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Review

On the edge: The use of infrared thermography in monitoring responses of intertidal organisms to heat stress



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ABSTRACT

Monitoring changes in the environment and the corresponding effects on biological systems still represents a major challenge in many marine and terrestrial ecological studies. Infrared thermography (IRT), and its application within the marine environment, represents an effective non-invasive tool for measuring the temperatures of organisms and their surrounding environment in situ. The use of IRT within the intertidal zone is particularly useful since habitat and organismal temperatures are highly variable across both fine spatial and temporal scales. We review the growing number of intertidal studies that utilise IRT to investigate the role of small-scale temperature variability in contributing to various demographic and ecological processes. In particular, we introduce two indicators of the thermal quality of intertidal habitats that can be readily used by ecologists but also management and conservation policy makers to assess the suitability of a given habitat for a range of species under actual and predicted climatic conditions. We also outline a range of potential applications involving IRT that have yet to be explored for monitoring coastal environments. These include combining photogrammetry, unmanned aerial vehicles and IRT to large-scale three-dimensional thermal maps of intertidal habitats. We also suggest ways in which this technology could facilitate environmental management objectives in a warming world, such as the identification and quantification of thermal refugia across various spatial and temporal scales. We affirm with previous studies that such thermal refugia are vital for the adaptation of intertidal communities to climate change and that IRT could facilitate more effective management and conservation of these areas. The IRT applications outlined in this review are by no means exhaustive or limited to rocky intertidal environments. We envision that IRT will become increasingly popular as environmental management agencies become increasingly concerned about global climate change and how to combat its negative consequences on ecosystems.

1. Introduction

1.1. Monitoring ecological responses to climate change

As biological systems and ecosystem processes continue to change in response to increasing temperatures associated with climate change it is paramount that environmental managers and conversation strategies incorporate the necessary tools for monitoring and predicting these future changes. In the past, this has largely been achieved by utilising long-term meteorological data but such records are usually somewhat removed from the actual conditions experienced by target organisms within their specific microhabitats (Lathlean et al., 2011; Stobart et al., 2016). Indeed, many recent marine and terrestrial studies have demonstrated that small-scale temperature variability can be extremely

heterogeneous and that this can have significant implications for the persistence and viability of species and populations in a warming world (Woods et al., 2015).

Infrared thermography (IRT) serves as a powerful non-invasive tool for rapidly detecting and measuring fine-scale variations in temperatures. Such measurements have proven to be particularly useful in measuring body temperatures of small ectothermic organisms (e.g. Chapperon and Seuront 2011a) as well as identifying and characterising small-scale thermal refugia utilised by such organisms during extreme heat events (e.g. Lathlean 2014). Due to the rapid attenuation of infrared radiation underwater, ecological studies that use IRT have largely been undertaken on terrestrial systems, whilst being limited to surfacing animals in aquatic ecosystems. In recent years, however, IRT has been used to investigate the thermal ecology and physiology of

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intertidal organisms, those species which live at the land-sea interface and are intermittently exposed by the receding tide.

Intertidal ecosystems are home to some of the world's most biologically diverse and productive communities but are particularly vulnerable to climate change because (i) many organisms in these ecosystems are already living at or close to their upper thermal limits (Stillman and Somero 2000; Somero 2010); (ii) rising sea levels and greater extreme temperatures are limiting the amount of suitable habitat available for these organisms; and (iii) anthropogenic activities and disturbances are generally the greatest along coasts. Therefore, the application of IRT within the intertidal zone has been quite crucial and is fast becoming widely used by marine ecologists and environmental managers alike (Lathlean and Seuront, 2014). This review outlines some the most common applications of IRT in the marine environment to date, focusing on several case studies undertaken across contrasting intertidal habitats, including rocky shores, mangrove forests and saltmarsh communities. It also discusses best practices and common pitfalls associated with using IRT within intertidal habitats, whilst identifying fruitful areas of future research and applications within aquaculture, resource management and conservation. In particular, we introduce two indicators of the thermal quality of intertidal habitats that can be readily used by ecologists but also management and conservation policy makers to assess the suitability of a given habitat for a range of species under actual and predicted climatic conditions.

1.2. Brief history of infrared thermography

The detection and quantification of infrared radiation has become one of the most diverse and important scientific applications since it was first discovered by Sir William Herschel in 1800 through his classic prism experiment to refract natural light. Initially used by astronomers to detect distant planets and hidden stars, infrared detection and imaging were quickly utilised for military purposes including target acquisition, night-vision and guided missile systems. Many commercial applications quickly followed as the relative cost and sophistication of infrared imaging technology became increasingly affordable and available. Such commercial uses to date include: surveillance, law enforcement, medical diagnosis, satellite imagery, electrical engineering, construction, pest control and veterinary science, just to name a few.

Since the first Earth Observation Satellite was launched in 1959, meteorologists and oceanographers have relied heavily on large-scale infrared images to monitor and forecast regional weather patterns and climate variability. Today, satellite-measured reflectances in the red, near infrared and infrared band of the electromagnetic spectrum are used by terrestrial ecologists to map large scale changes in vegetation cover (Vorovencii et al., 2013), primary productivity (Nouvellon et al., 2000) and photosynthetic efficiencies of entire ecosystems (Coops et al., 1998). Similarly, oceanographers utilise satellite images of sea-surface temperatures to produce detailed maps and models of oceanographic currents and surface properties. However, non-satellite-derived applications of infrared thermography (hereafter IRT) taken at small spatial scales have only come about in the last 20 years or so. Within the ecological literature, IRT was introduced in the late 1980s as a noninvasive tool for measuring body temperatures of lizards (Jones and Avery 1989). Since then IRT has become increasingly portable and sophisticated being used extensively for nocturnal surveys of bats, owls and rodents (McCafferty et al., 1998; Pregowski et al., 2004; Hristov et al., 2008; McCafferty 2013) and for tracking and quantifying the abundances of large mammals such as deer and polar bears (York et al., 2004; Butler et al., 2006). The most recent high-resolution infrared cameras have even been used to map fine-scale thermal properties of individual leaves and the implications on the thermoregulation of herbivorous arthropods (Caillon et al., 2014).

Whilst IRT is an effective method for capturing thermal variability on land, it is considerably less effective in the ocean, where infrared waves are rapidly attenuated by seawater. Many deep-sea fish are capable of detecting near infrared radiation (NIR) to capture prey and scientists have utilised NIR lights to observe the natural behaviour of deep-sea fish but such applications cannot be used to estimate temperatures of objects under water. Species living within the intertidal zone, however, are intermittently exposed to the atmosphere up to 12 h each day, which provide a unique opportunity to apply IRT to marine organisms (Lathlean and Seuront 2014).

2. Intertidal ecosystems - Bellwethers of climate change

2.1. Importance of intertidal systems

Apart from having a long history of ecological research, particularly rocky shores, intertidal systems constitute an important interface between the land and sea, and is characterised by steep environmental gradients. They also represent an important biome that is integral for the proper ecological functioning and cycling of nutrients within both terrestrial and marine environments. Although generally restricted to a 2-3 m band of rocky substrata around the edge of the ocean, rocky shores represent one of the most diverse and productive ecosystems on the planet. Despite the longstanding need to quantify the fluxes of carbon from continental margins to open ocean basins (Capone et al., 2006; Falkowski et al., 1998), scarce attention has been given to intertidal zones as a carbon source (Liu et al., 2000). Carbon fluxes and exchanges between the countless littoral shallow-water ecosystems and the open coastal zone have yet to be included in the global calculation of the carbon budget. Intertidal ecosystems have, therefore, been put forward as the 'missing carbon sink', characterised as a widespread network of 'small' sinks that capture an estimate of 1.8 \pm 0.5 PgC y⁻¹ (Guarini et al., 2008). Understanding the structure and function of intertidal habitats and their responses to future climate change is, therefore, of particular relevance to environmental managers and conservation programs that are concerned with sustaining the ecological and economic subsidies that these systems provide. For example, the worldwide value of ecosystem goods (e.g. food and raw materials) and services (e.g. disturbance regulation and nutrient cycling) provided by habitats from the intertidal zone out to the continental shelf break are estimated be over US\$14 trillion per year or \sim 43% of the global total (Costanza et al., 1997). Yet it is often these intertidal environments that are most at risk of anthropogenic disturbances such as land-clearing and over-exploitation. Furthermore, with many intertidal organisms already living at or close to their thermal limits intertidal communities may act as a sensitive bellwether for global climate change (Somero 2010; Somero, 2010Somero 2010; Denny and Harley 2006, Helmuth 2006).

2.2. Types of intertidal habitats

Intertidal habitats are as diverse as the biological communities they support and are generally categorised based on the type of substratum (hard or soft) and level of exposure (estuary or coast). Intertidal habitats with hard rocky substrata are commonly found in more exposed environments towards the entrance of estuaries and along the open coastline. These are collectively referred to as 'rocky shores' (Fig. 1a) and are usually topographically complex with numerous microhabitats including rock pools, crevices, boulders and emergent platforms. Along with a steep thermal gradient these microhabitats produce substrata with highly heterogeneous temperatures during aerial exposure, which can be captured effectively using IRT (see Fig. 2). Intertidal habitats with soft-sedimentary substrata can be found both within estuaries (e.g. mangrove forests; Fig. 1b; or coastal saltmarshes; Fig. 1d) or along open coasts such as sandy beaches (Fig. 1c). Sandy beaches are less topographically variable than rocky shores resulting in lower thermal heterogeneity. However, stranded wrack (i.e. seaweed) and other decomposing matter along the shoreline may increase thermal heterogeneity and produce microhabitats that would otherwise be non-existent (Fig. 1e). Soft sedimentary intertidal



Fig. 1. Illustrative photos of the various intertidal habitats and biological communities where infrared thermography can be applied: (a) exposed rocky shore, (b) mangrove forest, (c) sandy beach, (d) coastal saltmarsh, (e) wrack-line, and (f) mussel beds and associated communities.

habitats in estuaries experience considerably less wave action than sandy beaches enabling mangrove trees and saltmarsh plants to take root and increase the thermal heterogeneity of the underlying substrata (Fig. 1b,d). Such thermal heterogeneity, whether within coastal saltmarshes or rocky shores, is important for intertidal invertebrates as they seek to avoid unfavourable heat and desiccation stresses during aerial exposure. Intertidal habitats are also excellent study systems to investigate the role of ecosystem engineers, that is, organisms that create or modify environment conditions, in ameliorating heat stress on associated epifaunal and infaunal communities. These ecosystem engineers could include mussel beds (Fig. 1f), oyster beds, barnacles, macroalgae, mangrove trees or saltmarsh plants. Therefore, far from simply being a narrow band of homogenous habitats that belongs neither to the terrestrial or marine world, we find an incredibly productive and diverse range of habitats and biological communities that are completely compatible with the application of IRT.

3. Case studies from the intertidal

Taking advantage of the daily tidal cycle and the emergence of marine benthic communities, Helmuth (2002) first used infrared thermography to measure surface body temperatures of two species of intertidal invertebrates – the predatory seastar *Pisaster ochraceous* and the mussel *Mytilus californianus*, its preferred prey. Whilst Helmuth did not use replicate images to statistically analyse differences in body temperature of the two species, his initial application confirmed the unrealised potential of using IRT within intertidal ecology. It also revealed that organisms living under the same set of climatic conditions



Fig. 2. Visual and corresponding infrared image of a tropical rocky shore during low-tide. Notice the high thermal heterogeneity across fine spatial scales.

can display dramatically different body temperatures. This latter point has had significant repercussions on the field of global change biology and has sparked several lines of fruitful inquiry, including understanding how the strength and direction of species interactions will change with increasing temperatures (Helmuth et al., 2006). Since Helmuth's original application of IRT within the intertidal zone IRT has been used to measure variability in the surface and body temperatures of macroalgae in Hawaii (Cox and Smith 2011), limpets in New South Wales, Australia (Lathlean 2014; Fraser et al., 2016), littorinids in Chile (Rojas et al., 2013), Fiji (Chapperon and Seuront 2011a) and Hong Kong (Seuront and Ng 2016), neritids in South Australia (Chapperon and Seuront 2011b, 2012), barnacles in New South Wales (Lathlean et al., 2012; Lathlean et al., 2013), mussels in South Africa (Lathlean et al., 2016) and seastars in North America (Pincebourbe et al., 2013). We will now focus on these various case studies, organised by taxonomy, and outline what contribution they have made to the field of intertidal ecology.

3.1. Macroalgae

Despite the dominance of macroalgae on rocky intertidal shores worldwide, there have been very few studies that have used IRT to measure in situ surface temperatures of these important primary producers. This may be partly due to the lower vertical distribution of many macroalgae species which only emerge during the lowest monthly tides or otherwise remain awash in seawater, making it difficult to capture reliable IR images. Despite this, Cox and Smith (2011) successfully used IRT to measure the surface temperatures of six different macroalgae species on an exposed rocky shore in Hawaii. Here, the authors capture infrared images of macroalgae, and other intertidal organisms, taken haphazardly and perpendicularly to mid intertidal rocky substrata during two consecutive daytime low-tides. Individuals were outlined using appropriate thermal imaging software to calculate average surface temperatures for the various species' of algae. The major findings were that mean frond temperatures varied by up to 1.7 °C between species and that, depending on species, frond temperatures were between 0.4 °C and 1.5 °C cooler than the surrounding habitat. Whilst these results were not particularly ground-breaking, the authors argued that the significance in their work was in demonstrating the effectiveness of IRT as a non-invasive tool for measuring small-scale in situ temperature variability.

Another case study that utilised IRT to measure thermal properties of intertidal macroalgae involves unpublished work undertaken by one of the present authors (J.A. Lathlean). This work investigated the effects of macroalgae size on mean frond temperatures and the temperatures of the surrounding rocky substrata (Fig. 3). Similar to Cox and Smith (2011) the present author took infrared images of various sized macroalgae (*Ulva* spp.) haphazardly within the mid-shore region at three different locations in southeast Australia. Analysis of images revealed that mean surface temperatures of macroalgae decreased with increasing size and that a sharp thermal gradient existed on adjacent rocky substrata, with temperatures increasing dramatically within a few centimetres from the macroalgae (Fig. 3). These findings could be placed in the context of various direct and indirect species interactions between intertidal invertebrates and macroalgae. For example, many benthic invertebrates find refuge from heat and desiccation stress under the fronds of intertidal macroalgae during emersion and IRT could be used to better characterise this positive interaction e.g. by demonstrating the extent of thermal buffering within and adjacent to patches of macroalgae.

Note that a distinction needs to be made here between the application of IRT to measure the surface temperatures of intertidal macroalgae, of which there are few examples, and the numerous applications of Colour Infrared (CIR) multispectral imaging that have been used to estimate the abundance (Van der Wal et al., 2014), biomass (Murphy et al., 2006), distribution (Nezlin et al., 2007) and grazing pressures (Murphy and Underwood 2006; Underwood and Murphy 2008) of intertidal algae. Colour infrared images capture light within the near infrared region of the electromagnetic spectrum i.e. between approximately 1 μ m to 10 μ m in wavelength. This band of light behaves similarly to visible light and does not emit thermal radiation like wavelengths within the mid to far infrared band i.e. between 10 μ m to 150 μ m. Colour infrared cameras are extremely useful for other forms of quantitative imaging other than IRT and are regularly utilised in satellite remote sensing studies.

3.2. Molluscs

Due to their ubiquitous nature within the intertidal zone, molluscs have repeatedly served as model organisms when investigating the role of small-scale thermal variability on numerous ecological and evolutionary processes. This is true also for the application of IRT within the intertidal zone. So far, molluscan studies that have utilised IRT have investigated (i) the effect of individual size, morphology and mussel bed structure on individual body temperatures (Lathlean et al., 2016), (ii) thermoregulatory behaviours including aggregation formation (Chapperon and Seuront 2012; Rojas et al., 2013), shell orientation (Fraser et al., 2016), shell posturing behaviour (Seuront and Ng 2016; Ng et al., in press) and thermal refuge selection (Chapperon and Seuront 2011a; Lathlean 2014) and (iii) the effect of phototrophic endolithic parasites on body temperatures during extreme heat-events (Zardi et al., 2016) (Fig. 7).

Many of the initial applications of IRT within molluscan research were undertaken to simply validate the method of using surface shell temperatures as a proxy for internal body temperatures. This was an essential first step in demonstrating the potential use of IRT as a noninvasive tool in ecophysiology and should be repeated every time IRT is used to measure the body temperatures of a new study species as differences in the size, shape, colour and emissivity can alter the relationship between internal body temperatures and external shell



Fig. 3. Visual and corresponding infrared image of an exposed intertidal macroalgae. Notice not only the small-scale thermal heterogeneity within different parts of the algal fronds but also the 'thermal buffering' of the rocky substrata within close proximity.

temperatures. Caddy-Retalic et al. (2011) showed that shell temperatures of the intertidal gastropod Nerita atramentosa were significantly correlated with internal body temperatures measured with a digital thermocouple. These authors made comparisons of both the external ventral and dorsal surfaces with internal body temperatures for 50 individual gastropods (N. atramentosa) exposed to a range of temperatures (15-55 °C) under laboratory conditions. Thermal images of both the ventral and dorsal surfaces of N. atramentosa produced highly significant positive correlations with internal body temperatures. Next, using IRT Chapperon and Seuront (2011b) undertook comparisons between the external shell temperatures of N. atramentosa and the surrounding substrata within boulder fields and on open rock platforms and found them to be highly significantly correlated in both habitats. This example in particular demonstrated that IRT can be an effective non-invasive method for measuring body temperatures of intertidal snails in the field and that body temperatures of these snails in the field are largely influenced by the temperature of the surrounding substrata. Subsequent studies have, for example, also shown IRT as an effective tool for measuring the body temperatures of limpets (Fraser et al., 2016) and mussels (Lathlean et al., 2016). Nevertheless, a recent in situ study has demonstrated that shell temperature measured using IRT only explained \sim 50% of the variation of body temperature measured using thermocouples inserted into the mental cavity of the high shore ovsters Isognomon nucleus (T.P.T. Ng unpubl. data). This finding suggests that the effectiveness of shell temperature as a proxy for body temperatures may vary between different species and/or under different field conditions (e.g. depending on amount of solar radiation, wind speed, air temperature, etc.) and hence a considerable amount of cautions is still needed to be taken by inferring shell temperatures (measured by IRT) as body temperatures in the field.

One of the major advantages of using IRT over traditional singlepoint temperature measurements (e.g. thermocouples, iButtons, infrared thermometers) is that the images they produce allow for simultaneous measurements of multiple individuals, species and communities. This is particularly useful when the presence of absence of one species or individual influences the thermal properties of another. For example, shading by trees lowers the temperatures experienced by understorey plants and invertebrates (Fig. 4 a). Similarly, during aerial exposure barnacles on rocky intertidal shores ameliorate co-ocurring limpets and other invertebrates from direct ultraviolet radiation, and therefore heatstress (Fig. 4b). Using IRT, Lathlean (2014) demonstrated that a positive interaction existed between the small intertidal limpet Patelloida latistrigata and the barnacle Tesseropora rosea - its preferred biogenic habitat (Fig. 4b). Here, the distribution, as well as the abundance, of the barnacle T. rosea was shown to effect small-scale patterns of substratum temperatures as well as the abundance and distribution of P. latistrigata. The detection of such fine-scale processes was only possible through the use of IRT.

Like the intertidal barnacles found on rocky shores in Australia, IRT

has recently been used to characterise the small-scale thermal properties of intertidal mussel beds in South Africa and their ability to ameliorate individuals and associated invertebrate communities from heat and desiccation stress (Lathlean et al., 2016a). Using artificially constructed mussel beds comprised of the indigenous mussel Perna perna (Fig. 5), Lathlean et al. (2016b) investigated how the size, position and structure of mussel beds affected the body temperatures of individual mussels within each bed. Body temperatures were measured using IRT following successful validation of a strong positive correlation between shell surface temperatures and internal body temperatures ($r^2 = 0.96$). Results from this study revealed that body temperatures of small individuals reached higher 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 windward side of all beds displayed body temperatures 3–5 °C cooler than those on the leeward side. This sharp thermal gradient from one side of the mussel bed to the other is clearly visible in the infrared image (see Fig. 5b).

The effect of thermoregulatory behaviour on individual body temperatures is another important ecological process that is easily observed with IRT and has been explored in a number of recent studies (e.g. Chapperon et al., 2013; Rojas et al., 2013,b; Lathlean et al., 2016a,b; Seuront and Ng 2016). Like most terrestrial animals, intertidal mobile species benefit from resting in cool habitats by selecting shaded refuges such as crevices, barnacle tests or macroalgae. Chapperon and Seuront (2011a), for example, used IRT to show that the mangrove littorinid snail, Littoraria scabra, selected the bottom of mangrove roots as a refuge to reduce heat stress during the day but not at night. Forming aggregations is another common behavioural mechanism utilised by many intertidal gastropods to cope with thermal and desiccation stresses. Chapperon et al. (2013) and Rojas et al. (2013) both used IRT to demonstrate that aggregation behaviour reduced the amount of thermal stress experienced by two intertidal species of gastropods, N. atramentosa and Echinolittorina peruviana respectively. Similarly, Lathlean et al. (2016a) used IRT to demonstrate that increasing densities of the invasive mussel M. galloprovincialis within indigenous mussel beds limit the ability of P. perna to thermoregulate. Infrared thermography was also instrumental in successfully characterising the thermoregulatory effect of shell posturing behaviours (standing and towering) on body temperatures of two tropical littorinid snails, Echinolittorina malaccana and E. radiata under thermally stressful conditions (Seuront and Ng 2016). Shell standing is a common posturing response to increased heat-stress in many high-shore littorinid snails (Ng et al., in press). It usually involves individuals retracting their foot into their shell, closing their operculum and creating a mucus holdfast which allows them to lift themselves off the substratum and



Fig. 4. Infrared thermography can be a useful tool to investigate the thermal buffering properties of certain biogenic structures or ecosystem engineers. Within the intertidal zone ecosystem engineers that provide such thermal buffering include: (a-b) mangroves, (c) barnacles, and (d) mussels.

thus reducing heat flux through conduction as well as increasing the amount of convective cooling. This effect is magnified when an individual stacks on top of another to form a tower (Marshall et al., 2010). Since measuring body temperatures of standing or towering snails using traditional invasive method (e.g. thermocouples) may interfere with this behaviour, Seuront and Ng (2016) used IRT and successfully demonstrated that body temperatures of littorinids exhibiting these shell posturing behaviours were significantly lower (up to

 ~ 10 °C) than the individuals without showing these behaviours in the field during a low tide period in the summer. Seuront and Ng (2016) also effectively used IRT to illustrate decreasing littorinid body temperatures with increasing height within towers (Fig. 6).

The shells of many commercially important molluscs, including mussels and oysters, are often infested with endolithic parasites which bore into and discolour the exterior surface of the shell. In some cases infestations can be so severe that the parasites weaken the integrity of



Fig. 5. Manipulative cage experiment within the intertidal zone utilising IRT to investigate the effect of size and position of individual mussels on inter-individual variability in body temperatures.

the shell which subsequently depletes energy resources that would otherwise been used for growth, reproduction or byssal attachment. Consequently, shellfish aquaculture industries invest significant resources to ensure their livestock remain parasite and virus free. Contrary to this negative relationship between parasite and host, Zardi et al. (2016) used IRT to reveal that phototrophic shell-degrading cyanobacteria have a positive, cooling effect on mussel body temperatures during extreme heat-events (Fig. 7). 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 endoliths. Such results have broad ranging implications for our understanding of mutualistic and parasitic relationships and how these negative relationships might be expected to change under different climates. This study also demonstrates the potential use of IRT to identify and manage parasitic outbreaks amongst natural and cultivated populations of mussels and oysters which are commonly infested with endolithic cyanobacteria.

3.3. Crustaceans

Infrared thermography has also been used to investigate the effect of small-scale patterns of temperature variability on the recruitment processes of intertidal barnacles (Lathlean et al., 2012; Lathlean et al., 2013; Lathlean and Minchinton, 2012). Recruitment is a key life-history stage for many marine benthic invertebrates as it is the process by which pelagic larvae return to and repopulate the adult population. Settlement and recruitment are also the most vulnerable stages within the lifecycle of marine invertebrates since they often involve rapid metamorphosis and transition from a pelagic to benthic environment. For sessile marine invertebrates like barnacles, choosing where to settle and metamorphose is a critical and irreversible decision that will dictate the amount of biological and environmental stresses it will experience. For this reason, many intertidal barnacles are highly gregarious, choosing only to settle amongst adult conspecifics, using their presence to indicate the location of potentially favourable habitats.



Fig. 6. Digital and infrared images of a monospecific tower of *Echinolittorina malaccana* (left) and a heterospecific tower made of two *E. malaccana* and one *E. radiata* at the top (right) (recaptured from Seuront and Ng 2016). Pictures were taken during a summer low-tide on a tropical rocky shore in Hong Kong.



Fig. 7. (a) Detached intertidal mussels (*Mytilus galloprovincialis*) with one being completely covered in endolithic parasites which cause discolouration (right) and the other being almost completely free of parasites (left); (b) Infrared image of parasitized and unparasitized mussels.



Fig. 8. Digital and infrared images of intertidal barnacles during aerial exposure. Note the cooling effect of barnacle shading in the infrared image. Newly settled barnacles that settle in the shade of adult barnacles have been shown to have greater chances of survival due to reduced heat stress.

With the aid of IRT new insights can now be investigated into understanding how the small-scale thermal properties of rocky substrata influences the settlement patterns of intertidal barnacles. Lathlean et al. (2012) used IRT to quantify in situ temperature variability in substratum temperatures across a single rocky to assess how this within-site variability influenced the settlement and recruitment patterns of the intertidal barnacle Tesseropora rosea. Lathlean et al. (2012) found that substratum temperatures varied by up to 8.2 °C amongst quadrats placed within the same microhabitat on the shore (i.e. horizontal emergent rock). Amongst these quadrats the growth and survival of recently settled T. rosea decreased with increasing substratum temperatures. This suggests that different areas on the shore, even within the same microhabitat, can experience different rates of recruitment success based on differences in small-scale thermal properties. Likewise, at even finer spatial scales, Lathlean et al. (2013) found that T. rosea larvae settling on the shaded sides of adult barnacles experienced reduced temperatures and increased growth and survival (Fig. 8). This was the first time that such fine-scale temperature variation (i.e. at the scale relevant to individual larvae) was shown to impact early life history processes of a benthic marine invertebrate, and such processes can only be detected using IRT.

3.4. Echinoderms

As previously mentioned, the earliest application of IRT within the intertidal zone was carried out by Brian Helmuth on the predatory seastar *Pisaster ochraceous*, and its preferred prey *Mytilus californianus* (Helmuth, 2002). Since then, Sylvain Pincebourde and colleagues have worked extensively with using IRT to measure the body temperatures of *P. ochraceous* both within the laboratory (Pincebourde et al., 2008, 2012) and in the field (Pincebourde et al., 2013). In their initial

laboratory experiment, Pincebourde and colleagues wanted to understand how different levels of heat-stress during aerial exposure influenced the feeding rates of P. ochraceous. They hypothesised that increased temperatures associated with climate change would significantly alter the predator-prey relationship between P. ochraceous and M. californianus, and that this would have flow-on effects across the whole ecological community. They addressed this question by placing seastars into aquaria filled with live mussels (M. californianus) and exposed the animals to acute and chronic extreme heat events using heat lamps. Infrared images were used to calculate body temperatures of each individual seastar (calculated as the mean of five measurements taken within the centre of the body). This laboratory experiment demonstrated that feeding rates and growth of P. ochraceous are negatively affected by chronic heat-stress, (i.e. moderately high body temperatures sustained over consecutive low tides) compared to acute heat-stress (i.e. near-lethal body temperatures for a single low-tide) which actually had positive consequences on feeding rates and no effects on growth (Pincebourde et al., 2008). Following on from this experiment, Pincebourde et al. (2012) took this approach one step further by repeating the experiment and using fluctuating sea and air temperatures in various coincident and non-coincident patterns. Again, IRT was used to monitor the controlled body temperatures of seastars in aquaria in order to ensure individuals were exposed to the desired heat treatments. Interestingly, predation rate decreased as sea and air temperatures became temporally non-coincident (i.e. decreasing variability in seawater temperatures with increasing variability in air temperatures and vice versa). Such results are important because they highlight the need for more realistic laboratory experiments that incorporate natural levels of temperature variability, which can result in unexpected results on ecological and physiological processes.

Pincebourde and colleague's most recent application of IRT was to

assess the role of regional heterothermy, that is, within-body temperature variability, on the survival and rate of arm abscission in the seastar P. ochraceous under experimentally simulated heat-stress (Pincebourde et al., 2013). Using IRT, Pincebourde et al. (2013) were able to show that (i) survival decreased with increasing temperatures of the central disc, (ii) arms were generally warmer than the central disc for individuals that survived aerial heating, (iii) the central disc was warmer than the arms for individuals that died following aerial heating, (iv) when central disc temperatures of individuals reached 31-35 °C, arms reached 33-39 °C which induced arm abscission, and (v) arm abscission generally affected the arm that displayed the highest temperatures. These results represent the first application of IRT in assessing regional heterothermy, and its consequences for physiological processes, on a marine invertebrate. Such applications have only previously been attempted for veterinary purposes on much larger animals, like horses and marine mammals being kept in captivity. Due to the difficulty in detecting within-body temperature variability without IRT there may be numerous undocumented cases of regional heterothermy in marine invertebrates, which have important effects on individual physiology (e.g. limpets, Fraser et al., 2016).

4. Infrared thermography as a tool for monitoring the impacts of climate change

From the case studies above it appears that IRT represents an effective tool for investigating ecological processes from a unique perspective. It should also be clear that as infrared imaging technology has become increasingly portable, affordable and sophisticated the number and diversity of applications within the marine environment has steadily risen. However, the application of IRT within intertidal ecology is still very much in its infancy. We believe that IRT could play a key role in developing improved environmental management plans and policies for safeguarding these vulnerable systems to future climate change. For example, a unique feature of infrared thermography is its ability to produce instant thermal profiles of any particular surface from any number of angles. Combine this feature with new three-dimensional photographic techniques and light-weight unmanned aerial vehicles (i.e. drones) then environmental managers and ecologists have a powerful tool for producing fine-scale three-dimensional thermal maps of entire intertidal ecosystems at scales pertinent to individual organisms (Lathlean and Seuront 2014). Contrast this to the longstanding issue within ecological and environmental sciences where there is often a spatial mismatch between the size of the organisms and the grid sizes of distribution models, which are on average four orders of magnitude larger than the animals they study (Potter et al., 2013). Such thermal maps would significantly increase the computational power of ecological models designed to predict how and when specific flora and fauna are expected to respond to future climate change. Indeed, such thermal maps and models could be used to identify areas or microhabitats that (i) will act as thermal refugia for intertidal organisms during future extreme heat events, (ii) qualify for increased conservation status because they exhibit reduced thermal heterogeneity, or (iii) because of the increased likelihood of restoration success if a target species is transplanted to the area. Practically, the thermal quality of a given habitat could be quantified through a generalization of the body-to-substrate temperature ratio (BST) introduced by Chapperon and Seuront (2011a) as a standardized measure of the difference between substratum and organismal body temperatures, T_s and T_b . 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 synoptically provided in space and time through infrared thermography, it is then possible to produce an indicator of the suitability of the habitat:

where $T_b(i)$ is the organismal coma or lethal temperature. Areas where BST_c < 1 and BST_c > 1 will then be considered as viable or not for the species. More generally, the indicator BST_i could be generalized as

$$BST_c = T_{sc}/T_s \tag{2}$$

where T_{sc} is a critical surface temperature (either minima or maximal) returned by climatic scenarios and T_s the substrate temperature actually measured using IRT as scales pertinent to individual organisms. This approach is critical as (i) it explicitly takes into account habitat small-scale heterogeneity (e.g. crevices, pits, boulders and flat rocks) that defines a species thermal landscape, hence its realised ecological niche, and (ii) it may represent a first step to bridge the gap between field-based approaches that typically span from centimetres to tens of metres to climate scenarios which are typically coarse-grained (i.e. 10 km × 10 km); see e.g. Torossian et al. (2016) for a discussion on the mismatch between scales of observations and must needed biological details.

The use of IRT as a tool for monitoring and predicting changes in community structure is particularly appealing in an era where increasing temperatures are expected to affect different species within ecological communities in alternate ways. In recent years, much attention has been given to predict 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). Here, infrared thermography may not only offer 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 heatstress (see Lathlean et al., 2016b for example of where inter-individual variability in body temperatures of intertidal mussels was three to four times greater than interspecific variability). It is such inter-individual variability amongst populations that will largely determine whether a population will be capable of adapting to the rapidly changing climate. Therefore, infrared thermography can assist environmental managers and researchers to assess the ecological risks of natural or cultivated populations under climate change.

5. Some limitations of infrared thermography

Whilst marine ecologists have taken advantage of the increasingly lightweight and portability of infrared imagining cameras there still remain some challenges involved in using IRT within the marine environment, notwithstanding being restricted to the intertidal zone. The most obvious challenge is that of accounting for varying levels of emissivity (ɛ) for different objects. Emissivity relates to an objects ability to emit thermal radiation with values ranging from 0 for an object that reflects or transmits all electromagnetic radiation to 1 for a theoretical black body, which absorbs all electromagnetic radiation. Emissivity is hence the ratio of radiation actually emitted by the surface of an object (which is dependent on colour, texture and water content) and its theoretical radiation predicted from Plank's law. The difficulty in using IRT to measure surface temperatures within the intertidal zone is two-fold: first, different taxa within a single infrared image may display different emissivity values, and second, these emissivity values may change when organisms or substrata are wet (Lathlean and Seuront 2014). Morphological differences, whether intraspecific or interspecific, can be one reason individuals display different emissivity values. For example, the emissivity of intertidal macroalgae with flat surfaces are relatively constant at the scale of a few centimetres, but varies more significantly on algae with papillate surfaces and species composed of thin axes and branches (Van Alstyne and Olson, 2014). Fortunately, emissivity can be empirically estimated by simultaneously taking infrared images and in situ temperatures of the desired object with a calibrated thermocouple. Emissivity is then linked to in situ surface

(1)



Fig. 9. Examples of infrared images of two intertidal invertebrates (a) the snail *Cerithidea rhizophorarum*, and (b) the oyster *Isognomon isognomum* found within soft sediment mangrove habitats.

temperatures (T_{obj}) following the Stefan-Boltzmann law:

 $T_{\rm obj}$ = the 4th root of $[(\sigma \times T_{\rm ir}^4)/(\sigma \times \varepsilon)]$

where σ is the Stefan-Boltzmann constant (W⁻¹ m² K⁻⁴), T_{ir} is the temperature (K) of the object within the infrared image, and ε is the emissivity of the object. Emissivity is then adjusted so that both sides of the equation are equal. Such an approach has been used by a number of recent studies that have utilised IRT in measuring surface temperatures of intertidal substrata and organisms and have typically found emissivity values to fall within the range of 0.95-0.97 (Helmuth, 1998; Denny and Harley, 2006; Miller et al., 2009; Cox and Smith, 2011Cox and Smith, 2011Helmuth, 1998; Denny and Harley, 2006; Miller et al., 2009; Cox and Smith, 2011Cox and Smith, 2011Helmuth, 1998; Denny and Harley, 2006; Miller et al., 2009; Cox and Smith, 2011 Cox and Smith, 2011). So whilst emissivity values may make it slightly difficult to take infrared images at face value, the solution is relatively simple and once calculated emissivity values can be used repeatedly across multiple images. In some of the more recent thermal imaging cameras there are now built-in on-screen emissivity correction tools, making the calculation of emissivity in the field a very simple exercise.

Another limitation of IRT is related to the distance between the camera and a target object. For instance, in a recent study inferring the effect of distance on IRT estimates of thermal mosaic, Faye et al. (2016) showed that images taken from long distances (typically > 20 m) consistently led to underestimate surface temperatures by up to 3 °C. In addition, these authors showed that this bias is the result of complex relationship existing between atmospheric conditions, pixel size, and how solar radiation interacts with complex structures. The structural complexity of the surface itself had, however, negligible effect on the surface temperature bias. Note that the so-called pixel size effect (Faye et al., 2016) or minimum spot-size detection (Tattersall, 2016) is related to distance *d* as $SR = d \times \theta_{IFOV}$, where *SR* is the spatial resolution of the infrared camera, and θ_{IFOV} the instantaneous field of

view in radians, i.e. the angle over which the detector senses radiation. For instance, imaging an intertidal snail that is 1 cm long with a Fluke Ti25 camera that as a $\theta_{IFOV} = 0.0015$ rad would lead to a maximum distance at which the organism could reliably be resolved of d = 6 m. Now, as SR represents the size of one pixel, one may need more resolving capacity on the above-mentioned snail, e.g. 50 or 100 pixels, hence would require the image to be obtained at 13.3 and 6.7 cm, respectively. As a consequence, the choice of a thermal camera should be driven by ensuring that the resolution of a thermal camera is compatible with the targeted organisms and the related empirical constraints that are expected to be experienced either in situ or ex situ. More fundamentally, any objects of interest should practically occupy a sizable number of pixels in the final thermal image, and the potential presence of the distance effects mentioned above on temperature estimates should be empirically assessed, or at least explored mathematically.

6. Conclusions

From this review we can see that what was once primarily utilised by the military and medical professions has now being widely applied across multiple disciplines including marine ecological studies which, until recently, would not have been warranted since infrared radiation is quickly attenuated by even the smallest volumes of water. However, as in the majority of ecological concepts, intertidal habitats have served as excellent natural laboratories to test and refine ecological theories and methodologies. This is yet another example where during the history of science significant technological achievements have rapidly improved our understanding of the natural world. The application of IRT within intertidal ecosystems is still very much in its infancy as only a very few of the many diverse intertidal habitat types and taxa have been sampled. Most notably is the still relatively rare use of IRT studies undertaken within coastal saltmarsh and mangrove communities (but see Fig. 9a and b), which perform valuable ecological services including: (i) providing nursery habitat for many commercially important species, (ii) collecting and storing large amounts of organic carbon, and (iii) providing a natural defence against coastal erosion and storm damage. Other soft-sediment habitats like sandy beaches or coastal fore-dunes could also produce fruitful lines of enquiry. Finally, we discovered that IRT could play a vital role in understanding and managing how intertidal communities and their environment will be affected by increasing temperatures associated with climate change. One useful application in regard was to produce high-resolution thermal maps, which would facilitate the accuracy of large-scale ecosystem models used to predict biological changes at scales relevant to individual organisms. For these reasons we expect IRT to become increasingly popular and applicable to management as we continue to investigate how increasing temperatures will affect ecological processes from the level of the individual right up through to entire ecosystems.

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