REVIEW

Infrared thermography in marine ecology: methods, previous applications and future challenges

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ABSTRACT: Infrared thermography (IRT) is being increasingly utilised by animal physiologists and ecologists to investigate the role of thermal stress and small-scale thermal variability on the distribution and abundance of species. Due to the inability of infrared cameras to work underwater, ecological studies that use IRT have largely been undertaken on terrestrial systems, while fundamentally limited to surfacing mammals in aquatic ecosystems. In recent years, however, IRT has been used to investigate the thermal ecology of intertidal organisms, which are intermittently exposed. The aim of this paper was to summarise the rapidly growing application of IRT in marine ecology, to discuss best practises for using IRT in the marine environment whilst outlining some common limitations, and to suggest future research directions. IRT has been successfully used to count and track the movements of a range of marine mammals as well as to quantify previously unobserved nocturnal feeding patterns. On rocky intertidal shores, IRT has largely been used to assess thermoregulatory processes in gastropods, mussels and sea stars and the effect of heat stress on barnacle recruitment. Ground-truthing and calibration procedures still remain the largest drawback for the use of IRT in ecological studies. However, once the appropriate calculations and working procedures have been implemented, thermal imaging is a reliable and rapid tool for measuring environmental and biological temperature variability. We believe such techniques will become increasingly popular as global temperatures, and hence thermal stress, continue to rise.

KEY WORDS: Behavioural thermoregulation · Body temperature · Climate change · Ectotherms · Heat stress · Infrared camera · Rocky intertidal · Saltmarsh · Thermal imaging · Thermal refugia

INTRODUCTION

Infrared thermography (IRT) has emerged as a non-invasive tool for measuring the temperatures of organisms and their surrounding environment. Originally developed for military use, over the past 2 decades, IRT has become increasingly available for non-military purposes, including industrial and medical applications (Burnay et al. 1988, Kastberger & Stachl 2003). Applications of IRT are growing in physiology and ecology to investigate the role of thermal stress and small-scale thermal variability on the behaviour, distribution and abundance of species (e.g. Simmons 2005, Gauthreaux & Livingston 2006, Betke et al. 2008). Indeed, as ecosystems become increasingly threatened by climate change, IRT will represent a rapid and so-

phisticated method for assessing the health of individual organisms, populations and communities.

Within the ecological literature, IRT was introduced in the late 1980s as a non-invasive means to determine body temperature in lizards (Jones & Avery 1989), as small postural adjustments related to animal manipulations have long been known to alter heat balances (see e.g. the classical work of Heath 1965 on thermoregulatory behaviour of the horned lizards *Phrynosoma* sp.), and has since extensively been applied to terrestrial systems (McCafferty 2007). These include nocturnal surveys of bats, owls and rodents (McCafferty et al. 1998, Pregowski et al. 2004, Hristov et al. 2008, McCafferty 2013) and other environmental assessments involving insects, spiders, birds, snakes and lizards, deer and polar bears (York et al. 2004, Butler et al. 2006, Kohl et al. 2012, Pike et al. 2012, Pincebourde & Woods 2012). Whilst IRT is an effective method for capturing thermal variability on land, it is considerably less effective in the ocean, where infrared waves in the electromagnetic spectrum are rapidly attenuated by seawater (Widder et al. 2005). However, marine organisms living within the intertidal zone are routinely exposed to aerial conditions up to 12 h each day. Tidal cycles have long been utilised by marine ecologists, who in turn, have developed many broad ecological theories and applications (Connell 1972, Paine 1974, Sousa 1984). In recent years, several studies have taken advantage of this daily aerial exposure, and increasingly lightweight and portable thermal imaging systems, to investigate the role of local thermal variability on the physiology and ecosystem functioning of intertidal communities (Pincebourde et al. 2009, 2013, Caddy-Retalic et al. 2011, Chapperon & Seuront 2011b, 2012, Cox & Smith 2011, Lathlean et al. 2012, 2013, Chapperon et al. 2013, Lathlean in press). With this new and exciting application of IRT within the marine environment, it is important to establish some common working procedures, discuss the potential limitations of this technique and provide clear objectives for future research.

The aim of this paper is to summarise the rapidly growing application of IRT in marine ecology, to discuss best practises for using IRT in the marine environment whilst outlining some common limitations, and to suggest future research directions. We have specifically limited this review to those applications and techniques involving hand-held infrared cameras and do not make reference to the use of infrared images in satellite remote sensing, as they do not measure fine-scale spatial variability as IRT does.

MECHANICS OF IRT

Before summarising some of the recent applications of IRT within the marine environment, we provide a brief overview of thermal energy theory and subsequently describe how thermal infrared imaging works.

Thermal energy

Like any other imaging technique, IRT is based on the detection of electromagnetic waves and their conversion to electrical signals for visual display. All objects above absolute zero emit thermal energy as a result of their molecular motion. The wavelength of this radiation ranges from 0.7 μm (visible light) to 1000 μm (microwaves; DeWitt 1988, Kastberger & Stachl 2003). The 0.7–14 μm range is best suited for thermal infrared imaging and is further subdivided into near- (0.7–3 μm), mid- (3–5 μm) and far-infrared (8–14 μm). Most thermal infrared cameras operate within the far-infrared region of the spectrum, which is most appropriate for imaging the 90–740 K range (Kastberger & Stachl 2003) and produce images called 'thermograms'. However, unlike normal cameras, most infrared cameras do not distinguish between different wavelengths and therefore do not produce 'true' colour images. Instead, most infrared cameras use a single-colour channel sensor that detects different intensities for a specified range of infrared light, i.e. the higher the temperature of an object of interest, the greater the intensity of emitted radiation and thus the brighter the resulting image (Kastberger & Stachl 2003). As the human eye has limited capacity to differentiate such levels of light intensity, these monochromatic images are displayed in pseudo-colour.

Because infrared energy can be emitted by, transmitted through or reflected off an object, thermal imaging cameras use detailed algorithms to convert radiation intensity data to the temperatures displayed in an image. The purpose of these algorithms is to separate the radiation emitted by a surface from that transmitted through or reflected off an object. These algorithms involve several parameters including atmospheric temperature, relative humidity, distance from the object and emissivity (ε), which is the ability of an object to emit thermal radiation. For this reason, many field-based studies using IRT to measure body temperatures of endothermic animals are undertaken at night when the amount of solar reflectance is low (Cilulko et al. 2013). The low transmissivity of in-

frared radiation through water is the reason thermal imaging is ineffective under water. Provided atmospheric temperatures are similar to the internal temperature of the camera, relative humidity is low, distance from the object of interest is less than 1 m and emissivity values are accurate, most infrared cameras will return a thermogram with an accuracy of ±2°C or 2% of the thermal range, whichever is greatest. More recent models purport accuracies of ±1°C or 1% when images are taken within a restricted temperature range (Table 1). Still, care must be taken to ensure that temperatures estimated by thermal images accurately represent *in situ* temperatures of an object.

Equipment

The majority of modern infrared cameras can be divided into those with either cooled or uncooled infrared detectors. Most cooled infrared cameras are integrated with a cryo-cooler, which lowers the internal temperature of the imaging sensor to a temperature much cooler than ambient temperature (typically in the range 60–100 K) to reduce thermally induced noise. Specifically, cooled infrared cameras capture infrared wavelengths closer to the visual region of the electromagnetic spectrum and subsequently have greater thermal and spatial resolution than uncooled infrared cameras. However, cooled cameras are typically bulkier, more expensive and require considerably more maintenance than uncooled cameras. In 1998, AGEMA Thermovision® produced the first uncooled infrared camera representing a significant improvement from previous cooled models both in terms of function and practicality. These uncooled infrared cameras use a microbolometer to detect infrared radiation, typically between 7.5 and 14 μm, and transfer it to a measurable electrical charge. In comparison to cooled infrared cameras, these uncooled infrared cameras operate at ambient temperatures through the use of small internal sensor stabilizers that maintain congruency between the camera and external environment. Consequently, applications of these uncooled infrared cameras are more widespread, and recent technological advances have increased their portability and ruggedness and have reduced their cost (see Table 1). For this reason, this review will focus primarily on the use of uncooled thermal infrared cameras (CIR). Note, however, that a third category of infrared imaging cameras measures

Table 1. Specification summaries of popular portable uncooled infrared cameras used in recent thermography studies. Spatial resolution and minimum focus distance are based on a standard infrared lens with a 23°×17° field of view. Initial cost refers to an approximate price (AUD) of the camera when first released onto the market and does not account for inflation

Model	Year of production	Spectral range (μm)	Temperature range (°C)	Accuracy (°C)	Thermal sensitivity at 30°C	Spatial resolution (mrad)	Minimum focus distance (m)	Detector size (pixels)	Multispectral imaging (Yes/No)	Battery operating time (h)	Weight (kg)	Size (mm)	Initial cost ($10³)
AGEMA 570	1998	7.5–13	–40° to 500°	±2° or ±2%	0.1°	1.3	0.5	320×240	N	2	2.3	220×133×140	80
FLIR® ThermaCAM PM 595	1999	7.5–13	–40° to 1500°	±2° or ±2%	0.1°	1.3	0.5	320×240	N	2	2.3	220×133×140	80
FLIR® ThermaCAM PM 695	2000	7.5–13	–40° to 120°	±2° or ±2%	0.08°	1.3	0.5	320×240	N	2	2.4	220×133×140	100
FLIR® ThermaCAM S60	2002	7.5–13	–40° to 2000°	±2° or ±2%	0.08°	1.3	0.3	320×240	N	2	2.0	234×124×161	110
FLIR® ThermaCAM S65	2003	7.5–13	–40° to 2000°	±2° or ±2%	0.08°	1.3	0.3	320×240	N	2	2.0	100×120×220	110
FLUKE® TiR4	2003	7.5–14	–20° to 100°	±2° or ±2%	0.05°	1.3	0.15	320×240	N	3	1.9	162×262×101	30
FLUKE® Ti20	2005	7.5–14	–10° to 350°	±2° or ±2%	0.2°	2.7	0.15	128×96	N	3	1.2	254×102×178	10
FLIR® ThermaCAM SC640	2006	7.5–13	–40° to 2000°	±2° or ±2%	0.06°	0.7	0.3	640×480	N	3	1.7	120×145×220	90
FLIR® ThermaCAM BX320	2006	7.5–13	–20° to 100°	±2° or ±2%	0.08°	1.3	0.2	320×240	N	2	0.8	272×80×105	30
FLIR® ThermaCAM SC660	2008	7.5–13	–40° to 2000°	±1° or ±1%	0.03°	1.3	0.2	640×480	N	3	1.8	299×144×147	90
FLUKE® Ti25	2009	7.5–14	–20° to 350°	±2° or ±2%	0.09°	2.5	0.15	160×120	Y	3–4	1.2	270×130×150	11
FLUKE® TiR32	2010	7.5–14	–20° to 150°	±2° or ±2%	0.04°	1.3	0.15	320×240	Y	4	1.1	277×122×170	16
FLIR® ThermaCAM T640	2011	7.5–14	–40° to 2000°	±2° or ±2%	0.03°	0.7	0.25	640×480	Y	2.5	1.3	143×196×94	40
FLIR® ThermaCAM E30	2011	7.5–13	–20° to 120°	±2° or ±2%	0.1°	2.7	0.4	160×120	N	4	0.8	246×97×184	12
FLUKE® TiR125	2012	7.5–14	–20° to 150°	±2° or ±2%	0.08°	3.4	0.15	160×120	Y	4	0.7	284×86×135	7
FLIR® ThermaCAM E60	2013	7.5–13	–20° to 120°	±2° or ±2%	0.05°	1.3	0.4	320×240	Y	4	0.8	246×97×184	12
FLUKE® Ti400	2013	7.5–14	–20° to 1200°	±2° or ±2%	0.05°	1.3	0.15	320×240	N	4	1.0	280×120×170	12

wavelengths in both the visible and near-infrared bands of the electromagnetic spectrum. These colour-infrared cameras (CIR), however, produce images depicting the amount of reflected light and do not estimate surface temperatures. Consequently, they are primarily used as a method of undertaking field-based spectrometry rather than thermography (Murphy et al. 2004, 2005, Murphy & Underwood 2006).

Since the introduction of the first uncooled infrared camera in 1998 (i.e. AGEMA 570), technological advancements have continued to revolutionise a rapidly growing infrared industry. Most importantly, these improvements have led to increased performance and affordability of portable infrared cameras (Table 1), resulting in an increase in the number of ecological studies incorporating IRT (Fig. 1). The most obvious technological improvements relate to the increased accuracy, thermal sensitivity and spatial resolution of the cameras. For example, the accuracy of thermal imaging cameras has increased from ±2°C to ±1°C; thermal sensitivity has increased from 0.2°C to 0.03°C; and the size of microbolometer detectors, which determines the spatial resolution, has increased from 320 × 240 to 640 × 480 pixels over the past decade (Table 1). Despite these advances, the initial sale prices of thermal imaging cameras have continued to drop over the past 15 yr (Table 1). Another significant improvement to modern infrared cameras is the development of interchangeable lenses. These lenses, which come in a range of sizes, are capable of measuring thermal variability at ultra-fine spatial scales (50 to 100 µm), which is ideal for investigating thermoregulatory properties of small invertebrates.

Software and data analysis

One of the major advantages of using IRT is the ability to characterise fine-scale spatial variation in temperature. All modern infrared cameras come with user-friendly software packages without any additional cost, enabling researchers to analyse and export temperature data from their infrared images. Whilst the specific characteristics of these programs vary between manufacturers, the tools and analysis techniques are quite generic. These can range from numerous measurements of single pixels (Fig. 2a) to temperature frequency distributions of all pixels within a selected section of an image (Fig. 2b). Infrared analysis programs also allow the user to delineate areas within an image using simple or customised shapes (Fig. 2b). Another popular technique amongst thermographers is the profile analysis tool, which plots changes in temperature along a prescribed transect within an image (Fig. 2c). Note that a range of infrared cameras now have built-in digital cameras that blend digital and partially transparent infrared images into a single information-filled image.

RECENT APPLICATIONS OF IRT TO THE MARINE ENVIRONMENT

Portable hand-held infrared cameras were originally used by ecologists to estimate abundances of terrestrial mammals and birds, especially nocturnal species (Hristov et al. 2008, Cilulko et al. 2013). Within the marine environment, hand-held infrared cameras were first used to count and track the movements of whales, dolphins and seals (Perryman et al. 1999, Williams et al. 1999, Thomas & Thorne 2001; see Table 2 for a synthesis). Helmuth (2002) was the first to use IRT to measure the body temperatures of marine ectotherms in the field (i.e. the predatory rocky intertidal sea star *Pisaster ochraceus* and the intertidal mussel *Mytilus californianus*). Since then, IRT has been used to measure body temperatures of other intertidal invertebrates, including gastropods (Caddy-Retalic et al. 2011, Chapperon & Seuront 2011a,b, Chapperon et al. 2013, Rojas et al. 2013) and barnacles (Lathlean & Minchinton 2012, Lathlean et al. 2012, 2013).
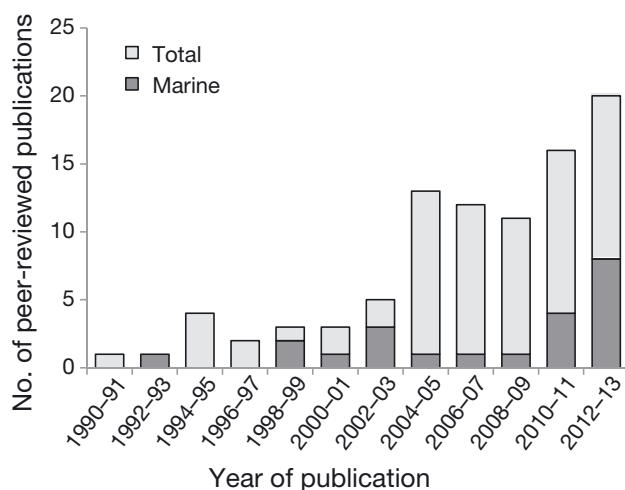

Fig. 1. Number of peer-reviewed ecological publications since 1990 that have used hand-held infrared thermography. Literature survey was undertaken within Scopus, the largest abstract and citation database of peer-reviewed literature, using the key words: 'infrared', 'thermography' and 'ecology'. Reference lists of documents found on Scopus were then cross-checked to ensure that any relevant documents not listed in this database were included
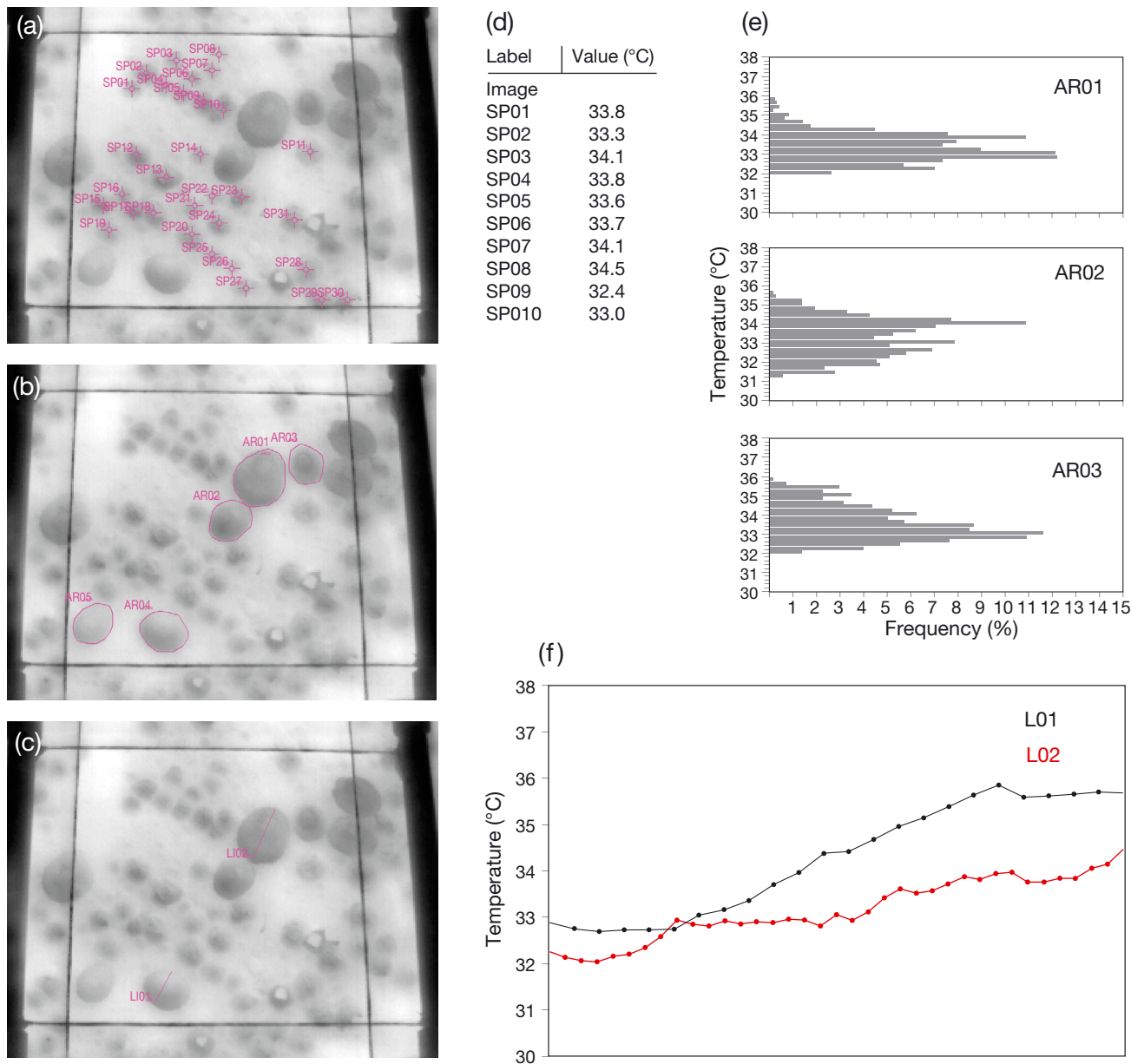
Fig. 2. Common tools for analysing infrared images: (a,d) spotmeter – allows user to select and record the temperature of numerous individual pixels; (b,e) tracing tool – used for delineating irregular regions of interest and producing temperature frequency distributions; (c,f) profile analysis – measures temperatures sequentially along a straight line. Images taken with a FLIR® ThermaCAM S65 camera and analysed with ThermaCAM Researcher Professional 2.10 software package. SP: spot; AR: area; L: line. In (e), only Histograms for Areas 1 to 3 are presented

Marine mammals

The application of thermal imagery to marine mammals (both pinnipeds and cetaceans) is limited to surfacing animals due to the extremely fast attenuation of infrared radiation in water. In addition, even surfacing animals are covered by a thin layer of water, which partially or completely masks skin tem-

perature, and the efficient thermal insulation of marine mammals further limits the temperature difference between the animal's skin and the surrounding water, especially when compared to terrestrial mammals. Infrared imaging of marine mammals nevertheless covers a wide breadth of applications that can be categorised into thermal physiology studies and field surveys.

Thermal physiology studies have been used to assess different aspects of thermoregulation, usually on captive animals. For instance, infrared images have been used to assess diving physiology and blood circulation in bottlenose dolphins (Williams et al. 1999, Meagher et al. 2002) and thermoregulatory evaporation in captive seals (Mauck et al. 2003). More recently, infrared imaging was use as a non-invasive tool to assess body condition in harbour seals and Steller sea lions (Mellish et al. 2013). Thermal imaging can also be used as a guide for the placement of heat flux sensors to study metabolic heat production of Steller sea lions (Willis et al. 2005) and to determine the effects of attaching bio-logging devices to the pelage of grey seals (McCafferty et al. 2007).

In contrast, field surveys do not require precise temperature measurements but simply detect individuals or dens by a warm signal against a cool background. Thermal imaging has been used to detect the blows of large whales (Cuyler et al. 1992) and monitor the nocturnal feeding habitats of Stellar sea lions in Prince William Sound (Alaska, USA; Thomas & Thorne 2001).

Specifically, infrared imagery of the nocturnal sea surface coupled to acoustic surveillance demonstrated that Stellar sea lions in Prince William Sound feed exclusively on Pacific herring, which are found closer to the surface at night (Thomas & Thorne 2001). Likewise, Perryman et al. (1999) compared day- and night-time estimates of migrating eastern Pacific gray whales by recording their blows with thermal imagery from an onshore research station in California, USA. Infrared imagery has also been used in aerial surveys to estimate the abundances of harbour seals (Duck & Thompson 2003), polar bears (York et al. 2004) and Atlantic walruses (Lydersen et al. 2012). Note, however, that the success of this approach relies on a relatively large temperature difference between the animals and the water surface and hence is likely to be optimised if conducted at night. For this reason, IRT may be less effective at detecting marine mammals at lower latitudes where water temperatures will be similar to surface body temperatures.

Table 2. Summary of marine ecological studies that used infrared thermography. Under 'image analysis', 'Yes' indicates that authors analysed infrared images to produce empirical data; 'No' indicates that authors simply present infrared images to visually illustrate a biological pattern

Ecological process	Camera model	Image analysis	Taxa	Source
Marine mammals				
Measuring body temperature	Agema Thermovision 880	Yes	Whale	Cuyler et al. (1992)
Measuring body temperature	FLIR ThermaCAM PM 595	Yes	Seal	McCafferty et al. (2007)
Evaporative cooling	Agema ThermaCAM 870	Yes	Seal	Mauck et al. (2003)
Peripheral blood flow	Agema ThermaCAM 570	Yes	Dolphin	Meagher et al. (2002)
Body condition	FLIR ThermaCAM P25	Yes	Seal, sea lion	Mellish et al. (2013)
Migration rates	Super-cooled AN/KAS-1A	Yes	Whale	Perryman et al. (1999)
Feeding patterns	Unspecified	Yes	Sea lion	Thomas & Thorne (2001)
Diving physiology	Unspecified	No	Dolphin	Williams et al. (1999)
Thermal physiology	FLIR ThermaCAM PM 695	Yes	Sea lion	Willis et al. (2005)
Rocky shores				
Measuring body temperature	FLUKE Ti20	Yes	Gastropod	Caddy-Retalic et al. (2011)
Aggregation behaviour	FLUKE Ti20	Yes	Gastropod	Chapperon et al. (2013)
Thermoregulation	FLUKE Ti20	Yes	Gastropod	Chapperon & Seuront (2011b)
Aggregation behaviour	FLUKE Ti20	Yes	Gastropod	Chapperon & Seuront (2012)
Temperature variability	Handy Thermo TVS-200 EX	Yes	Numerous	Cox & Smith (2011)
Temperature variability	FLIR ThermaCAM 695	No	Mussel, sea star	Helmuth (2002)
Recruitment	FLIR ThermaCAM S65	Yes	Barnacle	Lathlean et al. (2012)
Recruitment	FLIR ThermaCAM S65	Yes	Barnacle	Lathlean & Minchinton (2012)
Recruitment	FLIR ThermaCAM S65	Yes	Barnacle	Lathlean et al. (2013)
Thermal physiology	Unspecified	No	Sea star	Pincebourde et al. (2009)
Thermal physiology	FLIR ThermaCAM PM 695	Yes	Sea star	Pincebourde et al. (2013)
Desiccation stress	FLIR i40	Yes	Gastropod	Rojas et al. (2013)
Mangroves				
Thermoregulation	FLUKE Ti20	Yes	Gastropod	Chapperon & Seuront (2011a)

Rocky intertidal shores

Since its initial application in illustrating differences in body temperatures of rocky intertidal sea stars and mussels during low tide (Helmuth 2002), IRT has increasingly been used for quantifying thermal variability in the body temperatures of intertidal ectotherms and their surrounding microhabitats (Caddy-Retalic et al. 2011, Chapperon & Seuront 2011b, Cox & Smith 2011, Lathlean et al. 2012). Cox & Smith (2011) used thermal images to quantify spatial variation in temperature of an exposed tropical algal reef in O'ahu, Hawai'i, USA, and found considerable thermal complexity with habitats ranging from 18.1 to 38.3°C at a single point in time. Other attempts to capture this level of spatial variability in temperature without IRT have been made by deploying more than 200 temperature data loggers on a single rocky shore (Denny et al. 2011). This stresses the advantages of IRT compared to more traditional thermal methods as a tool to assess habitat thermal heterogeneity at scales compatible with the behavioural biology and ecology of individual organisms.

Caddy-Retalic et al. (2011) used a series of laboratory- and field-based experiments to assess the usefulness of IRT as a non-invasive method of estimating internal body temperatures of the intertidal gastropod *Nerita atramentosa* in South Australia. Here, the authors found a strong correlation between internal body temperatures measured with a temperature probe and the external surface temperatures of the shell measured with IRT. *N. atramentosa* has subsequently emerged as a model organism in using IRT to investigate thermoregulatory behaviour in intertidal ectotherms (Chapperon & Seuront 2011b, 2012, Chapperon et al. 2013). Specifically, IRT showed that *N. atramentosa* body temperatures were positively correlated with substrate temperature under various conditions of thermal stress (i.e. South Australian autumn and summer) on the low- and high-shore levels of a rock platform and a boulder field (Chapperon & Seuront 2011b). A follow-up study using IRT showed that both substratum and *N. atramentosa* body temperatures were more heterogeneous at scales ranging from a few centimetres to a few metres than between 2 distinct habitats (a boulder field and a rock platform) separated by 250 m and that aggregation behaviour significantly reduces both desiccation and heat stress during daytime on a boulder field but not on a rock platform (Chapperon et al. 2013).

To assess the thermal benefits of aggregation behaviour of *N. atramentosa* under cold thermal stress conditions, Chapperon & Seuront (2012) used IRT to show that the temperature deviation between aggregated individuals and their substrata was 2°C greater than the one observed between solitary individuals and their substrata. That is, individuals located in patch centres were significantly warmer than those located on patch edges; hence *N. atramentosa* experience a greater thermal advantage in aggregate centres.

Recently, laboratory experiments conducted on *Echinolittorina peruviana*, a littorinid snail common to the north-central shores of Chile, showed that under conditions of heat stress, the body temperature (assessed via IRT) of solitary individuals increases at a slower rate and remains significantly slower than that of aggregated ones, especially under conditions of low relative humidity (Rojas et al. 2013). This is consistent with results obtained from solitary and aggregated *N. atramentosa* individuals (Chapperon & Seuront 2011b, 2012, Chapperon et al. 2013) and mussels (Helmuth 1998), suggesting that the role of aggregation behaviour as an adaptation to thermal stress may be a general feature in intertidal ectotherms.

IRT has also been used to investigate the effect of small-scale thermal variability on the settlement and recruitment of the southeast Australian rocky intertidal barnacle *Tesseropora rosea* (Lathlean et al. 2012, 2013, Lathlean & Minchinton 2012). Growth and survival of newly settled barnacles was significantly lower within areas of the shore that infrared images revealed to be consistently hotter (Lathlean et al. 2012). Infrared images also indicated that increasing densities of barnacles reduce the temperatures of the surrounding rocky substrata by as much as 8°C during aerial exposure (Lathlean et al. 2012). At fine spatial scales, IRT found substratum temperatures to be 0.62°C cooler on shaded versus unshaded sides of adult barnacles and that survival of settlers increased the closer they were to adults (Lathlean et al. 2013). Such small-scale differences in temperature would have remained undetected without the use of infrared imaging technology.

A major advantage of IRT over other traditional methods of measuring temperatures (i.e. data loggers, thermocouples) is its ability to simultaneously measure and visualise the body temperatures of the whole organism. For example, Pincebourde et al. (2009) used IRT to show that the intertidal sea star *P. ochraceus* modulates its thermal inertia in response to prior thermal exposure. After exposure to high body temperature at low tide, sea stars increase the amount of colder-than-air fluid in their coelomic cavity when submerged during high tide, resulting in

a lower body temperature during the subsequent low tide. This buffering strategy has also been shown to be more effective when seawater is cold during the previous high tide. This ability to modify the volume of coelomic fluid provides sea stars with a novel thermoregulatory adaptive 'backup' when faced with prolonged exposure to elevated aerial temperatures. Follow-up studies further showed (1) that the temporal dynamics of thermal stress events substantially impact the predation rate of *P. ochraceus* (Pincebourde et al. 2012), and (2) that, under heat stress conditions, intertidal sea stars use their arms as heat sinks, actively drawing away heat from the core body, and they have the ability to ultimately excise at least 1 arm under prolonged heat stress (Pincebourde et al. 2013).

Preliminary investigations using IRT have also been undertaken to assess the role of ecosystem engineers and biogenic habitats in ameliorating thermal stress for species that are strongly associated with such structures. For example, on rocky intertidal shores of southeast Australia (Fig. 3), the abundances of the small acmaeid limpet *Patelloida latistrigata* are closely linked to densities of the habitat-forming barnacle *T. rosea*, presumably because they protect limpets from harsh abiotic conditions including heat stress (Creese 1982). However, recent thermographic analyses reveal that whilst increased barnacle densities reduce the levels of heat stress experienced by these small limpets, this decrease in temperatures does not explain their small-scale distribution and abundance (Lathlean in press).

Mangroves and saltmarsh habitats

Soft-sediment intertidal regions dominated by mangroves and saltmarshes represent another important area where IRT could be applied to the marine environment. To our knowledge, IRT has so far only been used in these environments to assess the behavioural thermoregulation of *Littoraria scabra*, a common littorinid species in Indo-Pacific mangrove forests (Chapperon & Seuront 2011a). That study showed a strong thermal heterogeneity of mangrove roots at the centimetre scale, with temperature gradients of ca. 5°C cm^{-1}. In contrast to what has been reported for *N. atramentosa*, *L. scabra* did not behaviourally thermoregulate through microhabitat selection or aggregation; instead, *L. scabra* actively selected specific substrate temperatures (22.5 to 33.4°C) rather than microhabitat type (Chapperon & Seuront 2011a). Considering the current shortage of published mate-

rials using IRT in these environments, we provide hereafter the results of several preliminary investigations undertaken in southern Australia (Jervis Bay, New South Wales) to illustrate the large amounts of thermal heterogeneity that characterise both mangroves and saltmarshes (Fig. 4). For example, crab burrows and mangrove pneumatophores both produce considerable fine-scale (10–100 mm) thermal heterogeneity for benthic invertebrates inhabiting mangroves (Fig. 4a,b). The thermal variability observed in saltmarshes at slightly larger spatial scales (1–10 m) appears to be largely governed by the abundance and spatial distribution of mangrove trees and succulent vegetation (Fig. 4c). Such thermal viability is likely to influence the thermoregulatory behaviour of a range of organisms, including gastropods and crabs.

LIMITATIONS

Whilst the application of IRT to the marine environment is opening up new avenues for research, it also presents some unique challenges. Below we outline the major difficulties involved in using IRT within the marine environment and suggest possible solutions to help minimise error.

Emissivity

Specific emissivity (ε) of objects relates to their ability to emit thermal radiation. Emissivity ranges 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, whether it is a mangrove root, a rock or a snail, and its theoretical radiation predicted from Planck's law. Emissivity plays an important role in the algorithms used to convert the amount of infrared energy to temperatures. Therefore, the difficulty of using IRT to measure thermal variability in the marine environment is 2-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. Emissivity can be empirically estimated by measuring *in situ* surface temperatures (T_{obj}) of an object (i.e. an organism or its substrate) with a small tipped temperature probe whilst simultaneously taking an infrared image. Emissivity is then linked to T_{obj} following the Stefan-Boltzmann law:
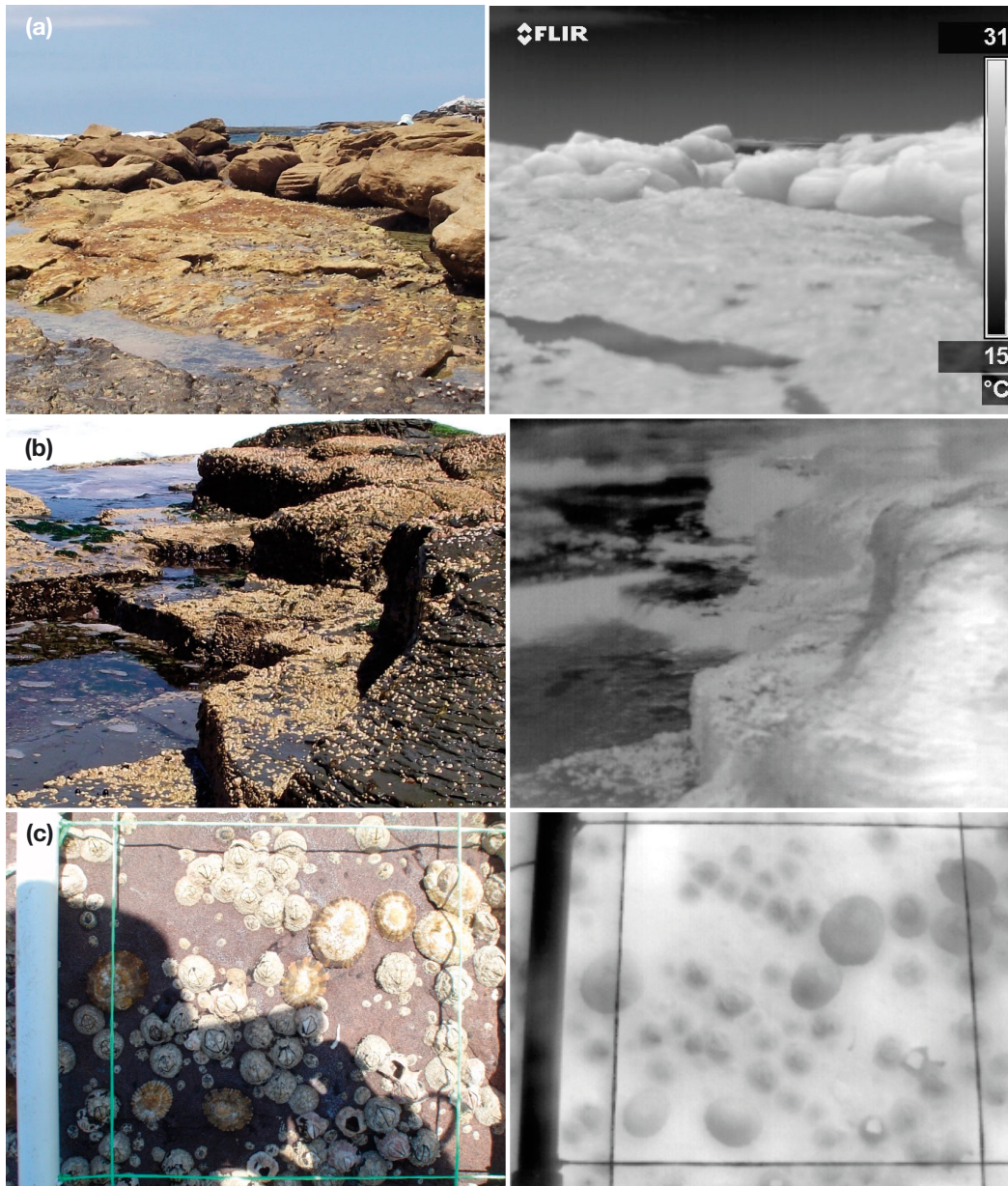
Fig. 3. Photographs (left) and infrared images (right) of rocky intertidal zones during daytime aerial exposure at (a) Little Bay and (b) Garie Beach, New South Wales, Australia. (c) Close-up images of the barnacles *Tesseropora rosea* and *Catomerus polymerus* and the limpets *Cellana tramoserica* and *Patelloida latistrigata*. Infrared images were taken with a FLIR® Therma-CAM S65 camera. Temperature scale is equivalent in all 3 infrared images

$$T_{obj} = \text{the 4}^{th} \text{ root of } [(\sigma \times T_{ir}^{4}) / (\sigma \times \varepsilon)] \qquad (1)$$

where σ is the Stefan-Boltzmann constant (W^{-1} m^2 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. Alternatively, most infrared image analysis programs allow users to estimate unknown emissivity values of an object if in the same image there is an object with a known emissivity value at the same temperature as the object with the unknown emissivity. In practice, this can be achieved by taking an infrared image of the object with an unknown emissivity with a small piece of black electrical tape (e.g. Scotch® Black Paper Tape; $\varepsilon = 0.95$) stuck to its surface (Chapperon & Seuront 2011b). Specifically, the surface temperature of the sticker is measured with an infrared device, then the surface temperature of the object is measured without the tape, and the emissivity is re-set until the correct
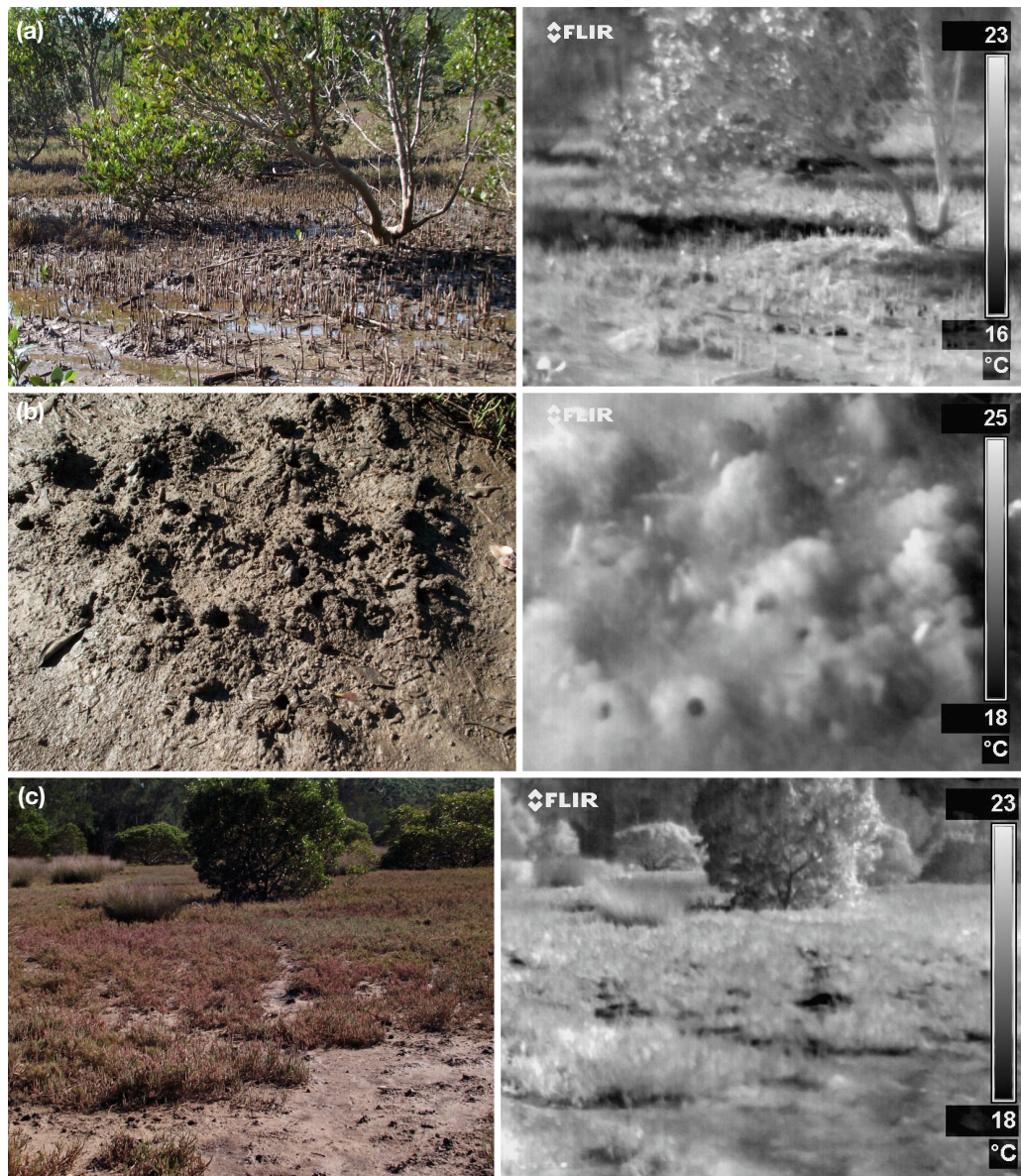
Fig. 4. Photographs (left) and infrared images (right) of (a,b) mangrove and (c) saltmarsh communities during daytime aerial exposure at Jervis Bay, New South Wales, Australia. Infrared images were taken with a FLIR® ThermaCAM S65 camera

temperature value is shown. The estimated emissivity is subsequently used for all temperature measurements of this specific material, either the surface of a rock or an organism. Alternatively, the surface of an object can be coated with a matte black paint (e.g. 3-M Black from Minnesota Mining Company or Senotherm from Weilburger Lackfabrik2, which both have an emissivity of ca. 0.95), and the above procedure can be repeated for coated and non-coated surfaces. This step is critical in any study assessing the thermal ecology of species of different colours or species exhibiting different phenotypes such as the

dogwhelk *Nucella lapillus* or the rough periwinkle *Littorina saxatilis*. So far, the emissivity of rocky intertidal substrata and organisms typically fall within the range of 0.95 to 1 (Helmuth 1998, Denny & Harley 2006, Miller et al. 2009, Cox & Smith 2011). Emissivity values calculated for a range of biotic and abiotic objects found on most rocky intertidal shores have been summarised by Cox & Smith (2011; see their Table 1). Emissivity can be easily corrected, as some of the latest generation thermal imagers (e.g. Fluke Ti25) have built-in on-screen emissivity correction capacity. However, care must be taken when

acquiring thermal images of wet surfaces in full sunlight, since this will increase the amount of reflected thermal energy. Most terrestrial studies using IRT avoid this source of error by undertaking sampling at night. However, for many intertidal organisms, thermal stress is greatest during the middle of the day when the sun is highest, and it is often their response to these intense periods of heat stress that ecologist are most concerned with. An alternative solution is to temporarily shade intertidal ectotherms while thermal images are being recorded or to undertake sampling when conditions are overcast, though the latter will result in measurements always being taken during thermally benign conditions; hence it is not recommended.

Environmental conditions

Increased concentrations of atmospheric gases (water vapour) and particles (dust) may also affect the ability of an infrared camera to accurately estimate surface temperatures. Airborne gases and particles lower atmospheric transparency, which in turn, affects the absorption and dissipation of infrared energy emitted by an object. This may be particularly prevalent within coastal regions where sea-spray and relative humidity are generally quite high. Therefore, infrared images taken within the marine environment should be accompanied by accurate measures of relative humidity. Along with distance between the object and the camera, these estimates of relative humidity are incorporated into the algorithms of most, if not all, infrared cameras. The use of IRT is therefore ideally suited for marine laboratory studies involving intertidal taxa since all external parameters affecting the reflection and absorption of infrared energy can be strictly controlled (Pincebourde et al. 2013).

Temporal variability

Whilst IRT is capable of capturing complex spatial patterns in thermal variability, some may criticise its inability to adequately capture temporal variability. Here, a single infrared image represents only a 'snap-shot' in time, and infrared video files are generally limited by the battery life of the camera (2–3 h) and/or external conditions (e.g. incoming tide). Temperature data loggers represent a cost-effective method for measuring broad-scale temporal and spatial temperature variability and are routinely used by inter-

tidal ecologists (Helmuth 1998, Helmuth et al. 2006, Denny et al. 2011, Lathlean et al. 2011) and could complement detailed spatial variability captured by IRT. Loggers have even been designed to match the thermal properties of several target organisms (Lima & Wethey 2009, Szathmary et al. 2009, Lathlean et al. in press). While infrared thermocouples enable point, non-contact measurements of body surface temperature (see e.g. Darnell & Munguia 2011), are more versatile than wired tissue-penetrating thermocouples (Iacarella & Helmuth 2011) and less expensive than the infrared cameras described above, they do not offer high-resolution synoptic measurements as do infrared cameras. This is, however, critical to assess the thermoregulatory behaviour of ectotherms, as surface temperatures of intertidal organisms are unlikely to be homogeneous over their entire bodies.

FUTURE DIRECTIONS

Thermal habitat mapping

An important characteristic of IRT is its ability to instantaneously quantify spatial variability in temperature. This attribute, along with the increasing portability of infrared cameras, has made it possible to map the fine-scale thermal properties of numerous habitats at scales pertinent to the individual organisms that actually experience those properties. Thermal mapping hence represents a promising tool for further assessments of the still relatively poorly explored relationship between habitat complexity and the resultant thermal properties of the organisms inhabiting them (Figs. 3 & 4). Such thermal mapping has already been undertaken on a range of rocky intertidal shores (Cox & Smith 2011, Lathlean et al. 2012) but has yet to be applied to soft-sediment habitats such as mangrove forests, mudflats and saltmarshes (see, however, our Fig. 4). With average temperatures and extreme heat events expected to increase with future climate change, IRT could be used to identify sites which could potentially act as thermal refugia for intertidal organisms as well as to monitor their effectiveness through time. This issue is particularly relevant in the context of climate change biology, as a major barrier in assessing where and when species may respond to altered climate lies in the spatial mismatch between the size of intertidal organisms and the grid sizes of distribution models, which are on average 4 orders of magnitude larger than the animals they study; see Potter et al. (2013) for a meta-analysis of the published literature in both aquatic and terrestrial ecology.

Species interactions

IRT could also be used to investigate the role of temperature in regulating the strength of species interactions. In ectotherms, body temperature strongly depends on the thermal inertia of the organisms, i.e. the time needed by an organism to reach its thermal equilibrium after a change in its environmental conditions (Monteith & Unsworth 2008). Thermal inertia is influenced by the mass, but also by the specific heat capacity and the thermal conductivity of an organism. As such, ectotherms with a larger mass, or those with a high heat capacity, take much longer to both warm up and cool down than smaller ectotherms or those with a low heat capacity. Large mussels are, however, buffered against rapid environmental changes because they have a higher thermal inertia (Helmuth 1998). A high thermal inertia may hence be considered as a competitive advantage, especially in environments with large and rapid temperature fluctuations. It should also be noted, however, as with endotherms, infrared images of ectotherms represent temperatures of an organism's surface, which does not necessarily reflect core body temperatures. This may be particularly true for larger species (and larger individuals within a species) that have a lower surface area to mass ratio. Along with being able to rapidly assess the effects of individual morphology on thermal physiology, IRT could provide further insight into the relationships between the dynamics of many habitat-forming species known to ameliorate neighbouring organisms from harsh abiotic conditions and their thermal properties. Macroalgae, for example, have frequently been cited as an important thermal buffer for many intertidal organisms (Dayton 1971, Bertness et al. 1999a,b, Leonard 2000, Beermann et al. 2013). IRT, which has yet to be applied to marine phycology (but see Van Alstyne & Olson 2014), could provide novel understanding of interspecific interactions between macroalgae and associated fauna which would otherwise remain undetected. For example, IRT could investigate whether the unique morphological characteristics of various intertidal algae influence their ability to buffer epifauna from thermal stress.

Thermoregulatory behaviour

To date, the majority of ecological studies that utilise IRT have been primarily interested in using this technology to improve estimates of population size of various terrestrial mammals and the detection of water stress in terrestrial plants (Stoll & Jones 2007). This bias towards large terrestrial endotherms and plants is somewhat surprising since thermal imaging is an extremely effective, non-invasive tool for investigating the influential role of environmental conditions on the body temperatures and thermoregulatory behaviour of both marine and terrestrial ectotherms alike. Even fewer studies have attempted to use IRT to take physiological measurements of marine invertebrates at the intra-individual level, but see Pincebourde et al. (2013). Surface temperatures of intertidal organisms are unlikely to be homogeneous over their entire bodies. Yet little is known about how or why regional heterothermy might exist in marine invertebrates, and IRT represents the only current technique capable of detecting and describing the driving mechanisms behind such processes. Furthermore, the use of IRT coupled with recently developed biomimetic technology could lead to further insights into the role of thermoregulatory behaviour and unique morphological characteristics on the physiological condition of numerous marine ectotherms. For example, IRT and specifically designed biomimetic loggers could be used to further assess the mushrooming behaviour in the limpet *Cellana grata* (Williams et al. 2005) and the shell lifting and stacking behaviour in the snail *Echinolittorina malacanna* (Marshall et al. 2010, Marshall & Ng 2013). Examples can already be found in the terrestrial literature on the use of both IRT and temperature data loggers (Scherrer & Körner 2010).

Underwater thermography

At present, the use of IRT has been largely restricted to intertidal habitats and surfacing marine mammals. This is because most infrared radiation is rapidly attenuated by seawater. However, recent studies in freshwater lakes and the deep ocean have used multispectral cameras fitted with infrared lights to observe benthic communities at night (Mills et al. 2005, Chidami et al. 2007). These cameras work by detecting near-infrared wavelengths (750–2500 nm) and therefore cannot, at present, be reliably used to estimate surface temperatures since most of the thermal energy emitted between 0 and 40°C is emitted within the mid- to far-infrared. Nonetheless, future technological advancements may enable these multispectral cameras to convert intensities of near-infrared light into reliable estimates of an object's temperature.

CONCLUSIONS

The ecological application of the fast developing infrared technology represents an example throughout the history of science where significant technological achievements have rapidly improved our understanding of the natural world. Whilst initially developed and used for military and medical applications, and extensively used by terrestrial ecologists, this review highlights the recent application of infrared technology to marine systems. Although fundamentally restricted to species found intermittently at the ocean surface, and within the intertidal zone, infrared technology can nonetheless provide insight into the thermal ecology and physiology of marine organisms. It is particularly relevant within intertidal ecosystems that include tremendously large and diverse environments, including rocky shores, sandy and muddy flats, mangroves and saltmarshes, which are among the most ecologically and socio-economically vital ecosystems on the planet, while increasingly threatened by climate change. As infrared technology continues to become increasingly sophisticated, portable and affordable, we consequently expect an ever-increasing number of marine ecologists incorporating IRT into their research, especially as temperatures continue to rise in response to climate change. Consequently, this review provides an outline for the best practices and procedures involving the use of IRT within the marine environment and hopefully helps seed further studies, as our journey to understand the impact of climate change on the physiology, behaviour and ecology of marine organisms is still at its early stage.

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