 2005; Dubois *et al.*, 2009) or behaviourally-driven selection of thermal refuges (Chapperon & Seuront, 2011a, b). Simultaneous high-resolution measurements of both environmental and organismal temperatures are, however, achievable with infrared thermography if appropriate conditions are met (see below).

Here, we first provide a brief history of infrared thermography. We next describe the fundamental physical principles behind infrared thermography and provide an overview of its importance to studies of the biology and ecology of molluscs. The general applications of infrared thermography to a range of physiological, biological and ecological questions are briefly considered. We then thoroughly review the thermal biology and ecology of molluscans, and the previous applications of infrared thermography to their study, including the still very limited amount of published information on the use of thermal imaging. We provide detailed recommendations for the proper use of infrared thermography. Finally, we consider promising areas for the future applications of infrared thermography in molluscan research, in particular in the context of climate change. These areas are illustrated using recent published and unpublished data taken from a wide range of environments and latitudes, to ensure a broad perspective.

A BRIEF HISTORY OF INFRARED THERMOGRAPHY

Even though no temperature-sensing device in a strict sense was available until the so-called Galileo thermometer in *c.* 1603 (Loyson, 2012), the ancient Egyptians had an intuitive knowledge of heat radiating from the human body. As reported by Herodotus (484–425 BC), they moved their hands across the surface of the body to scan and evaluate changes in temperature (Herodotus, 1954). Temperature changes were either localized to a specific area or detected over the entire body (Nunn, 2002; Allen & Mininberg, 2005). The ancient Egyptian practice was formalized in 400 BC by the Greek physician Hippocrates (460–370 BC), who wrote that “in whatever part of the body excess of heat or cold is felt, the disease is there to be discovered” (Diakides, Bronzino & Peterson, 2012: 132). The ancient Greeks covered the body in wet mud and the area that dried most quickly indicated the warmest region, and was considered the diseased part (Hodge, 1994). Hippocrates is even credited with describing an early version of a two-dimensional skin temperature-measuring device: a moist linen cloth covering an area of skin to produce an impression of surface temperatures by means of the change in cloth colour (Otsuka & Togawa, 1997).

Infrared radiation remained scientifically unknown until William Herschel (1738–1822) studied the heating effect of different colours of light. Building on Newton’s discovery that visible light could be refracted into distinct colour bands, Herschel used a prism to produce a spectrum of colours and measured their heating effect with thermometers (Fig. 1A). He discovered that this effect increased on moving from the blue to the red end of the spectrum. He also noticed that the ‘dark light’ just beyond the range of visible red also produced heat, providing the first evidence for an infrared form of light in part of the electromagnetic spectrum invisible to the human eye (Rogalski, 2012). This radiation, called ‘dark heat’ or ‘calorific rays’ (Herschel, 1800), can be reflected, absorbed and transmitted just like visible light (Barr, 1960, 1961), providing the first evidence for a thermal form of electromagnetic radiation (Rogalski, 2012). The visible light spectrum (as detected by the human eye under daylight conditions) is restricted to a narrow range of wavelengths (0.39–0.78 μm). In turn, the spectrum of infrared radiation ranges from 0.78 μm (i.e. just beyond the visible range) up to a wavelength of 1,000 μm (i.e. close to microwaves; Fig. 1B). The wavelength of infrared radiation utilized by infrared cameras ranges from 0.78 to 14 μm (Kastberger & Stachl, 2003) and can be subdivided into near-infrared (NIR; 0.78–1.7 μm), short-wavelength infrared (SWIR; 1–2.5 μm), mid-wavelength infrared (MWIR; 2–5 μm) and long-wavelength infrared radiations (LWIR; 8–14 μm). Of these four wavelength ranges, SWIR and especially NIR should not be considered as thermal bands in a strict sense, since they are close to the visible spectrum and share some of its properties (Vollmer & Möllmann, 2010).

MWIR and LWIR are the most commonly used bands in infrared thermography (Usamentiaga *et al.*, 2014). Infrared cameras operating in the MWIR and LWIR regions of the spectrum are

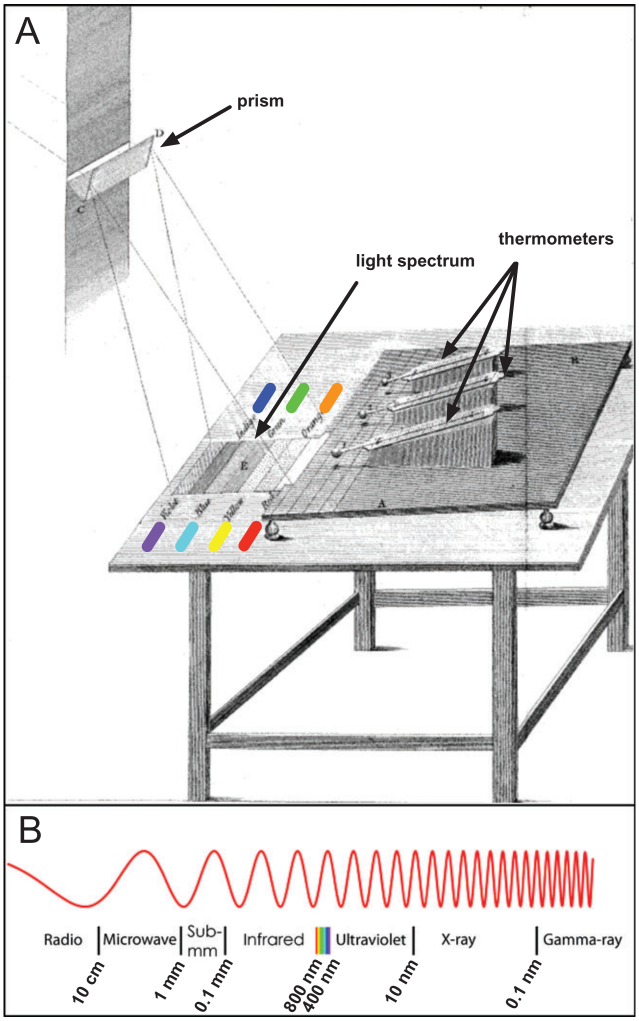

Figure 1. A. Experiment conducted by William Herschel (1738–1822) to demonstrate that the heating effect of the different colours of the visible spectrum increases from the blue end of the spectrum to the red (modified from Herschel, 1800). **B.** Schematic representation of the spectrum of electromagnetic radiation.

typically used for high and ambient temperature measurements (Usamentiaga *et al.*, 2014). Most thermal infrared cameras used in biological applications operate within the LWIR region, often referred to as the 'thermal infrared range' (Kastberger & Stachl, 2003; Lathlean & Seuront, 2014; Tattersall, 2016). LWIR cameras are preferred in biological applications as they are less influenced by the presence of moisture than MWIR cameras (Usamentiaga *et al.*, 2014) and because they are more affordable, portable and rugged (Lathlean & Seuront, 2014). Note, however, that MWIR cameras are less influenced by optical and electronic noise, and hence offer detection performances superior to those of LWIR cameras due to a reduced signal-to-noise ratio; in other words they typically make up for their reduced radiance detection by a much better detection accuracy (Usamentiaga *et al.*, 2014; see Jorge Aldave *et al.*, 2013, for a review of the relative performances of MWIR and LWIR cameras). The signal-to-noise ratio, however, depends also on the sensitivity of the infrared detector, which can either be cooled or uncooled. Cooled infrared cameras are designed to maximize detection performance through the incorporation of a cryogenic cooling system that reduces the internal temperature of the imaging sensor to much below ambient, in order to reduce the thermal noise induced by the camera components and the infrared sensor itself. These devices allow the detection of thermal radiation with an accuracy as fine as 0.025 °C (Usamentiaga *et al.*, 2014). Uncooled cameras, though less accurate, are generally preferred in biological applications (Kastberger & Stachl, 2003) as, without a cryogenic cooler, they are again more affordable, portable and rugged than cooled ones (Lathlean & Seuront, 2014). As an example, a cooled MWIR camera will offer superior performance with respect to an uncooled LWIR detector, even in the 15–55 °C range.

The pioneering work of Herschel led ultimately to the development of infrared sensors essentially used as thermal detectors (such as thermocouples and bolometers), which are still used today, and to the more sensitive and faster photon detectors. Thermal detectors were extensively developed in the 20th century, driven by military applications. The first bolometers were used for the remote detection of people (up to 200 m) and aircraft (up to 1,000 m) in 1914, the first infrared image converter in 1934 and infrared display units in 1939. The origin of modern infrared technology was rooted in the research and development effort conducted during World War II, followed by the ever-growing development of high-performance sensors, which have been extensively used for military, industrial and medical applications (see Biberman & Sendall, 2000; Vollmer & Möllmann, 2010; Rogalski, 2012, for reviews).

Infrared thermography now allows noninvasive and real-time visualization of fixed or transient changes in the long-wave radiant energy emanating from an object, hence allowing for the estimation of surface temperature of various substrata and organisms. Recent technological advances in thermal-imaging cameras (i.e. smaller size, reduced power requirements, and increased portability, ruggedness, resolution and sensitivity, together with a significant reduction in cost) have facilitated and expanded their use (Zalameda & Winfree, 2005; Lathlean & Seuront, 2014). This technology is particularly appealing in the research fields of thermal biology and ecology, landscape ecology, behavioural ecology and physiology, as it allows noninvasive measurements of surface temperature patterns over a very broad range of scales—ranging from ocean basins and continents (Kerr & Ostrovsky, 2003) to landscapes (Scherrer & Körner, 2010; Faye *et al.*, 2016; Faye, Dangles & Pincebourde, 2016) and individual organisms (Tattersall & Cadena, 2010; Pincebourde, Sanford & Helmuth, 2013; Tattersall, 2016). More detailed reviews of the history of the discovery of the infrared portion of the light spectrum and its major players, and the subsequent evolution of infrared detectors, have been given by Barr (1960, 1961, 1962), Hudson (2006) and Rogalski (2012).

FROM THE PHYSICS OF HEAT TRANSFER TO THE PHYSICS OF INFRARED THERMOGRAPHY

Heat is transferred by three mechanisms: radiation, conduction and convection. This is critical to understanding the physics of infrared imaging, as well as the thermal biology and ecology of ectotherms in general and molluscs in particular, because rates of both body heating and cooling fundamentally drive organismal energy budgets (Angilletta, 2013). These mechanisms and the fundamental physical laws that drive them are therefore briefly described. Readers interested in reaching a deeper understanding of the physics of thermal radiation and heat transfer are referred to Incropera *et al.* (2006) and Sundén (2012) for an introduction to these topics, and Ghoshdastidar (2012), Hahn (2012), Bejan (2013), Modest (2013), Balaji (2015), Howell, Mengüç, and Siegel (2015) and Stewart & Johnson (2016) for details of the physics and related computational tools.

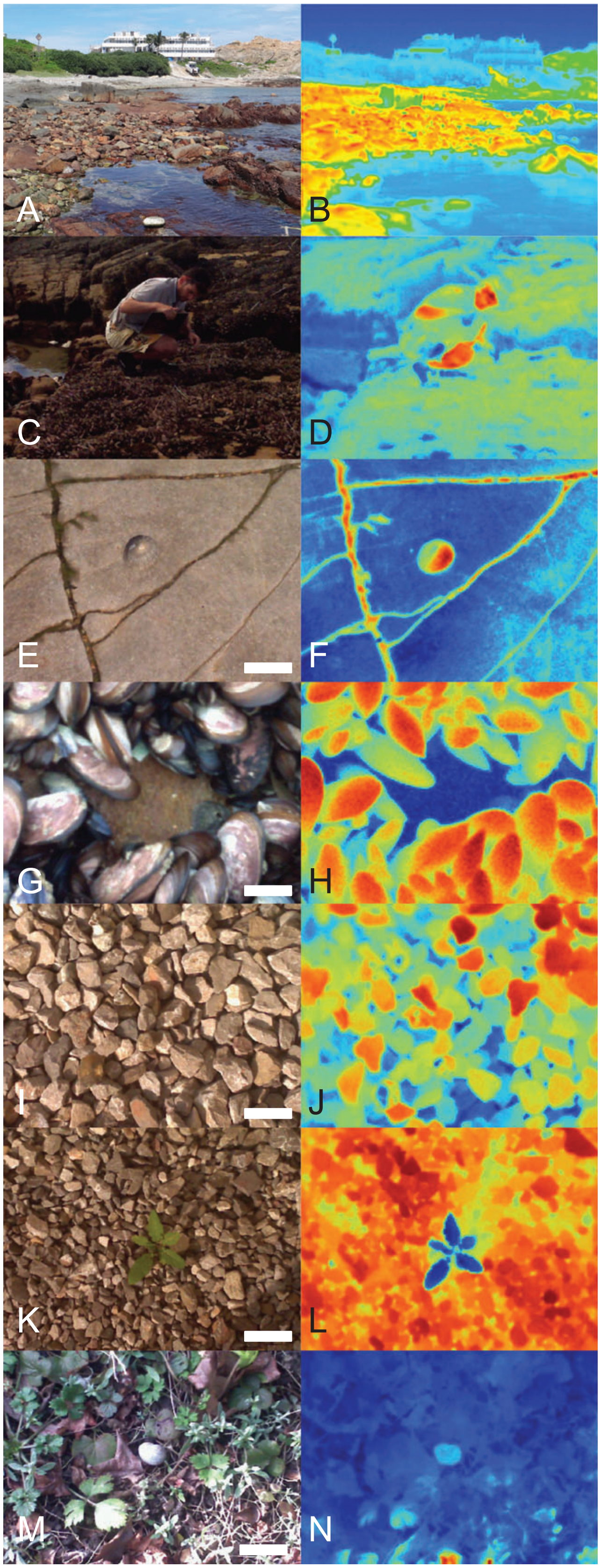

Figure 2. Digital images of various landscapes and organisms shown with the corresponding infrared images, i.e. thermograms, obtained with thermal cameras Testo 875-1iSR (A, B) and Fluke Ti25 (C–N). **A, B.** The Swire Institute of Marine Science, Hong Kong, with surrounding vegetation and rocky intertidal shore. **C, D.** One of the authors, J. Lathlean, at work on an intertidal rocky reef in Jorgensfontein, South Africa (note clear differences in body temperature signatures of exposed and nonexposed body parts. **E, F.** *Patella vulgata* on an intertidal rocky reef at Noirda Point, Audresselles, France (note hot thermal signatures of both limpet and crevices on a background of cooler rock). **G, H.** Native *Perna perna* and invasive *Mytilus galloprovincialis* in a mixed bed on an intertidal rocky reef, Jorgensfontein, South Africa. **I–L.** Rock assemblages of various sizes, the typical habitat of the pulmonate snails *Candidula unifasciata*, *Cernuella virgata* and *Cochlicella acuta*; Wierre-Effroy, France. Note thermal heterogeneity of rocks seemingly similar in shape, colour and size in both assemblages (**J, L**) and cool thermal signature of the vegetation (**L**). **M, N.** *Cornu aspersum* in its typical environment; Wasquehal, France. Scale bars = 5 cm.

Radiation

Both inanimate and animate objects with a temperature above absolute zero (i.e. –273.15 °C) emit thermal energy as a result of molecular motion. In addition, the main source of heat experienced on Earth comes from the sun's electromagnetic radiation, which transmits a fraction of its energy flux in the form of infrared radiation to Earth's atmosphere, water bodies and land masses (Phillips, 1995). All objects emit an energy flux ϕ. This flux of energy is detected by infrared or thermal cameras and converted to images called 'thermograms' (Fig. 2). By inducing a gradient of heat across the surface of a thin oil film, William Herschel showed that a visual interference pattern could be revealed by differential rates of evaporation, thereby producing the first visualization of temperature on a surface (Rogalski, 2012). To explain the relatively complex physics behind the use of a thermogram to estimate an object's temperature at a distance, we provide a short primer of essential concepts such as black-body radiation, Wien's displacement law of electromagnetic radiation, Kirchhoff's radiation law, the Stefan-Boltzmann law and emissivity, which need to be understood in order to conduct thermal measurements and interpret the subsequent thermograms reliably.

Black body radiation and Planck's law: A 'black body' is an ideal object that completely absorbs all the electromagnetic radiation that it receives at every wavelength. Note that the term 'black' does not refer to the colour of an object; rather, it describes how a black body behaves similarly with respect to all wavelengths. In fact, no objects in nature are true black bodies, because all objects emit electromagnetic radiation in part of the electromagnetic spectrum, dependent on their temperature. This concept is central to understanding how thermal imaging operates. It is summarized in Planck's law, which defines the spectral radiance of the electromagnetic radiation $I(\lambda, T)$ emitted by a black body in thermal equilibrium at a given temperature T as a function of the radiation wavelength λ according to the equation:

$$I(\lambda, T) = \frac{2hc^2}{\lambda^5}\frac{1}{e^{hc/\lambda kT} - 1} \qquad (1)$$

where h is the Planck constant ($h = 6.62607004 \times 10^{-34}\ \mathrm{m^2\,kg\,s^{-1}}$), k is the Boltzmann constant ($k = 1.38064852 \times 10^{-23}\ \mathrm{m^2\,kg\,s^{-2}\,K^{-1}}$) and c is the speed of light in a vacuum ($c = 299{,}792{,}458\ \mathrm{m\,s^{-1}}$). Eq. (1) implies that the spectral radiance $I(\lambda, T)$ peaks at a characteristic wavelength inversely related to black-body temperature (Fig. 3). For instance, the Sun (at $T = 5{,}800$ K) emits radiation that peaks in the visible part of the spectrum, at wavelengths of about 0.5 µm. In contrast, a human ($T = 310$ K) emits radiation peaking at around 10 µm, i.e. in the infrared part of the spectrum. This is formalized in the following law.

Wien's displacement law. Wien's displacement law describes how the spectral radiance of a black body peaks at a wavelength $\lambda_{\max}$ that is inversely proportional to the temperature (Fig. 3):

$$\lambda_{\max} = b/T \qquad (2)$$

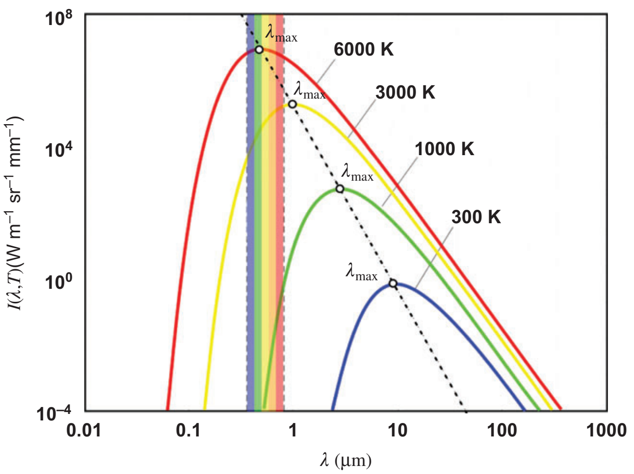

Figure 3. Spectral radiance of the electromagnetic radiation $I(\lambda,T)$ of an ideal black-body shown as a function of the radiation wavelength λ and temperature T following Planck's law. The peaks observed in spectral radiance for each black-body temperature lead to an inverse relationship between wavelength and temperature, i.e., known as Wien's law.

where b is Wien's displacement constant ($b = 2.8977721 \times 10^{-3}$ K m). Wien's law implies, for example, that the colour of stars is determined by their temperature. More practically, it implies that since sensors absorb infrared radiation within limited wavelength ranges according to the material of which they are made, the sensitivity of a given sensor needs to be matched to the range of temperatures being examined in order to achieve a maximum signal-to-noise ratio. For instance, for molluscan body temperatures in the range 15–55 °C (Chapperon & Seuront, 2011a, b; Seuront & Ng, 2016), λ_{max} ranges from 8.8 to 10.1 µm, which is within the range of sensor sensitivity used for biological applications (Kastberger & Stachl, 2003; Lathlean & Seuront, 2014; Tattersall, 2016), i.e. LWIR (8–14 µm).

Energy conservation law and Kirchhoff's radiation law: The energy conservation law states that, at thermodynamic equilibrium, at a given wavelength, the incident radiant energy flux F_i arriving at an object is either transmitted, absorbed or reflected; hence:

$$F_{\mathrm{i}} = F_{\mathrm{transmitted}} + F_{\mathrm{absorbed}} + F_{\mathrm{reflected}} \tag{3}$$

Or, equivalently:

$$\tau + \alpha + \rho = 1 \tag{4}$$

where τ, α and ρ are, respectively, the fractions of the incident radiation that are transmitted, absorbed and reflected, i.e. the transmittance, absorbance and reflectance coefficients. Eq. (4) can be simplified to $\alpha + \rho = 1$ as, in most materials, including biological surfaces, $\tau = 0$ (i.e. no fraction of the incident radiant flux is transmitted through the material), so all the incident radiation is either absorbed or reflected. Kirchhoff's law states that, because an ideal black body does not reflect any radiation, the conservation of energy implies that all the radiation absorbed by such a body is emitted, hence $\varepsilon = \alpha$, where the emittance coefficient (or emissivity) ε is the fraction of the black body energy that is emitted (Fig. 4). Since $\alpha + \rho = 1$, then $\varepsilon + \rho = 1$, which more prosaically translates as 'good absorbers are good emitters' (i.e. $\varepsilon = \alpha$) and its corollary 'good reflectors are poor emitters' (i.e. $\varepsilon + \rho = 1$). A notable consequence of these statements is that no physical object can emit more radiation than a black body, since emissivity is the ratio of the object's radiant flux (M_r) to that of a black body at the same temperature (M_b), that is $\varepsilon = M_r/M_b$. Emissivity then equals one ($\varepsilon = 1$) for an ideal black body, and $\varepsilon < 1$ otherwise (Fig. 4).

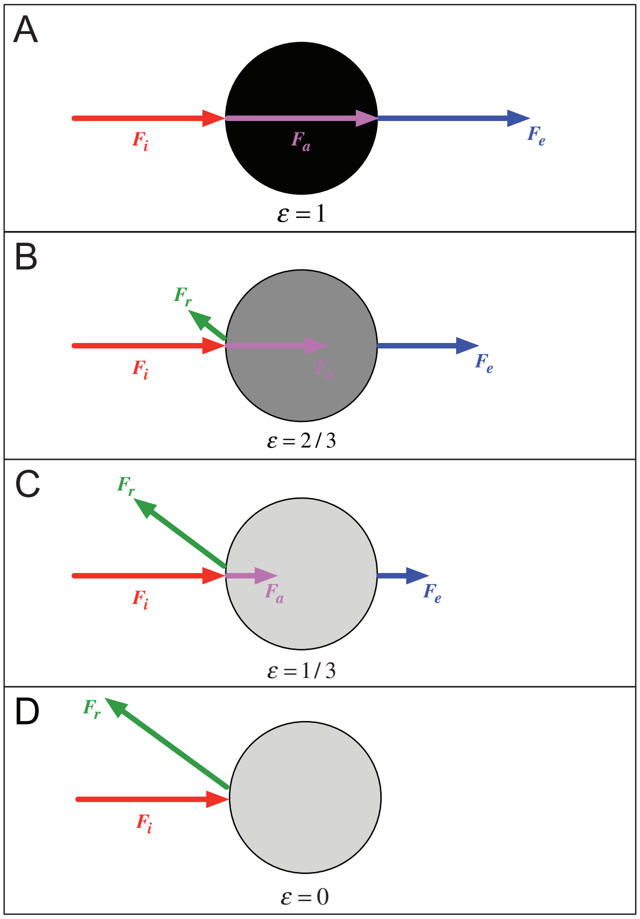

Figure 4. Schematic illustration of fate of an incident radiative energy flux F_i on a black body (**A**) and on grey bodies with various emissivities ε (**B–D**). **B.** $\varepsilon = 2/3$. **C.** $\varepsilon = 1/3$. **D.** $\varepsilon = 0$. Incoming radiation is totally absorbed (F_a) by a black body and owing to the conservation of energy all absorbed radiation has to be emitted (F_e), hence $F_a = F_e$. On a grey body a fraction of the incident flux F_i can be reflected (F_r), absorbed (F_a) or transmitted (F_t). For the sake of simplicity, F_t has been ignored, as it is usually negligible, hence $F_i = F_a + F_r$ (**B**, **C**). Under conditions of thermodynamic equilibrium, Kirschoff's law implies that the amount of radiation emitted (F_e) must be equivalent to radiation absorbed, thus Fe is usually equal to $F_a = F_i - F_r$, meaning that there is generally an inverse relationship between an object's emissivity and reflectivity. A grey body with a high emissivity (**B**) will then emit more energy than a grey body with a low emissivity (**C**). A perfectly reflective object (**D**) does not absorb any of the incident radiation, leading to $F_i = F_r$, hence $F_a = F_e = 0$.

Stefan-Boltzmann law: The Stefan-Boltzmann law describes how the total energy radiated per unit surface area of a black body across all wavelength per unit time (i.e. the radiant flux M_b) is directly proportional to the fourth power of the black-body temperature T:

$$M_b = A\sigma T^4 \tag{5}$$

where σ is the Stefan-Boltzmann constant ($\sigma = 5.66697 \times 10^{-8}$ W m^{-2} K^{-4}) and A the surface area. Note that Eq. (5) results from integrating Eq. (1) through all wavelengths λ from zero to infinity. For an object that does not absorb all incident radiation (often referred to as a 'grey body'), the Stefan-Boltzmann law has to be reformulated, taking account of the emissivity ε of the object (i.e. $\varepsilon < 1$), as:

$$M_r = A\sigma\varepsilon T^4 \tag{6}$$

Note that the emissivity of a grey body is constant and independent of the wavelength. Real objects cannot be considered as grey bodies in the strict sense, as their emissivity is neither constant nor independent of the wavelength (Usamentiaga *et al.*, 2014). However, emissivity varies slowly with wavelengths for solid objects (Usamentiaga *et al.*, 2014), which appear to have an approximately constant emissivity in the infrared region of the radiation spectrum. Emissivity is then typically assumed to be constant for narrow wavelength intervals. In practice, this means that real objects are treated as grey bodies by averaging their emissivity over the short intervals in which infrared sensors work.

Emissivity

According to Kirchhoff's law of thermal radiation (see above), the amount of energy emitted by an object is driven by its emissivity ε (Siegel & Howell, 2001; Fig. 4). Emissivity is the ability of an object to emit thermal radiation; it ranges between $\varepsilon = 1$ for a black body, a perfect absorber of thermal radiation (Fig. 4A), and $\varepsilon = 0$ for an object that reflects all electromagnetic radiation (Fig. 4D). Most objects selectively radiate electromagnetic radiation, with wavelength-specific emissivities from 0 to <1. In contrast, a grey body has a constant emissivity ($\varepsilon < 1$) across all wavelengths under consideration (see above), a property used in thermal modelling. As mentioned above in relation to the Stefan-Boltzmann law, one fundamental assumption of thermal imaging is that most objects behave like grey bodies with respect to infrared radiation and hence can be described using a single emissivity value (Fig. 4B, C).

Emissivity is independent of surface colour. For instance, white marble, limestone and coal share a similar emissivity of *c.* 0.95 in the infrared wavelength range, which *a priori* seems counterintuitive, because dark and white surfaces differ in their abilities to absorb visible light. Nevertheless, both dark and white surfaces absorb radiation very well in the infrared spectrum and hence share a comparable high emissivity. In contrast, emissivity does depend on surface texture. Smooth and polished surfaces reflect radiation very well and hence have a low emissivity. In turn, rough and textured surfaces reflect light less efficiently, so have a higher emissivity than smooth ones. These properties are best illustrated by Leslie's cube, a device used to demonstrate the differences in thermal radiation emitted from surfaces heated to the same temperature, but differing in colour and texture (Fig. 5; see Vollmer & Möllmann, 2010, for more details).

Water content is another factor that is likely to affect the emissivity of an object, since water is an excellent emitter of thermal radiation. The relationship between emissivity and both soil moisture and vegetation water content has been a prolific topic for decades (see Petropoulos, 2014; Srivastava, Petropoulos & Kerr, 2016, for reviews). Note, however, that wet surfaces have to be treated with caution, especially in the context of molluscan research where surface temperatures are frequently used as proxies of body temperature (Lathlean & Seuront, 2014; Seuront & Ng, 2016). Though water films have very high emissivity (typically $\varepsilon \geq 0.9$), wet surfaces reflect more incident radiation than dry ones (especially in full sunlight) and this effect increases when the viewing angle between the camera and the object decreases (Clark, 1976;

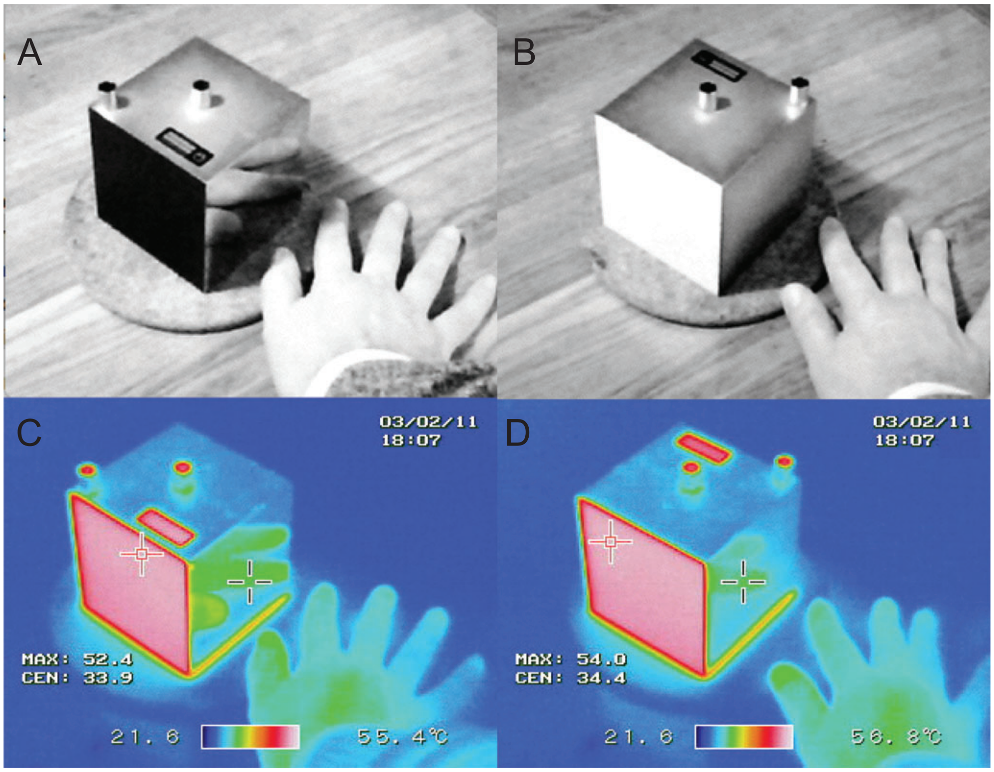

Figure 5. Digital (**A, B**) and infrared (**C, D**) images of Leslie's cube. This aluminium device shows how the nature (colour and texture) of surfaces of the different faces of the cube in thermal equilibrium (here 55 °C) influences their emission of thermal radiation. The two faces painted in black (**A**) and white (**B**) both emit thermal radiation strongly (red colour on thermograms **C, D**). In contrast, the reflective mirror-like polished (**A**) and unpolished (**B**) faces of the cube emit much more weakly (blue in **C, D**) and the reflected image of the warm hand is clear (**C**). Note that reflection of the hand on both aluminium faces is green, indicating a high emissivity surface near body temperature (37 °C). Photo credit: Pieter Kuiper, Public Domain, https://commons.wikimedia.org/w/index.php?curid=13303826.

Faye, Dangles & Pincebourde, 2016). As a consequence, these surfaces appear cooler than dry ones, which may lead to a systematic underestimation of ectotherm (including molluscan) body temperature using infrared thermography. This source of error could be limited by keeping the viewing angle close to 90° (Clark, 1976), by experimenting when conditions are overcast, or even avoided by carrying out measurements at night. Nevertheless, since thermal stress is obviously greatest during the middle of the day when the sun is highest, and it is often the response to these intense periods of heat stress that concern ecologists, none of the aforementioned solutions are recommended. A practical alternative would be to temporarily shade ectotherms while thermal images are being recorded. Note also that wet surfaces can actually be cooler than dry ones when evaporative cooling (i.e. the process by which the energy needed to convert water into vapour leads to heat loss; see below) takes place. Cooling the surface of the shell of a mollusc, however, does not imply a reduction in the core body temperature, as this would require thermal equilibrium—which only occurs after a delay that depends primarily on the size of the organism and the conductive properties of its tissues.

The emissivity of an object may also depend on its morphological complexity (Van Alstyne & Olson, 2014) and structural composition (Rubio, Caselles & Badenas, 1997). For instance, the emissivity of intertidal macroalgae with flat surfaces is relatively constant at the scale of a few centimetres, but varies more in algae with papillate surfaces and in species composed of thin stems and branches (Van Alstyne & Olson, 2014). These results may be related to the intrinsic changes in the angle θ between the infrared camera and the topologically complex surface. Note that the angle effect increases with decreasing values of θ.

It is essential to understand the properties described above and the implication that the visual appearance of the surface of an object may be a poor indicator of its emissivity. As discussed below, there are fundamental implications for the thermal biology of molluscs and for their abiotic and biotic environments. It must be stressed that, beyond the emissivity of an object and the absolute quantity of incident infrared radiation, both the orientation of its surface relative to the sun and its surface-to-volume ratio determine the amount of heat that is transferred to the object (Gates, 1980). This is particularly relevant for terrestrial and intertidal invertebrates in general, and in particular for molluscs and their substrata, which are heated up by both direct solar radiation (Fig. 6A) and solar radiation reflected by vegetation and topographic features (Fig. 6B) during the day; infrared radiation is also emitted at night, but reflected radiation strongly decreases. Heat radiation is subsequently emitted from both abiotic and biotic objects (Fig. 6C). Note, however, that while a significant amount of solar radiation is reflected by the atmosphere and clouds (*c.* 25%) and absorbed by the atmosphere (*c.* 2%), a variable amount of the radiation reaching the surface of the Earth (*c.* 50%; e.g. Miller & Wheeler, 2012) may be lost depending on the reflective properties of the objects (Fig. 6D).

Conduction

Conduction is the heat transfer between two objects in contact with one another. Heat travels down a thermal gradient, in exactly the same way that molecules move passively down a gradient in concentration; heat is, therefore, conducted from a warmer to a colder object. This property applies to both the heat conduction between an organism and its substratum (Fig. 6E) and the heat conduction between two organisms in contact with each other. Heat conduction also applies to a single object, when its core temperature differs from its surface temperature (Fig. 6F; Oke, 1987). Specifically, the rate of heat conduction from an object (either inanimate or animate) depends on (1) the conductivity (or rate at which it conducts heat), i.e. the amount of heat that flows per unit of time through a unit area with a temperature gradient of one degree per unit distance (Perry & Green, 2008; for living organisms, the higher their conductivity, the more energy they need per unit of body mass to maintain their heat balance); (2) the size (or volume), i.e. the smaller the object, the shorter the distance heat must travel; (3) the thermal inertia, which depends on the object's mass and heat capacity, and (4) the surface area that is physically in contact with other objects. As a consequence, the surface-to-volume ratio is a critical parameter, because both abiotic and biotic objects gain (or lose) heat via conduction from (or to) surfaces and objects they are in contact with, but also between their core and surface, when these are at different temperatures. In contrast to endotherms which have varying degrees of insulation (e.g. feathers, fur and/or fat deposits) that enable them to retain their internal heat (Fig. 7A, B) and hence to rely less upon external heat sources, ectotherms and their (vegetal or mineral) substrata have no insulation (Fig. 7C–F) and hence have a higher thermal conductivity (i.e. they easily gain or lose heat from/to the objects with which they are in contact). Note that insulation would be detrimental to ectotherms, because it would slow the rate of heat transfer into the body (Speakman, 2004); as an example, mammalian fur has a thermal conductivity that is more than one order of magnitude lower than mammalian tissue (Schmidt-Nielsen, 1997).

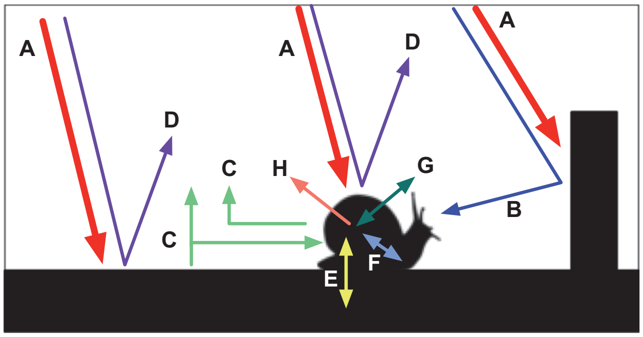

Figure 6. Diagram of the heat exchange pathways between a mollusc and its environment; these include radiation, conduction, convection and evaporation. Heat radiations originate directly from the sun (**A**) after a significant proportion (c. 30%) has been reflected by the atmosphere, clouds and the surfaces of land, lakes and oceans (**D**), and indirectly through reflected solar radiations, including diffuse scattering of radiation in the atmosphere (**B**) and from both abiotic and biotic objects (**C**). Conduction occurs between objects in contact with each other (**E**); conduction also occurs within a single object, when its core temperature differs from its surface temperature (**F**). Convective heat transfer occurs between an object and the surrounding moving fluid (i.e. water or air) (**G**). Evaporative cooling (**H**) is the process by which an organism's body temperature decreases through the energy required to convert liquid to gas; in contrast to radiation, conduction and convection, evaporation is not a mechanism of heat transfer but a source of latent heat.

Convection

Convection is the heat transfer between an object and the surrounding fluid, e.g. water or air, when they have different temperatures (Fig. 6G). In contrast to heat transferred via electromagnetic waves (heat radiation), heat convection is driven by the motion of the fluid surrounding an object (Denny, 1993; Cengel, 2003). Note that in the unlikely instance where the fluid surrounding an object is stagnant, heat transfer occurs in the form of conduction as described in the previous section. Heat convection can be subdivided into free convection and forced convection, where the motion of the surrounding fluid is driven, respectively, by the buoyant forces resulting from the changes in fluid density driven by a temperature gradient or by an external force such as advection or turbulence. As stated for heat conduction, the rate of heat transfer is

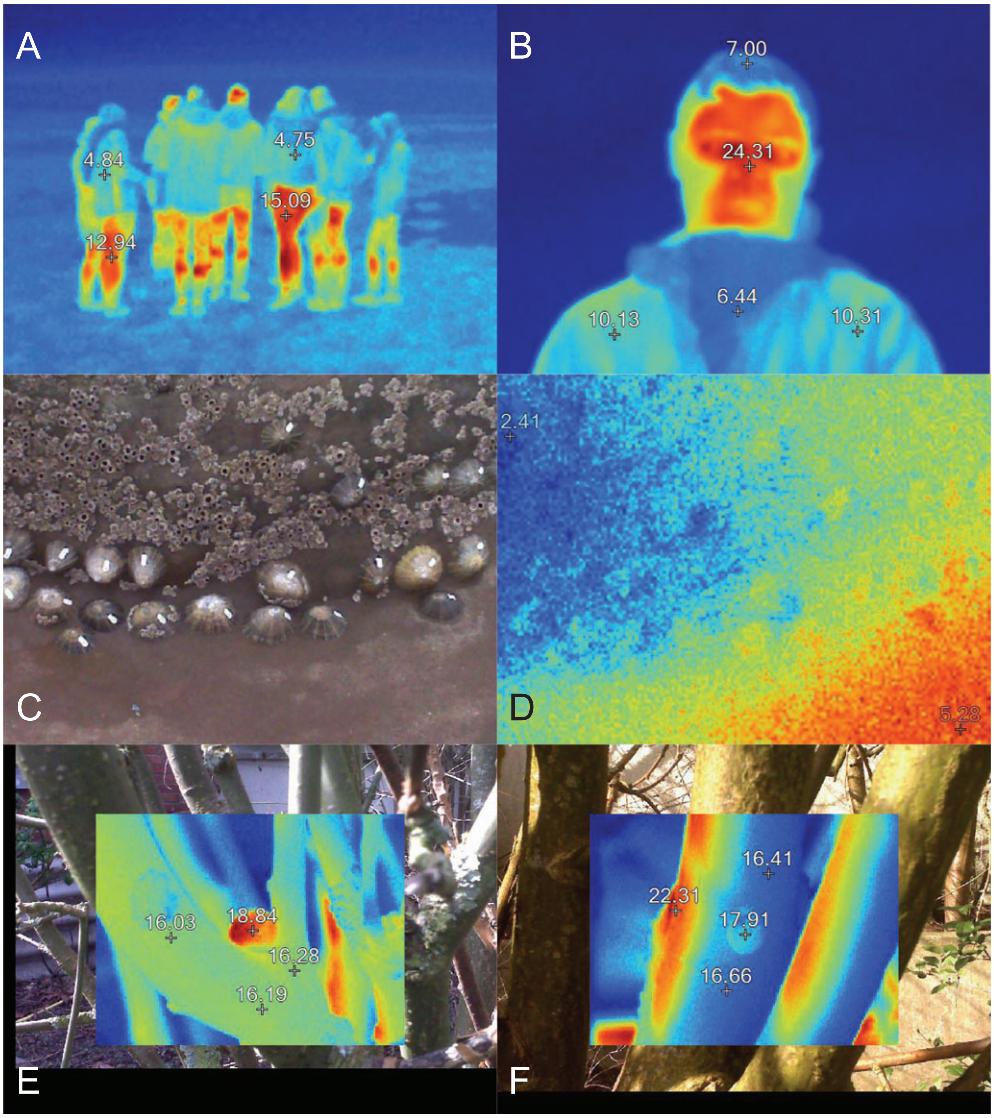

Figure 7. Illustrations of the effects of presence and absence of insulation in the thermal ecology of endothermic (**A, B**) and ectothermic (**C–F**) organisms. **A**. A group of students on a French rocky shore in winter (air temperature 3 °C), showing differences in thermal signatures of insulated (torsos with winter coats; surface temperature in range 4.5-4.9 °C) and noninsulated (legs with trousers; surface temperature in range 12.7-15.5 °C) body parts. **B.** Close-up of a student showing lower surface temperatures produced by insulation provided by hair and winter clothing, compared to face surface. **C, D.** Digital and thermal images of group of *Patella vulgata* on rocky intertidal substratum during overcast midday winter low tide in absence of wind, showing lack of thermal signature of the limpets. **E, F.** Thermal signature of *Cepaea nemoralis* resting on tree branches in sun (**E**) and shade (**F**), illustrating the direct link between solar radiations and body temperature in molluscs.

controlled by (1) the magnitude of the temperature gradient between the object and the fluid, (2) the area of contact between the object and its surrounding fluid, and (3) both the thermal and hydrodynamic properties of the fluid. For instance, water conducts heat 23–25 times faster than air, making water the more efficient medium for heat loss.

Evaporation

Evaporation is the process by which a liquid converts to a gaseous state. In contrast to radiation, conduction and convection, which are the three mechanisms of heat transfer (i.e. transport of thermal energy), evaporation is not a mechanism of heat transfer, but a phase transition between a liquid and a gaseous state that involves energy. As such, evaporation is a *source of latent heat*. If an object is covered by a film of water that evaporates, the surface of the object cools down, but the mechanism responsible for heat transfer is essentially convection, i.e. the energy from the surface is transported via water molecules into the surrounding air, and this is convection. In the present context, the energy needed to convert water to gas allows an organism to lose heat even if its body temperature is cooler than the environmental temperature (Fig. 4H; Denny, 1993). This process, referred to as evaporative cooling, is often the only mechanism available to organisms during prolonged exposure to solar radiation by which to dump excess heat efficiently, in an effort to maintain a safe body temperature. In its simplest form (e.g. panting or mouth gaping), evaporative cooling is a very effective strategy used by mammals, birds and reptiles to prevent overheating (Spotila, Terpin & Dodson, 1977; Tattersall & Gerlach, 2005). However, if the air is saturated with water (during periods of high relative humidity or in constantly humid environments), evaporation as a thermoregulatory mechanism becomes inefficient, because net evaporation ceases when the air can no longer absorb additional moisture (Speakman, 2004).

FROM THE PHYSICS OF HEAT TRANSFER TO THE THERMAL BIOLOGY AND ECOLOGY OF MOLLUSCS

This section briefly reviews how the fundamental mechanisms of heat transfer described above apply to molluscs, whether terrestrial or intertidal, that exchange heat with their environment intermittently through their foot during periods of locomotion and constantly through their shell. Note that because infrared thermography is not applicable in water (see Lathlean & Seuront, 2014) subtidal marine species and aquatic freshwater species are not considered hereafter.

Heat transfer and microhabitat selection

Microhabitat selection (e.g. of shaded topographical features) is common in both terrestrial and intertidal snails, and is generally considered as an adaptive behavioural response to thermal stress associated with heat radiation from the sun and heat conduction from the substratum (e.g. Chang & Emlen, 1993; Jones & Boulding, 1999; Chapperon & Seuront, 2011a; Cartwright & Williams, 2012). The roles of heat radiation, conduction and convection in driving microhabitat choice of molluscs are, however, difficult to disentangle. For instance, the mangrove snail *Littoraria scabra* selects its substratum based on the surface temperature of the substratum (Chapperon & Seuront, 2011a). The selected cooler substrata are, however, consistently located on the underside of *Rhizophora* roots and, hence, in the shade (Chapperon & Seuront, 2011a). The relative contribution of these three processes of heat transfer is also likely to be time-dependent (e.g. day *vs* night) and context-dependent (e.g. windy *vs* still). Sheltered microhabitats (e.g. crevices, vertical rock faces, gullies and logs) may reduce the effectiveness of convective cooling of individuals by air currents. For example, crevices have traditionally been considered to be thermal refuges for intertidal molluscs (Garrity, 1984). Recent studies have shown, however, that they may often be as thermally stressful as exposed surfaces—if not more so (Fig. 8A)—although they are selected by numerous molluscan species during summer (Chapperon & Seuront, 2011b; Chapperon, Le Bris & Seuront, 2013). These observations suggest that, under both thermal and desiccation stresses, some microhabitats may primarily act as refuges against desiccation related to convective cooling, especially when compared to a nearby flat substratum, so that microhabitat choice can be driven by humidity rather than temperature. This hypothesis is consistent with observations conducted on two sympatric xerophilic snails from southeastern Spain (*Iberus gualtieranus* and *Sphincterochila candidissima*) and two other sympatric snails (*Theba pisana* and *Otala lactea*) from a humid Mediterranean zone. Under similar conditions of heat stress, temperature was found to regulate microhabitat selection in the humid environment, while in the arid environment humidity also plays a critical role in habitat selection, even though differences exist between the sympatric species (Moreno-Rueda *et al.*, 2009). Note, however, that crevices may also offer a thermal refuge with higher temperature in winter, and hence be selected by gastropods (Fig. 8B, C).

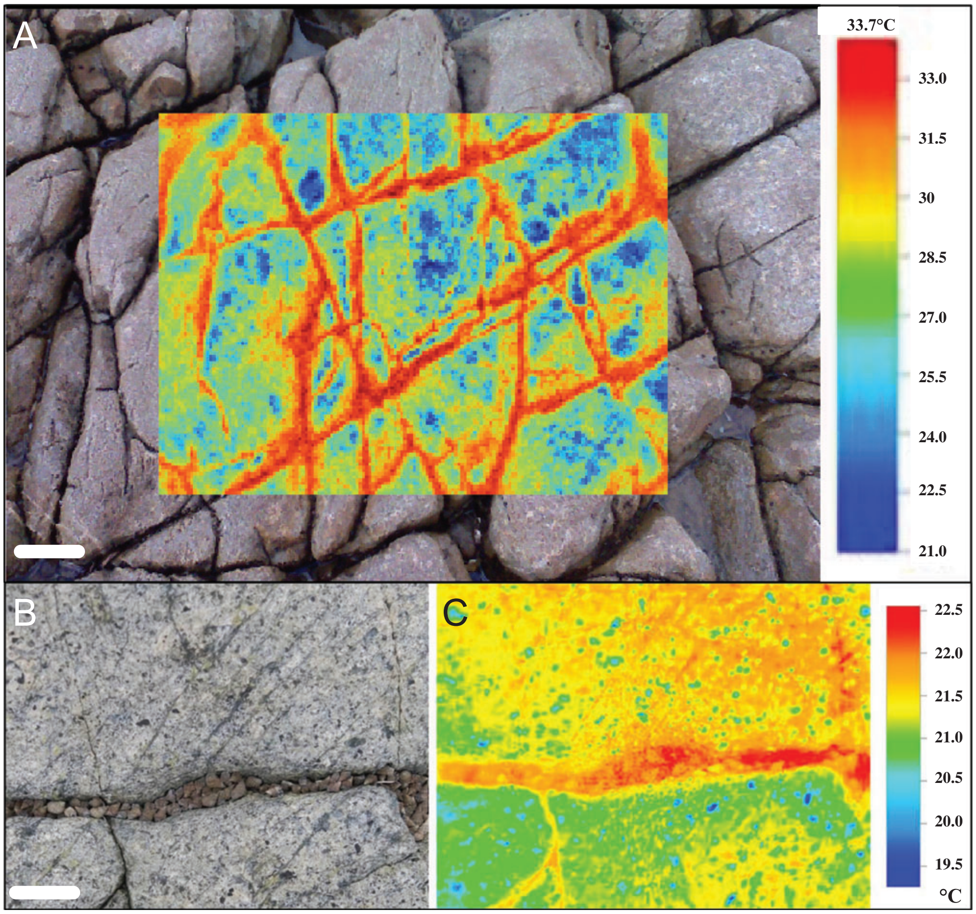

Figure 8. Digital and thermal images of crevices on (**A**) a horizontal rock platform in summer (Jorgensfontein, South Africa) and (**B**, **C**) a vertical rock platform in winter (Cape d'Aguilar, Hong Kong). Scale bars: **C** = 15 cm; **D** = 4 cm.

Heat transfer and shell characteristics

Polymorphism in shell colour or pattern is a common phenomenon in a range of molluscs, including terrestrial snails and intertidal bivalves and snails, and has been suggested to have an adaptive significance related to both predation (e.g. Johannesson & Ekendahl, 2002; Surmacki, Ozarowska & Rosin, 2013) and differential heat absorption. This has generated considerable research interests in climatic and microclimatic selection, and hence in the distribution of colour morphs at different spatial scales (e.g. Mitton, 1977; Johnson, 1980, 1981; Heller, 1981; Cowie & Jones, 1985; Etter, 1988).

In polymorphic terrestrial species, such as *T. pisana* and *Cepaea nemoralis*, shell colour and banding are strongly associated with habitat. Pale and unbanded *T. pisana* morphs are more common in open, exposed habitats, with higher frequencies of darker, banded snails in shrubby, shady habitats (Johnson, 1980; Heller, 1981). Yellow and banded *C. nemoralis* are more common in open than in shaded habitats (e.g. woodlands) where darker (pink or brown) and effectively unbanded morphs dominate (Cain & Sheppard, 1954; Parkin, 1971, 1972). These differences have been related to visual selection by avian predators (Surmacki *et al.*, 2013), but also to climatic and microclimatic selection. Climatic selection on both body and shell colour is supported by the large-scale latitudinal variation reported in *C. nemoralis* in Europe, where paler colours are favoured in areas of higher temperature because of their greater reflectivity of incident solar radiation, and darker colours in cooler areas because of their greater abilities to absorb radiation (Jones, 1973; Heath, 1975; Jones, Leith & Rawlings, 1977; Cowie & Jones, 1985; Chang, 1991). Such observations are also consistent with early field and laboratory measurements showing that fully banded/darker snails heat up more rapidly and reach higher temperatures than unbanded/lighter snails when exposed to radiant heat (Johnson, 1981; Cowie & Jones, 1985; Hazel & Johnson, 1990; Staikou, 1999; Di Lellis *et al.*, 2012). These observations have recently been ratified by the results of a 43-year survey showing that, despite changes in habitat towards greater shadiness (hence the expectation of visual selection for darker snails), the 1.5–2.0 °C temperature increase observed over the study period resulted in shells becoming lighter (Ozgo & Schilthuizen, 2012). Note that shell colour shows stronger and more consistent variation with habitat than do banding patterns, yellow shells being at higher frequencies in open habitats than in woods. There is, however, marked geographical variation in this relationship, which is stronger in southern England and northern France than elsewhere (Cameron & Cook, 2012). Further evidence for microclimatic selection comes from a 34-year survey of *T. pisana* colour polymorphism across an ecotone, which showed a consistent association of shell banding with habitat and a higher proportion of unbanded snails associated with hotter, sunnier summers (Johnson, 2011). Temporal variation thus supports the hypothesis of microclimatic selection, consistent with the spatial association with habitat. Direct quantitative and simultaneous measurements of air temperature, snail shell and body temperatures, and substratum temperature are, however, still missing, hampering the generalization of these results and prompting the need for further investigations into the thermal biology and ecology of land snails.

To our knowledge only a few studies have investigated potential differences in response to sunlight in molluscs of different colour morphs. Hamilton (1973) showed that the black *Tegula funebralis* heated up faster than the brown *T. brunnea* when placed in sunlight. This result should, however, be taken with caution given that *T. brunnea* and *T. funebralis* are subtidal and intertidal species, respectively. The observed differences may, however, be more related to the fact that *T. brunnea* and *T. funebralis* are not conspecific morphs (i.e. their shells do not differ in pigmentation alone) and have been exposed to different selection regimes in different habitats, rather than the result of actual pigmentation-related differences in the absorption of solar radiation by mollusc shells. *Mytilus edulis* with a higher degree of pale striping on their shells exhibited a lower body temperature than darker morphs under solar radiation (Mitton, 1977). Using empty (seawater-filled and sealed) *Nucella lapillus* shells exposed to natural sunlight, Etter (1988) showed that brown morphs heated up faster and attained higher temperatures than white morphs. This observation was consistent with experiments conducted on live snails, which showed that brown snails desiccated more rapidly and suffered greater mortality than white morphs (Etter, 1988). It is still unclear, however, whether the differences in shell size, shape, colour and surface patterning observed in molluscs (e.g. Reid, 1989) do significantly affect their ability to absorb thermal radiation. For example, Miller & Denny (2011) showed that body temperature variability related to shell structure and colour in littorinids was negligible (light shells were on average less than 0.5 °C cooler than dark ones) and Cox & Smith (2011) found nonsignificant differences in the emissivity of nine species of intertidal molluscs that varied in shape, size and colour. It is even unclear how differences in gastropod shell colour affect their ability to absorb and reflect thermal radiation. Darker shells are implicitly assumed to absorb more short-wave radiation, and hence to heat up more than lighter morphs under similar conditions, but different colour morphs also absorb and reflect other wavelengths (e.g. dark snail shells provide more protection against UV radiations than pale ones; Williams, 2016), which may impact the capacity to heat up and cool down and explain the lack of significant thermal difference between morphs (Scheil, Gärtner & Köhler, 2012).

Heat transfer and shell orientation

The orientation of even a stationary shell relative to the sun changes during the course of the day and hence its absorption of thermal radiation changes. Shell orientation has been reported as a behavioural adaptation to limit heat stress in some land species (e.g. *T. pisana*; McQuaid, Branch & Frost, 1979; Cowie, 1985). Shell orientation was, nevertheless, found to be random in the xerophilic Mediterranean land snail *Xeropicta derbentina* and unrelated to both shell surface and body temperature (Di Lellis *et al.*, 2012). In intertidal environments, *Nerita plicata* changes the direction of its shell to face the sun during emersion (Warburton, 1973) and the high-shore *Echinolittorina peruviana* adjusts its shell orientation to reduce the surface area perpendicular to the sun in order to maintain a lower body temperature during thermally stressful low tides in the summer (Muñoz *et al.*, 2005). Similar observations are lacking, however, in other species under similar conditions of heat stress (e.g. McQuaid & Schermann, 1988; Lang, Britton & Metz, 1998; Miller, 2008). The available results suggest that the role of shell orientation in thermal regulation may be both species-specific and context-specific. The interplay between heat stress and shell orientation may, however, be more complex than appears at first glance. Shell orientation is constrained by its shape (Cook & Jaffar, 1984; Garrity, 1984; Goodfriend, 1986; Okajima & Chiba, 2013) and may therefore be driven by functions that have nothing to do with the thermal nature of the environment, such as stability on the substrate (Bingham, 1972), wave action (Garrity, 1984) and mating (Marshall & Ng, 2013). High-shore snails may favour other behavioural strategies to minimize heat stress, as described in the next section.

Heat transfer, aestivation, foot withdrawal and postural behaviour

Both terrestrial and intertidal snails face the challenge of survival on substrata that may reach extreme temperatures, in arid and exposed habitats for the former and during daytime low tides for the latter. The amount of heat transfer through conduction from the substratum is, therefore, an important determinant of body temperatures of these animals (Helmuth, 1998; Staikou, 1999; Marshall, McQuaid & Williams, 2010). The problem is especially critical for terrestrial snails, which are very sensitive to desiccation due to their highly water-permeable skin (e.g. they can lose up to 40% of their body mass through evaporation in 2 h; Prior, 1989) and to overheating (Staikou, 1999). Note, however, that land snails are more sensitive to desiccation than intertidal snails because they have thinner shells, often lack an operculum, have large apertures, and do not benefit from the periodic occurrence of hide tides once or twice per day. As a consequence, terrestrial snails restrict their daytime activities to periods of favourable temperature and humidity (Staikou, 1999), are often active at night, climb on vegetation to escape the heat conducted from the substratum (Pomeroy, 1966, 1968; Yom-Tov, 1971) and use aestivation. Aestivation refers to a summer state of inactivity and reduced metabolism (5–30% of the normal rate) that can last for months (Guppy & Withers, 1999; Bishop & Brand, 2000) and is adopted during unfavourable conditions in order to save both water and energy (Pomeroy, 1968; Yom-Tov, 1971; McQuaid *et al.*, 1979; Herreid, 1977; Barnhart & McMahon, 1987; Withers, Pedler & Guppy, 1997).

High-shore intertidal snails, in particular rocky-shore littorinids, have also been reported to aestivate for days to weeks (Miller & Denny, 2011; Marshall, Baharuddin & McQuaid, 2013). In addition, they exhibit a suite of behaviours to reduce heat conduction from their substratum, as well as to reduce water loss through evaporation and/or increase convective cooling by air currents, and these behaviours are all coupled with foot withdrawal. Under dry conditions when exposed at low tide, snails may retract the foot into the shell, close the operculum and glue themselves to the rock with a mucus holdfast that allows them to detach their soft body from the substratum (Vermeij, 1971a; Bingham, 1972; Denny, 1984; Garrity, 1984; McMahon & Britton, 1985; Britton & McMahon, 1986; McMahon, 1990; Lang *et al.*, 1998). This simple behaviour provides enough support for littorinids to remain attached on rocks with minimal effort (Denny, 1984) and minimizes water loss from evaporation (Vermeij, 1971a; McMahon, 1990; Britton, 1992; Rojas *et al.*, 2013). It also minimizes conductive transfer from the substratum by reducing the amount of soft tissue and shell in contact with it, while maximizing the shell surface exposed to air currents, thus allowing increased heat transfer from the shell through convective cooling (Miller & Denny, 2011; Marshall & Chua, 2012). Individuals with the foot withdrawn have been found to be 3–5 °C cooler than those with the foot attached to the substratum and this effect was more pronounced in smaller species (Miller & Denny, 2011). Under conditions of extreme heat stress, improved convective cooling is achieved through shell-lifting (Garrity, 1984; Britton, 1995; Lang *et al.*, 1998; Wada & Ito, 2000; Miller & Denny, 2011), shell-standing (Lim, 2008; Miller & Denny, 2011; Marshall & Chua, 2012) and shell-stacking (Marshall, Mustafa & Williams, 2010), also referred to as towering (Seuront & Ng, 2016). Shell-lifting snails have their shell slightly lifted off the substratum with its aperture parallel to the substratum surface. Shell-standing refers to when snails attach to the substratum with their aperture facing perpendicularly to the rock surface (Marshall & Chua, 2012). Towering behaviour occurs when at least two snails (up to five have been observed; Seuront & Ng, 2016), glue vertically on top of each other to form a stack or tower, and all individuals involved in the tower may or may not adopt the former two postures (Lim, 2008; Marshall *et al.*, 2010; Marshall & Chua, 2012; Seuront & Ng, 2016). These various postural behaviours have all been shown to reduce snail body temperature, e.g. up to *c.* 10 °C in *Echinolittorina malaccana* and *E. radiata* (Seuront & Ng, 2016; Fig. 9A, B) and up to 5 °C in *Austrolittorina unifasciata* (Seuront, unpublished data; Fig. 9C). Note that towers can be either monospecific (Fig. 9A–C) or heterospecific (Fig. 9D), and there is a consistent decrease in snail size observed from the bottom to the top of a tower (i.e. in 96.2% and 97.6% of the towers observed in *E. malaccana* and *E. radiata*, respectively, and in 100% of the heterospecific towers; Seuront & Ng, 2016; Fig. 9). This seems to be consistent with an adaptation to heat stress, since heat transfer is inversely proportional to size in both stagnant and moving air, hence smaller individuals would theoretically benefit from a higher position in a tower (Seuront & Ng, 2016).

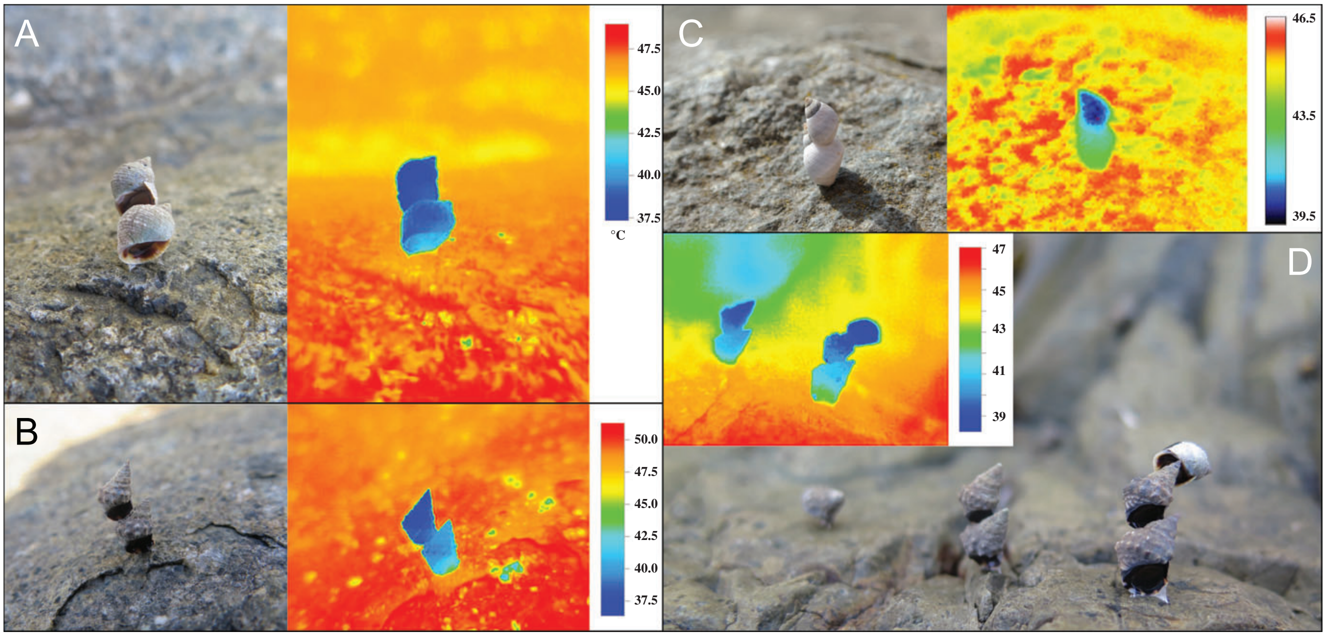

Figure 9. Digital and thermal images of shell-towering behaviour in *Echinolittorina radiata* (**A**), *E. malaccana* (**B**) and *Austrolittorina unifasciata* (**C**). This postural behaviour can lead to both monospecific (**A-C**) and heterospecific (here *E. radiata* and *E. malaccana*; **D**) towers, and consistently results in a decrease in both snail size and temperature from the bottom to the top of a tower.

Heat transfer, aggregation and gaping

Aggregations have commonly been observed in terrestrial snails and slugs (e.g. Mason, 1970; Chase, Croll & Zeichner, 1980; Giokas, Pafilis & Valakos, 2005; Mysak *et al.*, 2013; Chukwuka *et al.*, 2014; Korabek, Cejka & Jurickova, 2016), intertidal snails (Chelazzi, Innocenti & Della Santina, 1983; Chelazzi, Della Santina & Vannini, 1985; Tong, 1988; Mohammed, 1999), limpets (Keough, Quinn & Bathgate, 1997; Coleman *et al.*, 1999; Coleman & Hawkins, 2000) and chitons (Grayson & Chapman, 2004). Aggregations may help to retain moisture and reduce evaporation rates through the minimization of the surface area in contact with the atmosphere (Chase *et al.*, 1980). For instance, aggregated individuals of *E. peruviana* maintain water content and thermoregulate better than solitary ones (Rojas *et al.*, 2000) and aggregated individuals of *Nerita atramentosa* have higher water content than solitary snails. Note, however, that aggregation behaviour of *N. atramentosa* reduces both desiccation and heat stresses on boulder fields, but not on adjacent rock platforms, which indicates that the role of aggregation behaviour may be habitat-specific (Chapperon *et al.*, 2013). However, when individuals in an aggregation dry up after prolonged periods of heat stress, the beneficial cooling properties of such aggregations begin to break down (e.g. Chapman & Underwood, 1996; Stafford & Davies, 2004; Chapperon & Seuront, 2011a). Under hot and dry conditions, individuals within aggregations may even experience higher body temperatures than solitary snails (Chapman & Underwood, 1996); this effect may be due to reduced convective cooling when air currents are blocked by other individuals. Keeping warm through aggregation can, however, be beneficial during cold periods, as demonstrated in *N. atramentosa* (Chapperon & Seuront, 2012), although such thermal benefits of 'huddling up' have not been found in other rocky-shore species (*Echinolittorina malaccana* and *E. radiata*; Seuront & Ng, 2016).

Mussels are also characterized by the formation of dense and complex clusters (e.g. van de Koppel *et al.*, 2008; Erlandson, McQuaid & Sköld, 2011). Again, aggregated mussels often exhibit lower body temperatures than solitary ones (Helmuth, 1998). This observation is highlighted in the case of two species of intertidal mussel, the indigenous *Perna perna* and the invasive *Mytilus galloprovincialis*, that coexist in large aggregations on the south coast of South Africa. During emersion, *P. perna* exhibits periodic closure and opening of the shell (i.e. gaping); this behaviour allows the maintenance of aerobic respiration, but increases levels of water loss and the risk of desiccation, due to both evaporation and expulsion of water during valve closure. In contrast, *M. galloprovincialis* keeps its valves closed when exposed to air. This behaviour reduces the risk of desiccation, but decreases the efficiency of anaerobic respiration (Nicastro *et al.*, 2010). These different responses to aerial exposure, along with different byssal attachment strengths, are thought to determine the different vertical distributions of the two species (Branch & Steffani, 2004; Bownes & McQuaid, 2006; Zardi *et al.*, 2006; Hanekom, 2008). Recent laboratory experiments showed that the gaping behaviour of *P. perna* was ineffective in reducing the body temperatures of solitary mussels, but that when individuals were surrounded by conspecifics, evaporative cooling effects emerge for the entire cluster (Nicastro *et al.*, 2012). Consequently, increasing densities of *M. galloprovincialis* within *P. perna* beds may reduce the ability of individual *P. perna* to thermoregulate, while allowing *M. galloprovincialis* to 'steal' beneficial thermal properties from *P. perna* (Lathlean *et al.*, 2016a)—a seldom-studied process referred to as kleptothermy (see Brischoux, Bonnet & Shine, 2009; Corkery, Bell & Nelson, 2014). This hypothesis is consistent with observations that, during periods of severe heat stress, mortality rates of *P. perna* surrounded by nongaping *M. galloprovincialis* in the field were higher than those of *P. perna* surrounded by conspecifics (Nicastro *et al.*, 2012).

Heat transfer and evaporative cooling

There is a well known trade-off between drought resistance and thermoregulation in terrestrial snails (Rankevich, 1997). Thermoregulation requires water for evaporative cooling. Evaporative cooling is more effective for smaller snails because a smaller body size increases the surface-area-to-volume ratio, which in turn increases both absorption and radiation of heat (Rankevich, 1997; Schmidt-Nielsen, 1997). This is consistent with reports of higher water loss from small compared with large snails, which may lead to a more effective evaporative cooling and, therefore, also provide a possible explanation for the higher heat tolerance of small snails in a range of Mediterranean species such as *Xeropicta derbentina*, *Cernuella virgata* and *T. pisana* (Cowie, 1985; Dittbrenner *et al.*, 2009).

In intertidal snails, effective evaporative cooling is achieved by dripping mantle water over the body in low-shore species that are frequently immersed, but not in high-shore species (Garrity, 1984; McMahon, 1990; Britton, 1992). This process has been documented in a variety of neritids (Lewis, 1960, 1963; Vermeij, 1971b). *Nerita* species store water in the space between the shell and the body wall, and this water is released over the dorsal surface of the foot where evaporative cooling occurs (Vermeij, 1971b). For instance, *N. scabricosta* aggregates in multilayered clumps of up to 1,000 animals, where snails remained foot-attached to the rock or to conspecifics and trickle water from their shells (Garrity, 1984). Similarly, when *N. atramentosa* aggregated under a boulder are unexpectedly exposed to direct solar radiation, they became active nearly instantly, crawling onto each other and dripping their mantle water on each other's shells (Seuront, personal observations). Evaporative cooling hence allows intertidal species to remain active during periods of emersion, even under thermally stressful conditions. For example, evaporative cooling enables *Austrocochlea concamerata* and *N. atramentosa* to remain active for 2–3 h at 40 °C (McMahon, 1990). These results seem, however, to be species-dependent because, for example, in the mangrove whelk *Telescopium telescopium* the problem of water conservation outweighs the benefits obtained in regulating temperature via evaporative cooling (Lasiak & Dye, 1986). Some individuals of *N. atramentosa* appear to exhibit a lack of or limited evaporative cooling abilities (McMahon, 1990).

APPLICATIONS OF INFRARED THERMOGRAPHY IN NON-MOLLUSCS: A BRIEF REVIEW

The rationale behind the use of infrared thermography differs fundamentally between endotherms (mostly birds and mammals) and ectotherms (invertebrates, amphibians, reptiles and most fish). Endotherms produce their own heat and hence must have mechanisms to conserve and release this heat as necessary. In contrast, ectotherms derive their body heat from their environment and use behavioural mechanisms to utilize the range of physical processes driving heat exchange.

One of the most common applications of infrared thermography in endothermic animals (see Tattersall, 2016, for a review) relates to temperature measurements of the body areas responsible for heat exchange; this exchange is achieved by modifying and controlling blood flow (via vasoconstriction and vasodilatation) into these areas, which experience a much greater range of cutaneous blood flow than elsewhere (Johnson *et al.*, 1986). Such areas (hereafter referred to as 'thermal windows') include the ears, feet and nose of mammals, and the bills, feet and facial skin of birds (Tattersall & Cadena, 2010; Tattersall, 2016). Infrared thermography has now been applied extensively to assess endotherm body temperature of these thermal windows, e.g. in ostrich, emu and cassowary (Phillips & Sanborn, 1994), mole-rats (Sumbera *et al.*, 2007), seals (Mauck *et al.*, 2003), bats (Reichard *et al.*, 2010) and elephants (Weissenböck *et al.*, 2010). It has also been applied in the study of conservation of body heat radiation in birds in relation to feather colour (Dove *et al.*, 2007) and of various aspects of human thermoregulation (Bouzida, Bendada & Maldague, 2009; Fournet *et al.*, 2013; Adamczyk *et al.*, 2016). The infrared thermal signature of endotherms has also been used remotely (1) to assess the health of both captive and wild animals (Lavers *et al.*, 2005; Mellish *et al.*, 2013) and (2) to identify and enumerate a range of terrestrial and marine mammals (Cronin *et al.*, 2007). Infrared thermography enables study of the abundance and behaviour of small nocturnal mammals such as bats (Sabol & Hudson, 1995; Hristov, Betke & Kunz, 2008), which are difficult to visualize when emerging from their caves at night.

Infrared thermography also found many applications in both vertebrate and invertebrate ectotherms (see McCafferty, 2007; Tattersall & Cadena, 2010; Lathlean & Seuront, 2014; Tattersall, 2016, for reviews). Briefly, infrared thermography has been used to assess various aspects of reptile biology and ecology such as respiratory cooling (Tattersall & Gerlach, 2005; Tattersall, Cadena & Skinner, 2006), habitat choice (Krochmal & Bakken, 2003; Croak *et al.*, 2008; Lelièvre *et al.*, 2010) and the potential links between skin colour and body temperature (Tattersall, Eterovick & De Andrade, 2006). Thermal-imaging technology provides a reasonable approximation to internal body temperature for small vertebrate ectotherms (i.e. <20–50 g) with relatively low thermal inertia (Jones & Avery, 1989; Tattersall, Eterovick & De Andrade, 2006). Its use is more problematic with large ectotherms because (1) regional heating by solar radiation can lead to major differences in the surface temperature throughout the body, without necessarily a similar change in core body temperature, and (2) many of these ectotherms may regulate head or brain temperature rather than body temperature (Tattersall & Cadena, 2010). Finally, infrared thermography is also increasingly used to estimate body temperature in small invertebrates such as insects and spiders (e.g. Rehnberg, 2002; Hunt *et al.*, 2011; Pike, Webb & Shine, 2012) and to assess the thermal heterogeneity of their habitats (Pincebourde & Woods, 2012; Caillon *et al.*, 2014). There are a few studies in which infrared imagery has been used to assess various aspects of non-molluscan intertidal ectotherms, such as the sea star *Pisaster ochraceus* (Helmuth, 2002; Pincebourde, Sanford & Helmuth, 2008, 2013) and barnacles (Lathlean & Minchinton, 2012; Lathlean, Ayre & Minchinton, 2012, 2013).

INFRARED THERMOGRAPHY IN MOLLUSCAN RESEARCH: WHERE WE ARE SO FAR

The use of infrared thermography in molluscan research is currently limited to intertidal species. Infrared thermography was first used to measure temperature variability in *Mytilus californianus* (Helmuth, 2002), while more recent work has investigated the effect of parasitism on *M. galloprovincialis* and *Perna perna* (Zardi *et al.*, 2016). The thermal relationship between *M. galloprovincialis* and *P. perna* has further been explored through investigations of the effects of (1) varying densities of the two species on the thermal properties of both natural and artificial mussel beds during periods of aerial heat stress of various intensities (Lathlean *et al.*, 2016a) and (2) bed size and the size structure of individuals within beds on small-scale variability in body temperatures (Lathlean *et al.*, 2016b). Intertidal gastropods have also been investigated through the lens of infrared thermography, initially from a purely methodological perspective to compare invasive and noninvasive measures of body temperature in *Nerita atramentosa* (Caddy-Retalic, Benkendorff & Fairweather, 2011). Subsequent studies have assessed (1) aggregation behaviour associated with heat stress in *N. atramentosa* (Chapperon & Seuront, 2012; Chapperon *et al.*, 2013) and *Echinolittorina peruviana* (Rojas *et al.*, 2013); (2) thermoregulation through thermal refuge selection in the mangrove snail *Littoraria scabra* (Chapperon & Seuront, 2011a) and the rocky-shore *N. atramentosa* (Chapperon & Seuront, 2011b); (3) heat stress associated with free space in the limpet *Patelloida latistrigata* (Lathlean, 2014); (4) shell-posture behaviours associated with thermoregulation in *E. malaccana* and *E. radiata* (Seuront & Ng, 2016) and patterns of orientation in relation to thermal stress in the limpet *Cellana tramoserica* (Fraser *et al.*, 2016).

Noticeably, and despite the long-lasting interest in assessing various aspects of thermoregulatory behaviour in a range of terrestrial and freshwater snails, e.g. *Theba pisana* (McQuaid *et al.*, 1979), *Lymnaea auricularia* (Cabanac & Rossetti, 1987), *Biomphalaria glabrata* (Lefcort & Bayne, 1991), *Lymnaea* sp. (Żbikowska, 2001) and *Planorbarius corneus* (Żbikowska *et al.*, 2013), we are not aware of any attempt to investigate the thermal ecology of terrestrial molluscs through infrared thermography. Despite the potential that infrared thermography is offering, and the need for it in the field of molluscan research, there are several limitations that need to be carefully examined to ensure the robustness of thermal images and subsequent temperature measurements and interpretations.

INFRARED THERMOGRAPHY IN MOLLUSCAN RESEARCH: CAUTIONS AND LIMITATIONS

Emissivity

As stressed earlier, the emissivity of an object (i.e. its ability to emit thermal radiation) fundamentally influences how that object interacts with and emits radiation. Emissivity consequently plays a critical role in the algorithms used to convert the amount of infrared energy to temperatures in most infrared cameras. For biological tissues, the convention has been to use a value of ε between 0.95 and 0.98 (Hammel, 1956; Best & Fowler, 1981; Rubio *et al.*, 1997; Tattersall, 2016), even though the exact value of ε is unlikely to produce much error, since slight variations in the chosen emissivity value lead to minimal variations in the resulting temperatures for high-emissivity objects (Usamentiaga *et al.*, 2014). This is not necessarily the case in molluscan research, as (1) the shells of most molluscs vary in shape, colour and ornamentation, and (2) their biotic or abiotic substrata drastically vary in shape, structure and colour (see Fig. 2A–D, I–L). For example, the emissivity of intertidal macroalgae with flat surfaces is relatively constant at the scale of a few centimetres, but varies more significantly in algae with papillate surfaces and species composed of thin axes and branches (Van Alstyne & Olson, 2014). The use of infrared thermography to measure surface temperatures of molluscs and their substrata in terrestrial and intertidal environments is then potentially limited because (1) different taxa/substrata within a single infrared image may display different emissivity values due to their difference in shape, colour, surface aspect and ornamentation, and (2) these emissivity values may change when organisms or substrata are wet (Lathlean & Seuront, 2014). While the latter limitation may be more difficult to tackle given the temporary nature of the wetted state of a surface, two distinct, though conceptually similar, remedial procedures are described here as a first step to ensure that the temperature measurements provided by infrared thermography are representative of the actual temperature of an object.

First, emissivity can be empirically estimated by simultaneously taking infrared images (T_{IR}) and the *in situ* temperature of the same object with a calibrated thermocouple (T_{Object}), and subsequently adjusting ε on the infrared camera until $T_{IR} = T_{Object}$. This approach has been used in a range of studies that used infrared thermography to measure the temperature of intertidal organisms and their substrata, and they have consistently yielded emissivity values in the range 0.95–1.00 (Helmuth, 1998; Denny & Harley, 2006; Miller, Harley & Denny, 2009; Cox & Smith, 2011). Second, emissivity can be estimated by comparing surface temperature estimates to those of substances of known ε. As recommended by most thermal-imaging companies, this can be achieved in practice by sticking a piece of black electrical tape (e.g. Scotch® Black Paper Tape; $\varepsilon = 0.95$) onto the surface of interest, which is then heated up to a temperature of *c*. 40 °C above ambient temperature (Tattersall, 2016). The surface temperature of the tape is then measured with an infrared device, the surface temperature of the object is measured without the tape, and the emissivity ε is reset until the two temperatures match one another (Lathlean & Seuront, 2014). Alternatively, the surface of an object can be coated with a matt black paint (e.g. 3-M Black from Minnesota Mining Company or Senotherm from Weilburger Lackfabrik2, which both have an emissivity of *c*. 0.95) and the above procedure repeated for coated and noncoated surfaces. The estimated emissivity is subsequently used for all temperature measurements of this specific material, either the surface of a (abiotic or biotic) substratum or an organism. In molluscan research, this solution is problematic for shell-less species, either marine or terrestrial, since it involves destructive sampling of the surface, and is impossible to perform on the skin of living animals due to convective and conductive heat exchange from the circulating blood beneath. Since biological tissues are composed primarily of water and organic compounds, emissivity values >0.95 are often assumed, with 0.98 being widely reported as appropriate for human skin (Tattersall, 2016). For shelled molluscs, however, this procedure can be relatively easy to apply under controlled conditions. Note that in instances where surfaces with different emissivity values are considered, one should consider the emissivity of each surface in any subsequent analysis to get reliable temperature measurements. This is easily achieved since many infrared cameras have built-in on-screen emissivity correction capacity and/or come with software that can be used to set *a posteriori* different emissivity values to specific areas of a thermal image, hence actual temperatures of surfaces with distinct emissivity can be estimated through an appropriate post-processing procedure (Faye *et al*., 2016). Note, however, that for biological tissue the exact emissivity value is unlikely to produce much error, since most biological surfaces consist of similar substances (Tattersall, 2016).

Distance matters

The distance *d* between the camera and a target object is another potential source of bias in temperature estimates using infrared thermography. A recent study inferring the effect of distance on infrared-thermography estimates of the thermal properties of vegetation and landscape mosaics showed that images taken from long distances (typically >20 m) consistently underestimated surface temperatures by up to 3 °C (Faye, Dangles & Pincebourde, 2016). Interestingly, the structural complexity of the surface itself had negligible effect on the surface temperature bias (Faye, Dangles & Pincebourde, 2016). The authors explained the aforementioned bias in terms of atmospheric composition and the pixel-size effect. Specifically, a larger distance implies more air between the object and the camera, leading to more attenuation, mostly due to water vapour in the atmosphere. Therefore, the distance should be a user-set parameter in any camera software in order to account for the air path, and the user must always measure relative humidity (especially for outdoor observations) as an additional input parameter.

The so-called ‘pixel-size effect’ (Faye, Dangles & Pincebourde, 2016), or ‘minimum spot-size detection’ (Tattersall, 2016), refers to the change in pixel size with distance, which modifies the temperature measured by an infrared camera. One of the most fundamental consequences of this effect occurs at the physical boundary between an object and its surroundings, because both elements may be included in the same pixel, depending on the shooting distance. In this case, the pixel integrates the infrared information originating from both elements, as a combination of the different temperatures at the sub-pixel scale (Murphy *et al*., 2014). This subpixel temperature combination at the physical borders of the studied surface can be avoided by removing the surface boundary edge, i.e. the boundary pixels, in the infrared image. More precisely, the pixel size effect can be related to *d* by the function: $SR = d \times \theta_{IFOV}$, where *SR* is the spatial resolution of the infrared camera (the size of one pixel) and θ_{IFOV} the instantaneous field of view in radians (the angle over which the detector senses radiation). For example, infrared images of a mollusc 1 cm long being visualized with a Fluke Ti25 camera ($\theta_{IFOV} = 0.0015$ rad) should be taken at the maximum distance at which the organism could reliably be resolved, at $d = 6$ m. Since *SR* is the size of one pixel, additional resolving capacity may be required in this example, e.g. 50 or 100 pixels, requiring the image to be obtained at 13.3 or 6.7 cm, respectively. In a real study of the thermal ecology of the intertidal snail *Littorina saxatilis* in the size range 5 to 8 mm conducted with a Fluke Ti25 camera, the infrared images were taken at less than 30 cm from the snails to ensure a minimum pixel resolution of 0.5 mm (L. Seuront, unpublished data).

In this context, the choice of a thermal camera (and implicitly the objective lens attached to it) should be driven by the requirement that the resolution of the camera is compatible with the targeted organisms and the related empirical constraints that are predicted either *in situ* or *ex situ*. In practice, the objects of interest should occupy a number of pixels that allows a spatial resolution of *c*. one tenth of the object size in the final thermal image, and the potential distance effects mentioned above should be empirically assessed, or at least explored mathematically.

Atmospheric effects

Natural objects do not behave like black bodies, because their emissivity ε is typically lower than 1. As such, a portion (i.e. $1 - \varepsilon$) of the radiation arriving to the infrared-imaging device originates from the background environment. This background-reflectance temperature can simply be equated to air temperature in indoors applications of infrared thermography (FLIR, 2007). In outdoor applications, the average sky temperature should be considered as the background-reflectance temperature, noting that this temperature will vary with the time of day and cloud cover. Fortunately, in contrast to smooth and polished anthropogenic surfaces that reflect infrared radiation very well (and hence have a low ε), the emissivities of abiotic and biotic objects that are relevant to molluscan research are high. Consequently, the error caused by background reflectance in the estimated temperature is low, producing a maximum error in absolute temperature that is proportional to the reflectivity of the object ($1 - \varepsilon$), which is typically about 5% (Tattersall, 2016). Variations in solar radiation are also known to affect infrared measurements (Faye *et al*., 2016), in particular because under full-sun conditions significant short-wave reflection is likely to occur (Tattersall, 2016). These facts imply that measurements of short-wave reflectance as well as solar radiant flux have to be performed to ensure that they are stable during the capture of infrared images in full sunlight.

A range of atmospheric gases, especially carbon dioxide, ozone and water vapour, influence the radiant energy detected by infrared sensors (Vollmer & Möllmann, 2010). Water vapour is, however, by far the most important absorber of radiation over the range of wavelengths detected by infrared cameras (Vollmer & Möllmann, 2011). The degree to which air absorbs infrared radiation depends on the wavelength. In the MWIR and LWIR bands, this absorption is low, allowing more radiation to reach the sensor of the camera (Usamentiaga *et al*., 2014). Atmospheric attenuation of infrared radiations is also dependent on the distance between a thermal camera and a target object, and typically increases with distance, e.g. infrared radiations are attenuated by up to 10% over a path length of 100 m and by more than 90% over 10 km. Though Faye, Dangles & Pincebourde (2016) recommended reducing the shooting distance to the lowest possible in order to yield more accurate surface temperatures, this is not always possible. This is where atmospheric radiative-transfer models could be used to correct the surface temperatures according to atmospheric composition. For example, MODTRAN 6 (MODerate resolution atmospheric TRANsmission) includes the effects of molecular and particulate absorption/emission of the atmosphere present between the thermal sensor and the studied object in its solution of the radiative-transfer equation (Berk *et al.*, 2014). For most ecological and biological applications, and in particular in molluscan research, measurements are likely to be conducted at distances between a few centimetres and a few metres, rather than at the scale of kilometres. Humidity nevertheless influences infrared measurements and should ideally be measured, or at least estimated. Most thermal-imaging software incorporates empirical atmospheric-transmission curves for estimating and correcting the loss of signal resulting from the water vapour pressure and distance (Holst, 2000). Note, however, that for the applications of infrared thermography at distances ranging from a few centimetres to a few metres, the effect of atmosphere is negligible and can therefore simply be neglected.

On the reliability of shell temperature vs *body temperature*

A fundamental assumption behind the use of infrared imaging in molluscan research is that there is a relationship between the surface (i.e. tissue or shell) temperature and the actual body temperature. Knowledge of this relationship is absolutely necessary to ensure the reliability of noninvasive surface-temperature measurements as a proxy for internal body temperature. In an early infrared-imaging study of the intertidal *Nerita atramentosa*, Caddy-Retalic *et al.* (2011) reported highly significant linear relationships between mantle temperature T_m and the maximum temperature of shell thermal images $T_{S_{\max}}$ when thermal images were taken from ventral and dorsal views of the shell in the range 15–55 °C. In order to avoid handling the snails, they recommended use of the dorsal thermal maximum to predict internal mantle temperature, according to the relationship:$T_m = 1.121 T_{S_{\max}} - 2.884$. Infrared imaging of shell surface temperatures have subsequently been used as a proxy for mantle temperatures in other intertidal snails, e.g. *N. atramentosa* (Chapperon & Seuront, 2011b, 2012; Chapperon *et al.*, 2013), *L. scabra* (Chapperon & Seuront, 2011a), *Echinolittorina peruviana* (Rojas *et al.*, 2013), *E. malaccana* and *E. radiata* (Seuront & Ng, 2016), in the limpets *Patelloida latistrigata* (Lathlean, 2014) and *Cellana tramoserica* (Fraser, 2014; Fraser *et al.*, 2016) and in the littoral bivalves *Perna perna* and *Mytilus galloprovincialis* (Lathlean *et al.*, 2016a, b; Zardi *et al.*, 2016). With the exception of two studies (Caddy-Retalic *et al.*, 2011; Lathlean *et al.*, 2016a) that explicitly demonstrated the linear relationship between body temperature and shell temperature, most of the above-mentioned studies did not directly test this on their model systems, instead making the implicit assumption that surface temperature was an accurate proxy of mantle temperature. Also note that in an earlier work, Helmuth (2002) illustrated the potential use of infrared thermography through images of large beds of *Mytilus californianus* without further quantification of mussel body temperature.

In this context, we quantify hereafter the relationship between internal body temperature (measured invasively using a thermocouple inserted through a hole carefully drilled into the shell to avoid damaging underlying tissue) and surface temperature (estimated with infrared thermography) based on a range of terrestrial (*Candidula unifasciata*, *Cepaea nemoralis*, *Cernuella virgata*, *Cochlicella acuta* and *Cornu aspersum*) and intertidal molluscs representative of various climates (*Afrolittorina africana*, *A. knysnaensis*, *Austrolittorina unifasciata*, *Nodilittorina pyramidalis*, *Echinolittorina malaccana*, *E. radiata*, *E. hawaiiensis* (= *Littorina picta*; smooth and ornamented morphs), *Littorina littorea*, *L. saxatilis* (black, white, yellow and striped morphs), *Melarhaphe nerotoides*, *Littoraria pintado*, *Mytilus edulis*, *M. galloprovincialis*, *N. atramentosa*, *Nucella lapillus* (black, white, brown and striped black/white morphs) and *P. perna*). Note that in contrast to Caddy-Retalic *et al.* (2011), who estimated T_m from the maximum temperature of the dorsal surface of *N. atramentosa*, we recommend considering instead the average surface temperature of the whole shell (T_S) as recorded through infrared thermography. This measure represents a better metric of the thermal conditions experienced by a mollusc than $T_{S_{\max}}$, which may be strongly biased by e.g. the shape of the shell and its orientation towards the sun (L. Seuront, unpublished data). In addition, the equation used by Caddy-Retalic *et al.* (2011), i.e. $T_m = 1.121 T_{S_{\max}} - 2.884$, suggests that $T_{S_{\max}}$ typically underestimates and T_m overestimates respectively for low and high temperatures, which is not the case when T_S is considered (Fig. 10). The T_m of all the above mentioned species and morphs was highly significantly correlated with their surface temperature in the range 20–55 °C ($P < 0.001$). More specifically, the slope α in the relationship $T_m = \alpha T_s + \beta$ never differs significantly from the theoretical expectation $\alpha = 1$ ($P > 0.05$). This indicates that T_m and T_s covary at the same rate in the temperature range 20–55 °C, and hence that mollusc surface temperature can be considered a reliable proxy of internal temperature. Note that this conclusion holds for each of the aforementioned species, irrespective of the size of the individuals. The thermal inertia is, however, species-dependent and size-dependent (L. Seuront, unpublished data).

More generally, though shell temperature and body temperature are consistently significantly correlated in a range of molluscan species, some of these relationships have been derived from laboratory experiments conducted under standardized conditions of heat stress, i.e. in the presence of a single source of heat and in the absence of air movement. These conditions differ from those in the field where molluscs are exposed to multiple heat sources and heat-transfer processes (Fig. 6) and may (Fig. 11B, C), or may not (Fig. 11A), control their body temperature through postural behaviour. In addition, when investigated *in situ*, molluscs may potentially have been exposed to fluctuating thermal radiation before being scrutinized through the lens of infrared thermography. Further information about the potential links between the size and colour of various mollusc species and the rate of heat transfer is therefore still needed, to ensure that shell temperature is indeed a

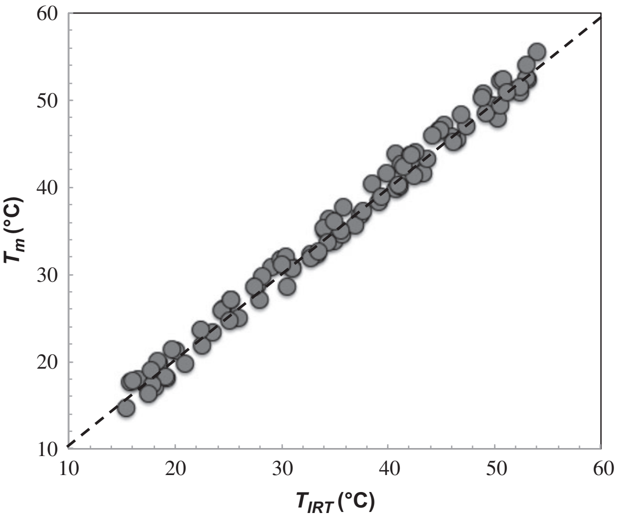

Figure 10. Thermocouple laboratory measurements of mantle temperature (T_m) of *Nerita atramentosa* as a function of the average shell surface temperature assessed using infrared imaging (T_{IRT}), showing that T_{IRT} is a reliable proxy of mantle temperature. The dashed line is the first bisectrix $T_m = T_{IRT}$.

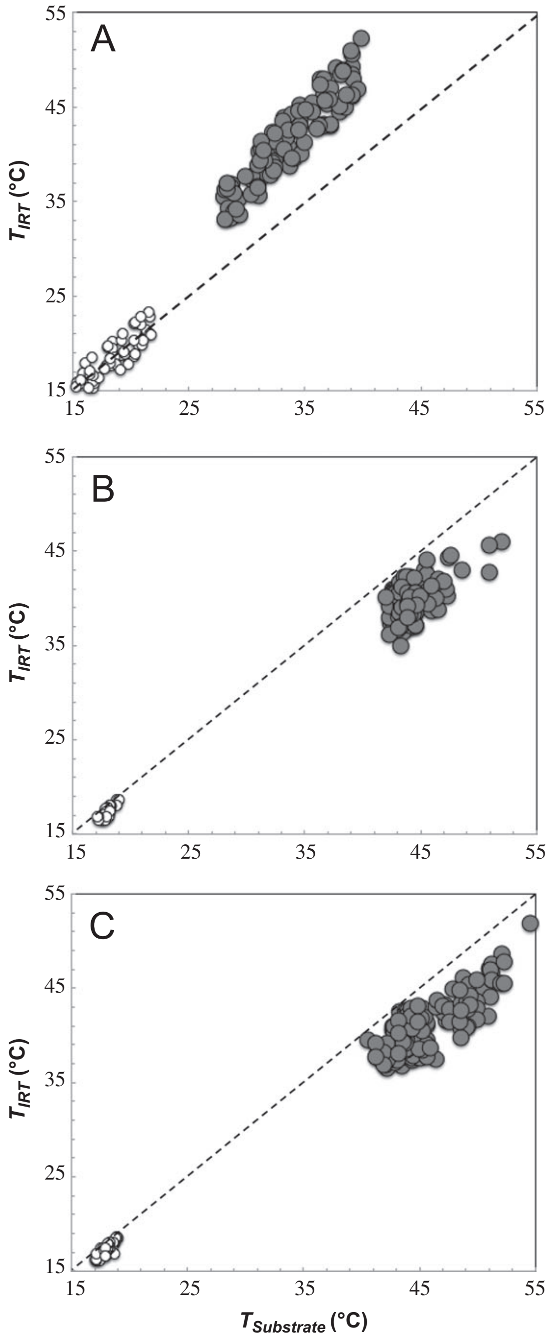

Figure 11. Field measurements of mantle temperature (T_{IRT}) of *Nerita atramentosa* (**A**), *Echinolittorina malaccana* (**B**) and *E. radiata* (**C**) as a function of their substratum temperature in winter (open circles) and summer (grey circles). The dashed lines are the first bisectrix $T_{IRT} = T_{Substratum}$. (**B** and **C** modified from Seuront & Ng, 2016: fig. 1.)

reliable proxy of body temperature. In particular, assessing the thermal inertia of different species, sizes and morphs, under different conditions of radiation and/or when radiation changes, will provide valuable information on how thermal inertia may help molluscs tolerate short periods at or above lethal temperatures.

Demystifying the link between colour and heat

As defined in the sections describing the physics of heat transfer and of infrared thermography, surfaces of different colours may have a similar emissivity and hence share a similar ability to absorb and emit infrared radiation. This understanding must inform the interpretation of surface temperature measured by infrared thermography and the proper set-up of an infrared camera. On the other hand, the colour of an object does have critical implications for its temperature, as colour defines the way it absorbs and reflects visible light, and hence the quantity of light energy being transferred to that object and subsequently converted to heat. This issue is very simple when comparing black and white objects. Because these objects have a similar emissivity, they both absorb light very well in the infrared spectrum. However, a black object absorbs most of the light in the visual spectrum, which is why it appears black. In turn, a white object reflects most of the light in the visual spectrum. Black objects hence overall absorb more heat than white ones, and thus exhibit higher temperature, when exposed to light (Fig. 12A–C). This is not the case, however, when black and white objects are sheltered from solar radiations (Fig. 12D, E), which illustrates the fundamental difference between direct and indirect radiative heat transfer.

INFRARED THERMOGRAPHY IN MOLLUSCAN RESEARCH: CURRENT APPLICATIONS AND FUTURE PROSPECTS

For the sake of generality, the case studies discussed below are based on thermal images taken in a range of environments under different climatic regimes ranging from temperate to tropical latitudes (France, Spain, South Africa, Australia and Hong Kong) using four different thermal-imaging cameras. The images are analysed with the corresponding firmware and software, to provide the reader unfamiliar with thermal imaging with a range of examples of the capabilities offered by this emerging technology. The thermal cameras used were (1) Fluke Ti20 (Fluke Corporation, Everett, WA), (2) Fluke Ti25, (3) Testo 875-1iSR (Testo AG, Germany) and (4) FLIR ThermaCAM S65 (OR), and the resulting thermal images were analysed using, respectively, InsideIR 4.0 v. 2006, SmartView v. 3.2.639.0, IRSoft v. 3.1 and ThermaCAM Researcher Professional v. 2.10 software packages. The thermal performances of the cameras are very similar, with sensitivities ≤ 0.2 °C (Fluke Ti20), ≤ 0.09 °C (Fluke Ti25), < 0.05 °C (Testo) and 0.08 °C (FLIR) and accuracy is 2% or 2 °C, whichever is greater (Fluke and Testo) and fixed at ±0.2 °C (FLIR) by recalibrating the camera every 2 min. The emissivity (ε) was consistently set at 0.95 (Chapperon & Seuront, 2011a, b; Seuront & Ng, 2016).

We discuss both recently published and unpublished data taken from a wide range of environments and latitudes, using various terrestrial and intertidal species of molluscs. We highlight, based on studies conducted both *in situ* and *ex situ*, the many applications of infrared thermography to molluscan research ranging from individual thermoregulatory behaviour to landscape and community ecology, hence covering spatial scales ranging from millimetres to hundreds of metres.

Mapping mollusc habitat thermal heterogeneity

One of the major advantages of using infrared thermography rather than traditional single-point temperature measurement devices (e.g. thermocouples, iButtons and infrared thermometers) is that the images they produce allow for simultaneous measurements of multiple individuals, species and communities. Thermal imaging is particularly useful to assess the thermal properties of contrasting adjacent microhabitats (e.g. horizontal and vertical flat rocks and crevices; Fig. 8). The thermal contrast between flat surfaces and crevices discussed above (Fig. 8) is but one case of the influence of overall topographic complexity. As another example (Fig. 13), anthropogenic south-facing intertidal seawalls characterized by

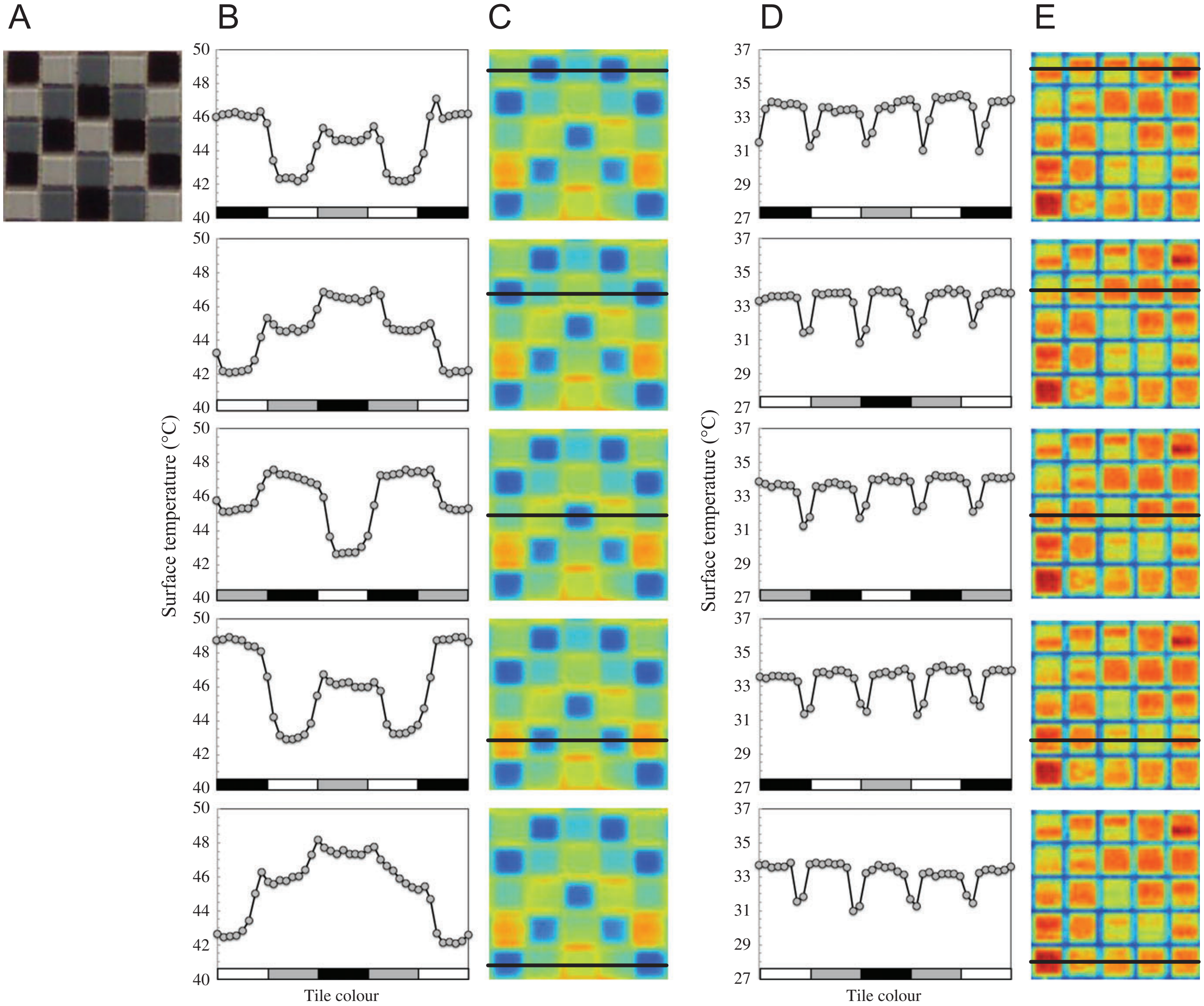

Figure 12. Illustration of the effect of the colour of a surface on its thermal properties. Surface temperature of a chequerboard made of black, grey and white tiles (**A**) was measured using infrared thermography under direct sunlight at 28 °C (air temperature) in absence of wind (**B, C**), and in shade where air temperature was 33 °C (**D, E**). Under direct sunlight, surface temperature of tiles was very heterogeneous both locally along horizontal transects (**B**) and globally (**C**), and colour-dependent with $T_W < T_G < T_B$ (where T_W, T_G and T_B are, respectively, surface temperatures of white, grey and black tiles). In contrast, under shaded conditions, surface temperatures were nearly uniform (**D, E**), with $T_W = T_G = T_B$. This is shown by shape of temperature transects traced across the board (black lines in **C** and **E**); temperature varied as a step-function dependent on tile colour in the sun (**B**), but was independent of tile colour in shade (**D**). Note that sharp decrease in temperature observed in (**D**) between the temperature plateaux is an artefact related to the temperature of the substratum beneath the tiles, which were not tightly jointed.

distinct topographic complexity were investigated within 1 h under similar conditions of air temperature and solar radiation and were distinguished by their respective thermal heterogeneity, which increased with topographic complexity. The thermal properties of even flat surfaces are affected by their orientation, colour and biogenic cover, which can result in considerable temperature changes over only a few centimetres, as illustrated by a sea wall (Fig. 14A, B). A vertical cement-coated outside wall of a house exhibits a finer-scale variation in its surface temperature in the range 0.5–1 °C (Fig. 14C, D), which is likely to be related to topographic complexity at the sub-centimetre scale and to the even finer-scale heterogeneity of its internal components. These examples illustrate that even slight differences in topography, colour, biogenic cover and internal structure can affect the thermal signature of a substratum, creating thermally complex landscapes.

Thermal imaging is also advantageous when the presence or absence of one species or individual influences the thermal properties of another. For example, shading by trees typically lowers the temperatures experienced by understorey plants and invertebrates (Fig. 15A, B). Similarly, the distribution of the barnacle *Tesseropora rosea* on Australian rocky shores was shown to affect the small-scale patterns of substratum temperature, and hence the abundance and distribution of the small limpet *Patelloida latistrigata* (Lathlean, 2014; Fig. 15C, D). Other ecosystem engineers such as mussels generate thermally favourable free space, protecting associated invertebrate communities and individuals from heat and desiccation stress (Lathlean *et al.*, 2016a; Fig. 15E, F).

The detection of all the above-mentioned small-scale thermal properties of the habitat, though essential to understanding of the physiology, biology and ecology of individual molluscs, could not

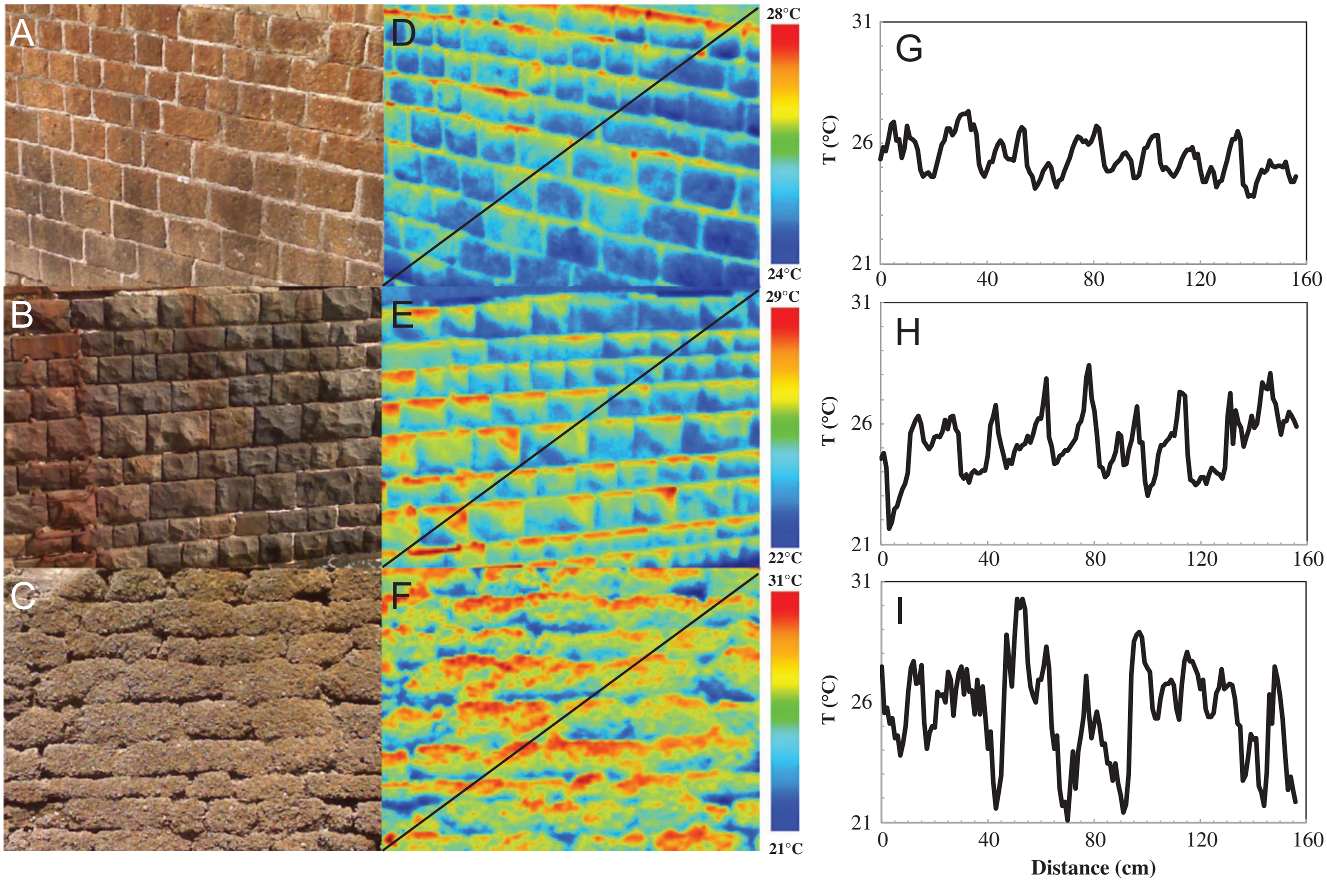

Figure 13. Three anthropogenic surfaces (**A, B,** south-facing intertidal seawalls located in Dover harbour, England; **C,** Le Portel, France) of increasing topographic complexity (from **A** to **C**), shown together with corresponding infrared images (**D–F**). The spatial patterns of surface temperatures observed along transect drawn across thermal images (black lines in **D–F**) show that while no significant differences exist in the mean temperature (**D, G:** T = 25.4 ± 0.8 °C; **E, H:** T = 25.2 ± 1.2 °C; **F, I:** T = 25.4 ± 2.3 °C) the thermal heterogeneity markedly increases with topographic complexity. Note different temperature scales in **D**–**F** and **G**–**I**, and lower temperature observed in crevices (**F**).

have been captured by traditional single-point temperature measurements and was only possible through the use of infrared thermography.

Mollusc size and shape matters when feeling the heat

Body size is an important parameter to consider in thermal ecology, because heat conduction depends on the distance heat has to travel and on the surface-to-volume ratio (see account of physics of heat transfer, above).

To illustrate the potential effect of size on heating rate and maximal body temperature, we generated heating curves using biomimetic models (Helmuth, 1998; Denny & Harley, 2006; Denny *et al.*, 2011; Miller & Denny, 2011) of the high-shore gastropod *Austrolittorina unifasciata*. Biomimetic snails of different sizes (5 mm: $n = 3$; 10 mm: $n = 7$; 15 mm: $n = 5$) were created using hollowed out *A. unifasciata* shells filled with 3 M Scotchcast 2130 Flame Retardant Compound (Lima & Wethey, 2009). Biomimetic snails were fitted with fine K-type thermocouples and maintained at 20 °C in a cooler until they were fixed with cyanoacrylate glue (Loctite Superglue) onto flat limestone with the aperture orientated towards the substratum ($T_{\text{substratum}} = 40 \pm 1$ °C) either (1) in direct sunlight or (2) in shade. Shading was achieved following Marshall & Chua (2012) by using 7, 12 and 17-mm diameter discs supported directly above the shells by fine wires leading from the surface; this ensured only the shells and not the surrounding surfaces were shaded. The difference in the temperature dynamics between the sunned and shaded biomimetic shells demonstrated the direct and indirect effects of heat transfer towards *A. unifasciata*. The former were heated by direct solar radiation, convection and conduction from the substratum, while the latter were affected only by convection and conduction (Marshall & Chua, 2012). Simultaneous recordings of the snail models were made every 30 s between 11 am and 1 pm on a rocky platform in Lincoln National Park (Australia) on 12 March 2013, when air and limestone surface temperatures were 28 ± 1 °C and 40 ± 1 °C, respectively. The temporal dynamics of the temperature T_i of *A. unifasciata* models of size i were consistently highly significant ($P < 0.01$) fitted by equations of the form, $T_i(t) = T_0 + (T_{\max} t/(t_m + t))/k_i$, where T_0 and $T_{\max}$ are, respectively, the initial and maximal temperatures of the models ($T_0 = 20$ °C), t the time, t_m the time at which $T_i(t) = T_{\max}/2$, and k_i an empirical constant. No significant differences were found in the maximal temperature $T_{\max}$ (43.9 °C ± 0.5 SD) reached by biomimetic snails of different sizes when exposed to solar radiation (Kruskal-Wallis test, $P > 0.05$; Zar, 1999). In contrast, t_m differed significantly with size (Kruskal-Wallis test, $P < 0.05$)—the smaller the snails the shorter t_m (3, 7 and 13 min for snails 5, 10 and 15 mm in length, respectively). The difference in $T_{\max}$ estimated for sunned and shaded models also differed significantly with size ($P < 0.05$) ($\Delta T = 2.1$, 1.6 and 1.4 °C for models 5, 10 and 15 mm in length, respectively). These results are consistent with previous work (Marshall & Chua, 2012) and indicate that (1) the smaller the snail, the faster it warms up, (2) snails of different sizes eventually attain similar maximal

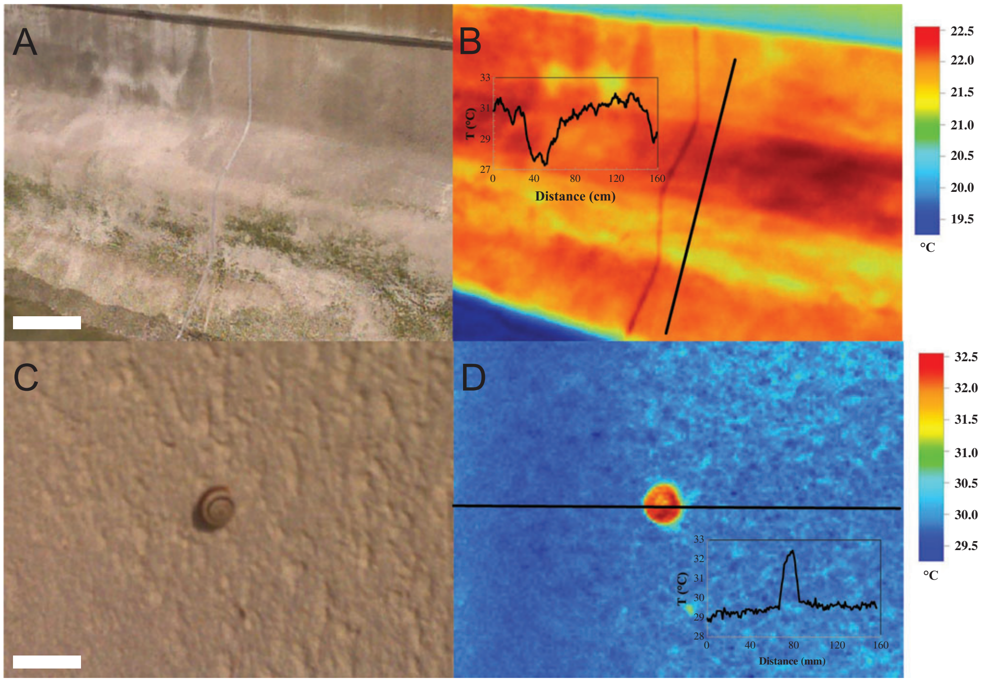

Figure 14. Digital (**A, C**) and thermal (**B, D**) images of high-shore seawall in Dover harbour, England in spring 2015 (**A, B**) and of *Cernuella virgata* glued with a mucus holdfast to outside wall of a house in Wierre-Effroy, France, during a hot summer in August 2016 (**B, D**). Slight changes in verticality, colour and biogenic cover of the seawall lead to clear differences in surface temperature (**A, B**). In contrast, the structurally uniform wall is thermally homogenous, making thermal signature of *C. virgata* highly conspicuous (**C, D**). Scale bars: **A** = 30 cm; **C** = 2 cm.

temperatures (in less than 2 h under the conditions considered here), and (3) the effect of direct solar radiation is minor, representing between 3.9% and 6.1% of the overall heating.

A similar approach was used to assess the effect of shell shape on the heating rates of four species of co-occurring gastropods, *Gibbula cineraria*, *G. umbilicalis*, *Phorcus* (=*Osilinus*) *lineatus* and *Littorina littorea*. The shell surface-to-volume ratio was approximated by the shell aspect ratio (S_{ar}) calculated as S_{ar} = shell height/shell width. Heating rates were estimated for each species for standardized snail sizes in the range 10.7–12.0 mm using the biomimetic approach described above. The biomimetic snails were maintained at room temperature (15 °C) on granite tiles and subsequently placed under infrared lamps (Phillips PAR38) until they reached a stable temperature. Significant differences were found between S_{ar} (Kruskal-Wallis test, and subsequent multiple comparison procedure, $P < 0.05$; Zar, 1999) with S_{ar}(*G. umbilicalis*) < S_{ar}(*G. cineraria*) = S_{ar}(*P. lineatus*) < S_{ar}(*L. littorea*). No significant differences were found in $T_{\max}$ (44.9 °C ± 0.5 SD) reached by biomimetic snails of the four species (Kruskal-Wallis test, $P > 0.05$). In contrast, t_m differed significantly with size (Kruskal-Wallis test, $P < 0.05$) and t_m was longer for a smaller S_{ar} (14 min for *L. littorea*, $S_{ar} = 0.73 \pm 0.05$; 18 and 19 min for *G. cineraria*, $S_{ar} = 0.58 \pm 0.04$, and *P. lineatus*, $S_{ar} = 0.56 \pm 0.03$; 23 min for *G. umbilicalis*, $S_{ar} = 0.53 \pm 0.02$). Species with a higher surface-to-volume ratio, i.e. higher S_{ar}, heat up significantly more quickly than flatter species.

Lastly, using artificially constructed mussel beds composed of *Perna perna*, Lathlean *et al.* (2016b) investigated how the size, position and structure of the beds affected the body temperatures of individual mussels within each bed (Fig. 16). Results revealed that small individuals reached higher body temperatures than large individuals, irrespective of mussel-bed size. However, contrary to expectations, average body temperatures and heating rates of individuals within large mussel beds were generally greater than for individuals within small mussel beds. This was thought to be due to differences in convective cooling of large and small mussel beds, since individuals on the leeward side of all beds displayed body temperatures 3–5 °C greater than those on the windward side (Fig. 16A, B).

Thermal heterogeneity within a community

A major advantage of using infrared thermography as a tool for measuring *in situ* thermal variability is that it can simultaneously record fine-scale differences in the body temperatures of numerous individuals within a community. This is particularly relevant in community ecology as all species may not deal similarly with thermal stress, even if they live in the same microhabitat. In this context, inter-individual thermal variability may shed new light on our understanding of key ecological concepts such as keystone species and the stability of community structure (Paine, 1969, 1995). More generally, this is important in an era when increased temperatures associated with climate change are expected to impact different species within ecological communities in different ways. In recent years, much attention has been given to identifying which species within communities are most vulnerable to further increases in temperature, in order to predict how changes in their relative abundance may impact the direction and strength of species interactions (Kordas, Harley & O'Connor, 2011). Infrared thermography can reveal how multiple species within a community respond to contemporary and future levels of heat stress, thus providing a glimpse of how such communities may respond and adapt to climate change.

One recent case study that explores this process using infrared thermography was undertaken on rocky intertidal communities along the south coast of South Africa (Lathlean *et al.*, 2016a). Here, the invasive mussel *Mytilus galloprovincialis* is found interspersed among mid-intertidal aggregations of the indigenous mussel *Perna perna*. While belonging to the same family, these two species display different behavioural responses to heat stress during aerial exposure. During emersion, *P. perna* exhibits periodic closure and opening of the shell (gaping); this behaviour allows the maintenance of aerobic respiration, but increases levels of water loss

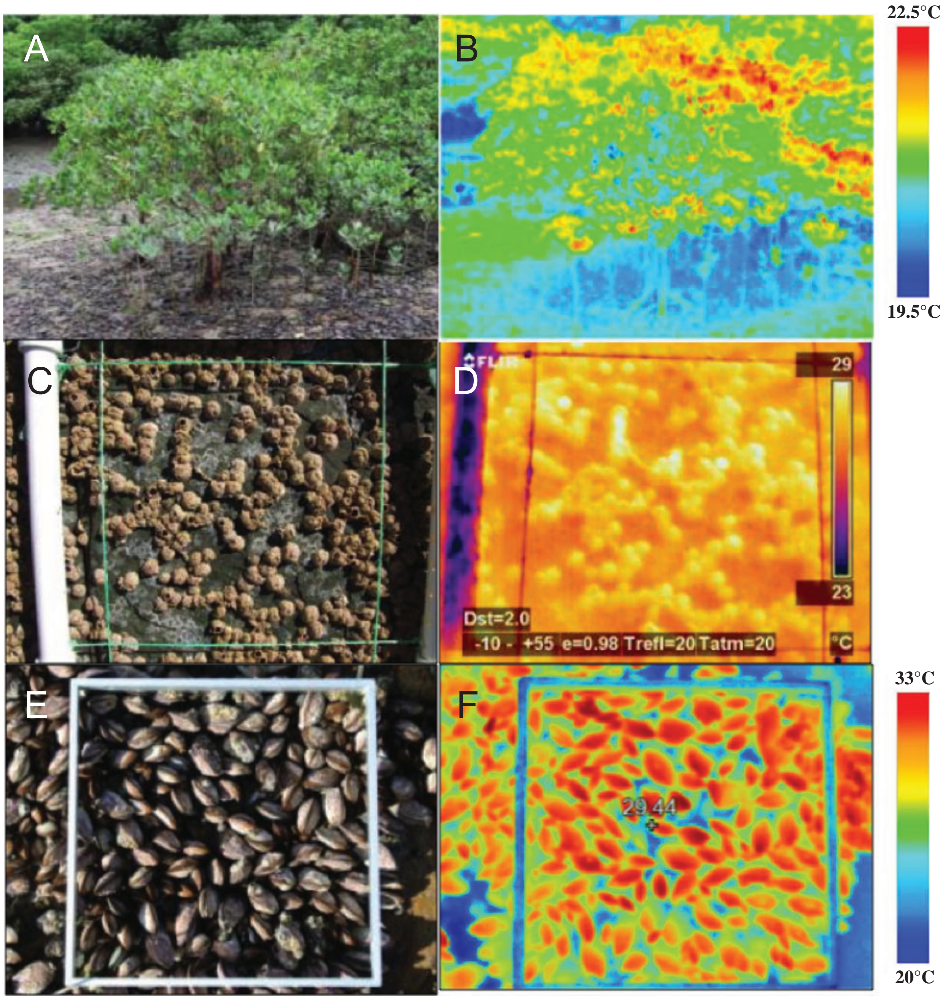

Figure 15. Digital and infrared images illustrating the thermal buffering properties of biogenic structures such as mangrove vegetation (**A, B**), ecosystem engineers such as the barnacle *Tesseropora rosea* (**C, D**) and the mussels *Perna perna and Mytilus galloprovincialis* (**E, F**).

and the risk of desiccation due to both evaporation and expulsion of water during valve closure. In contrast, *M. galloprovincialis* keeps its valves closed when exposed to air. This behaviour reduces the risk of desiccation, but decreases the efficiency of anaerobic respiration (Nicastro *et al*., 2010). These differences in thermoregulatory behaviour result in dramatically different body temperatures, even though individuals are found within the same microhabitat. Through the use of infrared thermography, Lathlean *et al.* (2016a) were able not only to show that *P. perna*, when aggregated, maintained lower body temperatures than *M. galloprovincialis* during exposure to identical levels of heat stress, but also that when interspersed among aggregations of *P. perna* the invasive *M. galloprovincialis* benefitted from the evaporative cooling behaviour of the former. Without the use of infrared thermography this interaction could have only been discovered had the researchers simultaneously (though unrealistically) taken thousands of intrusive thermocouple measurements of both species in the field. The use of biomimetic loggers to measure body temperatures of the two species would also have been inappropriate, since such devices cannot model differences in thermoregulatory behaviour of living animals.

Intertidal mussels may play an important role as ecosystem engineers, their sometimes extensive aggregations serving to buffer associated epifaunal communities from unfavourable conditions such as heat stress and wave exposure. The effectiveness of mussel beds in providing thermal refugia for other intertidal molluscs may vary depending upon geographic location as well as on the size and structure of the mussel beds themselves. Recent research has used infrared thermography show that both the size of mussel beds and the size of individual mussels within the bed, influence the amount of heat stress experienced by both mussels and their epifaunal communities (Lathlean *et al*., 2016a). Infrared images have also been used to demonstrate high inter-individual variability in body temperatures of mussels within beds. Thermal gradients of 4–5 °C were found to exist across mussel beds as small as 20 cm^2 during extreme heat events with mussels on the windward side displaying cooler temperatures than those on the leeward side of the mussel bed (Lathlean *et al*., 2016b; Fig. 16A, B). Noticeably, the observed inter-individual variability in body temperatures was three to four times greater than interspecific variability. Observations using infrared thermography have also shown that body temperatures of adjoining mussels orientated perpendicular to the sun can differ by up to 2–3 °C (J.A. Lathlean, unpublished data). Such inter-individual variability within mussel beds may have significant implications for predicting how these ecosystem engineers, and by extension their associated invertebrate communities, may respond and adapt to the increasing frequency and intensity of extreme heat events associated with climate change. Thus, infrared cameras are an important tool for marine conservationists and environmental managers interested in monitoring and predicting responses of molluscan populations to climate change.

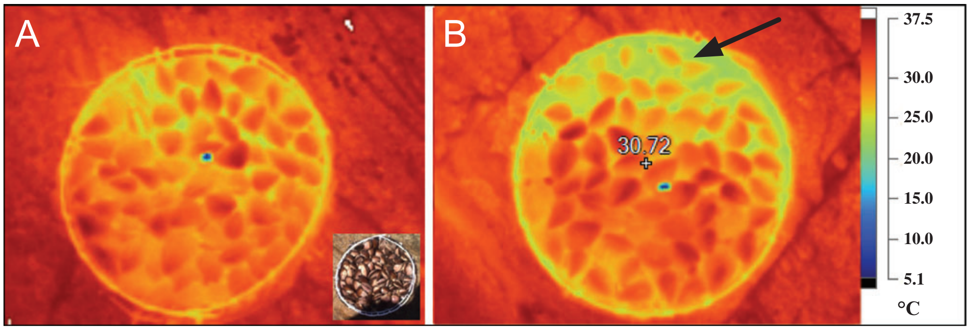

Figure 16. Thermograms of artificial *Perna perna* beds (20 cm in diameter; inset) observed on a flat rocky reef at Jorgensfontein, South Africa, in absence (**A**) and presence (**B**) of wind (direction indicated by arrow in **B**). Individuals on windward side of beds displayed body temperatures 3–5 °C lower than those on leeward side, explained by convective cooling.

Thermoregulatory behaviour

Despite the widely acknowledged role of a suite of postural behaviours in both marine and terrestrial molluscs to reduce heat conduction from their substrata, as well as reduce water lost through evaporation and/or increase convective cooling by air currents (as reviewed above), little is yet known about the mechanisms driving these behaviours. Marshall & Chua (2012) showed that shell-standing behaviour was triggered by the presence of a temperature gradient in the boundary-layer air close to (<4 mm) the solar-heated rock surface and was not observed when snails were heated in the absence of this gradient. Seuront & Ng (2016) showed that postural behaviours (including shell-lifting, shell-standing and towering) occurred in summer, but not in winter, in the high-shore *Echinolittorina malaccana* and *E. radiata*. While these results suggest that postural behaviour may be driven by the temperature of the substratum, Seuront & Ng (2016) did not find any significant relationship between the type of postural behaviour and substratum temperature. Recent fieldwork conducted on *Austrolittorina unifasciata* in Australia and *Littorina saxatilis* in Spain nevertheless indicated that postural behaviour only occurred when substratum temperature reached a critical temperature (L. Seuront, unpublished data; Fig. 17). Thus *L. saxatilis* started exhibiting shell-lifting and shell-standing behaviour at substratum temperatures above 36 °C (Fig. 17A). In *A. unifasciata*, shell-lifting and shell-standing occurred above 38.8 °C, and shell-towering above 41 °C (Fig. 17B).

Though further work is needed to decipher the relationship between the temperatures of molluscs, that of their substrata and their postural behaviour, infrared thermography presents the unique and desirable advantage of allowing multiple measurements of body and substratum temperatures, which is not achievable using traditional single-point temperature measurement devices such as thermocouples, iButtons or infrared thermometers.

Mollusc colour polymorphism and thermal properties

The potential role of shell colour in regulating body temperature of molluscs is still poorly investigated, despite shell colour polymorphism being a common feature of the populations of many marine and terrestrial molluscs (e.g. Mitton, 1977; Clarke *et al.*, 1978; Clarke, 1979; Johnson, 1980, 1981; Heller, 1981; Raffaelli, 1982; Cain, 1983, 1988; Cowie & Jones, 1985; Etter, 1988; Rehfeld, 1997). The relevance of this aspect of mollusc thermal ecology is illustrated by two examples: the effect of shell colour modification by parasites on body temperatures of mussels and the effect of shell colour on the body temperature of the highly polymorphic *Littorina saxatilis*.

The shells of many molluscs, including mussels and oysters, are often infested with endolithic parasites, which bore into and discolour the exterior surface (Kaehler, 1999; Zardi *et al.*, 2016). In some cases infestations can be so severe that the shell is weakened

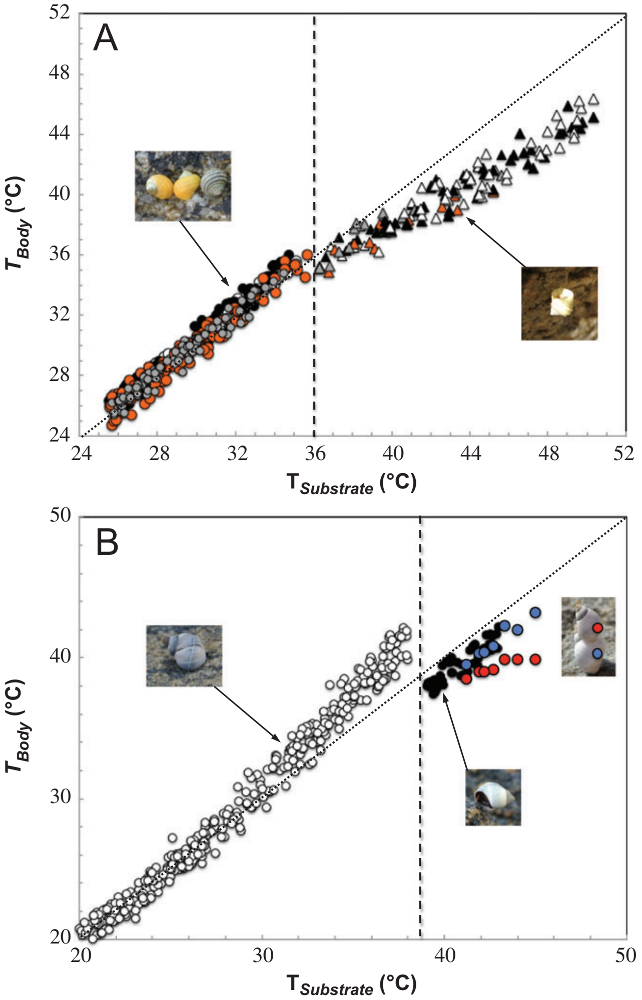

Figure 17. Body temperature (T_{Body}) of the high-shore *Littorina saxatilis* (**A**) and *Austrolittorina unifasciata* (**B**), shown as a function of their substratum temperature ($T_{Substrate}$). Dotted line is first bisextrix, $T_{Body} = T_{Substrate}$; vertical dashed line is critical temperature above which snails exhibit postural behaviour. In **A** the black, grey, orange and white points represent four *L. saxatilis* morphotypes, respectively black, black-and-white striped, orange, and white; circles and the triangles represent, respectively, individuals lying flat on substratum and shell standing. In **B** the white, black, red and blue points represent, respectively, *A. unifasciata* exhibiting no postural behaviour, shell-lifting/shell-standing, and individuals at top and bottom of towers.

and must be strengthened by internal shell deposition, resulting in depletion of energy resources (Kaehler & McQuaid, 1999; Zardi *et al.*, 2009). Contrary to this negative relationship between parasite and host, Zardi *et al.* (2016) used infrared thermography to reveal that phototrophic shell-boring cyanobacteria have a positive, cooling effect on mussel body temperatures during extreme heat events (Fig. 18A). This beneficial effect was due to the white discolouration of the shell and the increased rugosity of the shell surface caused by the excavation activity of the cyanobacteria. Such results have implications for our understanding of mutualistic and parasitic relationships and how these relationships might be expected to change under different climates. This study also demonstrates a potential use of infrared thermography to identify and manage parasitic outbreaks among natural and cultivated populations of mussels and oysters, which are commonly infested with endolithic cyanobacteria.

The polymorphic intertidal snail *L. saxatilis* is a particularly relevant species for thermal study as it has an unusually wide latitudinal distribution (ranging from South Africa to Svalbard; Reid, 1996; Branch *et al.*, 2010), it occurs in diverse habitats (from sheltered estuaries to highly exposed rocky shores; Clarke, Mill & Grahame, 2000), it is found at most intertidal levels (Sokolova *et al.*, 2000), and can withstand temperatures of up to 35 °C for at least several hours during summer low tides and up to 47 °C during short-term acute heating events (Sokolova *et al.*, 2000). Despite the extreme variability in shell coloration in *L. saxatilis* (Reid, 1996) and the amount of work conducted on the selective forces controlling colour polymorphism (Ekendahl & Johannesson, 1997; Johannesson, 2003, 2016), there is still a paucity of information on the potential links between shell colour and body temperature of *L. saxatilis*. Selection processes related to colour include visual selection for cryptic coloration by predators (Johannesson & Ekendahl, 2002; Surmacki *et al.*, 2013) and physiological selection arising from the genetic correlation between shell colour and the physiological response to salinity (Sokolova & Berger, 2000) and to direct thermal selection (Berger, Bogdanov & Sergievsky, 1995).

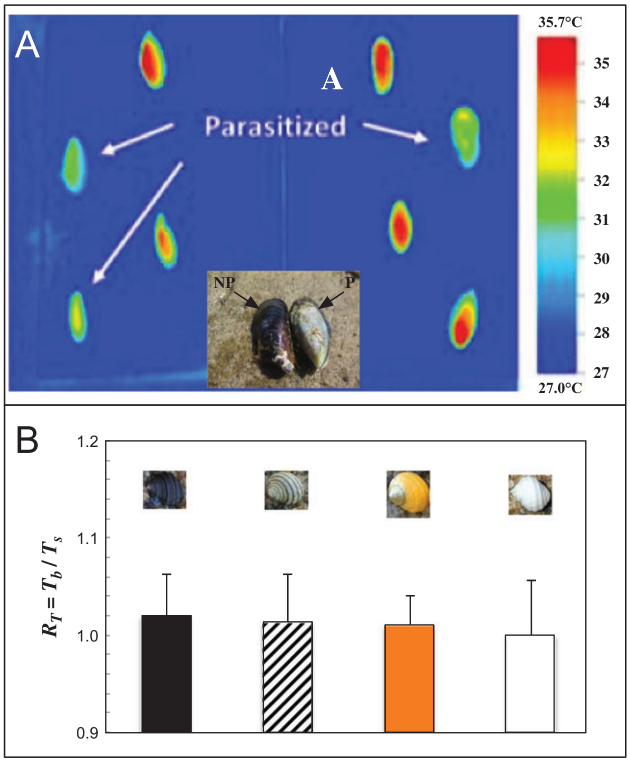

Figure 18. Illustration of effect of different shell colours on mollusc body temperature. **A.** Infrared images of South African *Perna perna*, showing decrease in body temperature of individuals completely covered by endolithic parasites that cause discolouration (inset, P), when compared with individuals free of parasites (inset, NP; modified from Lathlean *et al.*, 2017: fig. 7). **B.** The ratio R_T (a standardized measure of difference between body temperature T_b and substratum temperature T_s) of the highly polymorphic high-shore *Littorina saxatilis* did not differ significantly between colour morphotypes (insets) and did not differ significantly from $R_T = 1$, indicating (1) absence of an effect of shell colour on *L. saxatilis* body temperature and (2) thermal homogeneity between *L. saxatilis* and its substratum.

The potential differences in heating rate and maximal body temperature of colour morphs have been investigated by generating heating curves using biomimetic snails of the four colour morphs (black, white, yellow, and black-and-white striped; Fig. 18B) of a high-shore Galician *L. saxatilis* population (L. Seuront, unpublished data). Biomimetic snails (prepared following Lima & Wethey, 2009) were fixed with cyanoacrylate glue onto flat granite rocks with aperture towards the substratum under direct sunlight or in shade (created following Marshall & Chua, 2012, as described above). For each colour morph, shells (6–7 mm in diameter) were fitted with fine K-type thermocouples (glued inside the shell) and their temperatures simultaneously recorded every 30 s until they reached stable maxima. All measurements were conducted over 2-h periods around solar midday under sunny conditions (solar irradiance 975–1035 $\mathrm{W\,m^{-2}}$) in the absence of wind with air temperature ranging between 34.2 and 35.6 °C and substratum temperature in the range 42–45 °C. Using a protocol similar to that described above (see example of *A. unifasciata* of different sizes), it was shown that the temperature of the four biomimetic colour morphs converged towards $T_{\max}$ within 60 min. No significant differences were found in $T_{\max}$ between morphs ($P > 0.05$; $T_{\max} = 41.3 \pm 1.4$ °C), though the temperature of the black morph increased significantly faster than in other morphs ($P < 0.05$). The heating rate (estimated as t_m, the time needed to reach a temperature $T_{\max}/2$) was significantly faster (on average twice as fast) in the biomimetic snails exposed directly to the sun ($P < 0.05$). This result indicates that direct and indirect heat transfers have comparable contribution to *L. saxatilis* body temperature. The absence of differences in $T_{\max}$ between morphs is consistent with field observations of T_b and T_s of the four colour morphs of *L. saxatilis* considered here; in which the body-to-substratum temperature ratio (BST = T_b/T_s; introduced by Chapperon & Seuront, 2011a, as a standardized measure of the difference between substratum and snail body temperatures) did not significantly differ between morphs ($P > 0.05$; Fig. 18B). These observations are congruent with both evidence of dark morphs heating up faster than light ones (Etter, 1988) and of the absence of temperature differences in intertidal molluscs varying in structure, shape, size and colour (Miller & Denny, 2011; Cox & Smith, 2011). They nevertheless suggest a decoupling between the heating rate and the maximal temperature reached by molluscs of different colours.

Infrared thermography: a tool for monitoring the impacts of climate change on molluscs?

A major difficulty for climate-change biologists is the spatial mismatch between the size of organisms and the resolution at which global climate data are collected and modelled: the grid sizes of climate models are on average four orders of magnitude larger than the animals they study (Potter *et al.*, 2013; Torossian, Kordas & Helmuth, 2016). This is particularly critical for minute organisms, because microclimatic conditions often deviate substantially from those generated by the available models (Faye *et al.*, 2014; Hannah *et al.*, 2014; Scheffers *et al.*, 2014a), hindering opportunities to study biotic responses to global warming (Storlie *et al.*, 2014; Scheffers *et al.*, 2014b; Pincebourde & Casas, 2015). There is an urgent need for microclimatic modelling at spatial scales appropriate to organisms, so that mechanistic models at individual levels can be incorporated into models of species distribution and vulnerability to climate change (Potter *et al.*, 2013). Monitoring microclimates at scales relevant to individual organisms is, however, a daunting task owing to the diverse spatial and temporal patterns of microclimatic variation, while climate change at a global scale generates even more complexity (Woods, Dillon & Pincebourde, 2015).

As emphasized in the present work, one of the essential features of infrared thermography, especially when compared with traditional single-point temperature measurements, is that thermal images allow for simultaneous measurements of multiple individuals, species and communities. Combining infrared thermography with new three-dimensional photographic techniques, spectrometers and lightweight unmanned aerial vehicles (i.e. drones) may be a first step in producing fine-scale thermal maps of entire ecosystems at scales pertinent to individual organisms (Lathlean & Seuront, 2014; Faye *et al.*, 2016). In this context, we suggest that infrared thermography could play a major role in developing and improving environmental management and conservation plans for systems vulnerable to future climate change in general, and for both terrestrial and intertidal molluscs in particular. Such thermal maps would increase the computational power of ecological models designed to predict how and when specific organisms will respond to future climate change. This approach could be used to identify areas or microhabitats that (1) will act as thermal refugia for intertidal organisms during future extreme heat events, (2) qualify for increased conservation status because they exhibit reduced thermal heterogeneity, and (3) present increased likelihood of restoration success if a target species is transplanted to the area. These issues are pertinent for molluscs that live in particularly heterogeneous habitats, since a recent study showed theoretically that ectotherms thermoregulate more accurately when thermal resources are spatially dispersed than when clumped (Sears *et al.*, 2016). This prediction was supported by observations of thermoregulatory behaviours of lizards in outdoor arenas with known temperature distributions.

In practice, the thermal quality of a given habitat could be quantified through a generalization of BST. For instance, knowing the thermal tolerance limit of a species (i.e. heat coma and lethal temperatures) and the thermal property of a given habitat recorded in space and time through infrared thermography, it is possible to produce an indicator of the suitability of a habitat to an organism (or species) i as: $\mathrm{BST}_i = T_b(i)/T_s$, where $T_b(i)$ is the organismal coma or lethal temperature of i. Areas where $\mathrm{BST}_i < 1$ and $\mathrm{BST}_i > 1$ will then be considered as viable or not for the species. More generally, a critical BST_i could be defined as: $\mathrm{BST}_c = T_{sc}/T_s$, where T_{sc} is a critical surface temperature (either minimal or maximal) returned by climatic scenarios and T_s the substratum temperature actually measured using infrared thermography at scales pertinent to individual organisms (Lathlean, Seuront & Ng, 2017). This approach is notable because (1) it explicitly takes into account small-scale heterogeneity of habitat (e.g. crevices, pits, boulders and flat rocks) that defines a species' thermal landscape, and hence its realized ecological niche, and (2) it represents a first step to bridge the gap between field-based approaches that typically span from centimetres to tens of metres to climate scenarios that are generally coarse-grained (i.e. 10 × 10 km). Torossian *et al.* (2016) have discussed the mismatch between scales of climatic observations and the much-needed biological details.

In an era where much attention has been given to predicting which species are going to be 'winners' or 'losers' under future climate-change scenarios (Somero, 2010), as well as how changes in the relative abundance of different species may impact the direction and strength of species' interactions (Kordas *et al.*, 2011) and demographic responses (Kordas & Harley, 2016), the use of infrared thermography as a tool for monitoring and predicting changes in community structure is appealing. This is important for both natural and harvested mollusc populations that are under increasing threat of both ocean warming and acidification (Barton *et al.*, 2012). As recently stressed (Lathlean *et al.*, 2017), infrared thermography not only offers a glimpse of how multiple species within a community may respond to contemporary and future levels of heat stress, but can also reveal which individuals within a population are most susceptible to elevated heat stress (e.g. Lathlean *et al.*, 2016b). If genetically determined, it is this inter-individual variability among populations that will largely determine whether a population will be capable of adapting to the rapidly changing climate.

CONCLUSIONS: MOLLUSCAN RESEARCH MAY WELL FEEL THE HEAT

Both the reviews and the case studies presented here demonstrate that infrared thermography is an effective tool for investigating a range of ecological patterns and processes from a unique perspective. In particular, it has the desirable advantage over traditional single-point temperature measurements (e.g. thermocouples, iButtons and infrared thermometers) in that the images it produces allow for simultaneous measurements of multiple molluscan individuals, species and communities. However, even though the number and diversity of ecological applications of infrared thermography has steadily risen over the last two decades, due to increasingly portable and affordable infrared-imaging technology, its use in molluscan research is still in its infancy. This is especially true in terrestrial ecosystems, where only a very few of the many mollusc habitat types and taxa have been sampled (e.g. Lathlean & Seuront, 2014; Lathlean *et al.*, 2017). Uniquely, infrared thermography has the potential to bridge the long-acknowledged gap between scales of actual observations and the much-needed biological details (Potter *et al.*, 2013; Torossian *et al.*, 2016). This is achievable through a better quantification of microclimates across appropriate spatial and temporal scales, so that mechanistic models at the individual levels can ultimately be better incorporated into models of species distribution and vulnerability to climate change. In this context, we suggest that infrared thermography should play a key role in understanding and managing how molluscan species, populations and communities and their environments will be affected by increasing temperatures associated with climate change. It is apparent from both the inherent complexity of patterns and processes involved in molluscan thermal biology, and from the wide range of applications of infrared thermography in molluscan research, that our journey towards understand the ecology of molluscs from a bottom-up approach—through the lens of infrared thermography—is still in an early stage.

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