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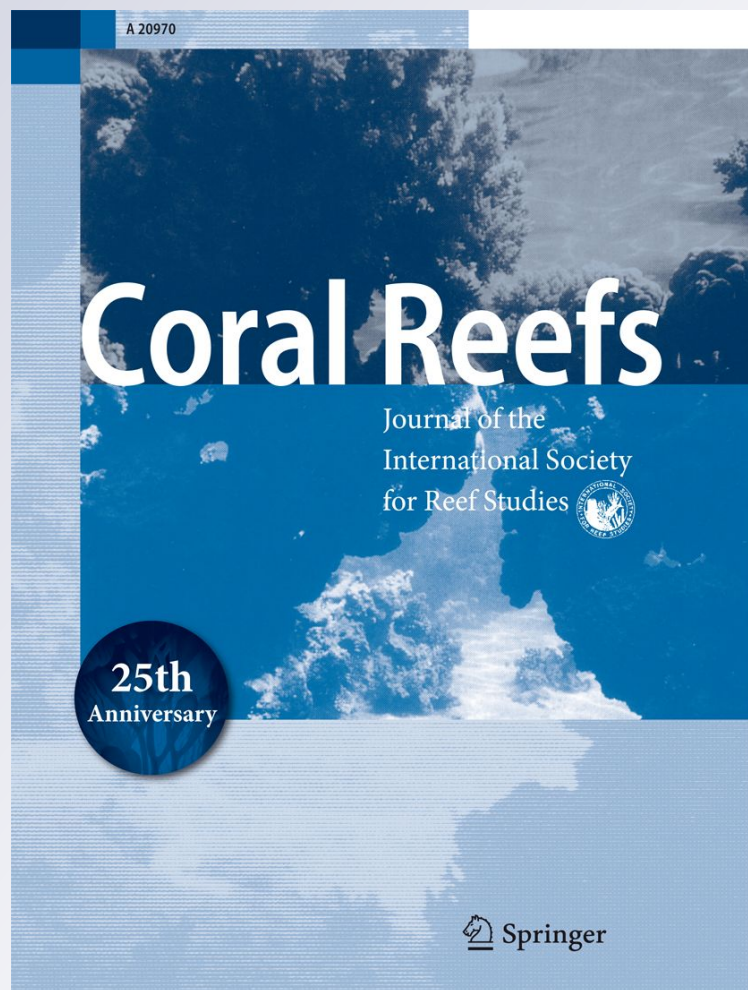
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Thermal ecology on an exposed algal reef: infrared imagery a rapid tool to survey temperature at local spatial scales

T. E. Cox · C. M. Smith

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Abstract We tested the feasibility of infra-red (IR) thermography as a tool to survey in situ temperatures in intertidal habitats. We employed this method to describe aspects of thermal ecology for an exposed algal reef in the tropics (O'ahu, Hawai'i). In addition, we compared temperatures of the surrounding habitat as determined by IR thermography and traditional waterproof loggers. Images of reef organisms (6 macroalgae, 9 molluscs, 1 anthozoan, and 2 echinoderms), loggers, and landscapes were taken during two diurnal low tides. Analysis of IR thermographs revealed remarkable thermal complexity on a narrow tropical shore, as habitats ranged from 18.1 to 38.3°C and surfaces of organisms that ranged from 21.1 to 33.2°C. The near 20°C difference between abiotic habitats and the mosaic of temperatures experienced by reef organisms across the shore are similar to findings from temperate studies using specialized longterm loggers. Further, IR thermography captured rapid temperature fluctuations that were related to tidal height and cross-correlated to wave action. Finally, we gathered evidence that tidal species were associated with particular temperature ranges and that two species possess morphological characteristics that limit thermal stress. Loggers provided similar results as thermography but lack the ability to resolve variation in fine-scale spatial and temporal patterns. Our results support the utility of IR thermography in exploring thermal ecology, and demonstrate the steps needed to calibrate data leading

to establishment of baseline conditions in a changing and heterogeneous environment.

Keywords Tropical · Intertidal zones · Global climate change · Thermal stress · Thermography · Method

Introduction

Nearshore coastal habitats with fluctuating tidal conditions and discrete zones of organismal distribution have long been recognized as model system to study the influence of abiotic factors on species distributions (Stephenson and Stephenson 1949; Benson 2002). Since the groundbreaking research of Connell (1961), it is recognized that physical abiotic stress often determines intertidal species upper distributional limits while biological interactions are more influential closer to subtidal zones. Recently this paradigm has been expanded to incorporate how physical factors such as temperature can alter biological interactions like predation and competition (Wetthey 1984; Hoegh-Guldberg and Pearse 1995; Sanford 1999; Schneider and Helmuth 2007; Pincebourde et al. 2008). Indeed temperature, which influences a wide variety of physiological processes, is often cited as the single most important abiotic factor impacting the ecology of marine organisms (Helmuth 2002; Somero 2002), and increasingly marine environments are subjected to that stress (IPCC 2007).

Temperature is likely a more important ecological driver in the tropics than at other latitudes (Tewksbury et al. 2008). Tropical marine habitats can be abiotically stressful for organisms (Moore 1972) as tropical species not only experience some of the highest temperatures and irradiances worldwide (Beach and Smith 1996), but they also can be acclimated to narrow thermal regimes (Stillman and

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Somero 1996; Tewksbury et al. 2008). For example, an increase of a few degrees above normal conditions in shallow marine waters results in coral bleaching (Brown 1997; Jokiell and Brown 2004; IPCC 2007). Thermal stress could be greater for intertidal reef organisms as the pool of water buffer drains away and many tropical habitats in which numerous species reside lack shade from canopy-forming algae (Abbott and Huisman 2004 but see Beach and Smith 1996). Few examples of intertidal habitats in tropical areas confirm this hypothesis as organisms reside in cooler cracks and crevices (Menge and Lubchenco 1981), invertebrates exhibit cooling behaviors and morphologies (Vermeij 1971, 1973; Garrity 1984; Williams and Morritt 1995), and even species compete for cooler microhabitats (Wethey 1984). Along the subtropical to tropical Main Islands of Hawai'i, where micro-tidal conditions persist for a marine fauna with temperate and tropical ancestry (Kay 1979; Abbott 1999), very little is known about nearshore thermal conditions nor the ecological influence of temperature. Bird (2006) shows that temperature and distributional patterns of animal and algae by functional groups are correlated on wave dominated shores in Hawai'i. The thermal variability and fine-scale thermal distribution patterns have yet to be examined.

Thermal ecology is difficult to investigate in any intertidal zone (Helmuth 2002; Tomanek and Helmuth 2002; Fitzhenry et al. 2004). This difficulty lies in the complexity of the environment as temperature can vary over different temporal and spatial scales (Helmuth and Hoffmann 2001; Helmuth et al. 2006a, b). Tides, waves and even local weather act to rapidly alter temperatures and their magnitudes and timing can dictate the degree of heating or cooling (Helmuth et al. 2002). Habitat structure and location alter temperatures as the very nature of incoming and outgoing tides results in hotter temperatures for organisms found at higher tidal elevations (Somero 2002). However, angle of the shore and crevices can provide cool microhabitats and afford high zone species thermal protection (Helmuth 1998). Thus, to capture and account for this level of variation requires numerous efforts and large numbers of traditional waterproof loggers and probes.

The success of technologies can be gauged by their application to answer novel scientific questions. Thermography is clearly a useful approach in measuring sea surfaces temperatures collected by aerial infrared (IR) techniques, further thermal data from offshore surface buoys are combined with these data to characterize thermal stress and to predict the impacts of global climate change (Schneider and Helmuth 1997). Our approach is to employ this established technology to ascertain the localized temperatures experienced by reef organisms on low tides. Recent local scale efforts with IR technology have been useful in a laboratory setting to describe temperatures of

captive sea stars (Pincebourde et al. 2009) and casually in the field to examine habitats (Schneider and Helmuth 1997; Helmuth 2002). This approach has yet to be applied rigorously to quantitatively assess temperatures in an intertidal reef.

The purpose of this study is to explore the feasibility of using IR thermography in an intertidal system to study aspects of thermal ecology. We use this technique to describe in situ temperatures that occur on diurnal low tides in a little studied intertidal reef, O'ahu, Hawai'i. Specifically, we examine (1) if reef organisms are associated with particular thermal habitats (2) if these organisms have characteristics that allow them to remain cooler than their surrounding substrates, and (3) the spatial and temporal temperature heterogeneity that occurs during spring diurnal low tides. Finally, to test the efficacy of our methods we compare temperatures from IR thermography to traditional waterproof loggers and discuss the feasibility of this technique to rapidly assess temperatures at varying spatial scales.

Materials and methods

Site selection

We examined shore temperatures during low tides at Diamond Head, O'ahu (21°15'20.67"N, 157°48'38.94"W). The exposed reef platform at Diamond Head is composed of limestone with a small offshore reef that protects this intertidal zone from large onshore waves. The community is observably zonate (Kay 1979; Abbott 1999; Hoover 2002; Abbott and Huisman 2004) with small molluscs (*Echinolittorina hawaiiensis*, *Nerita picea*, and *Siphonaria normalis*) occurring closest to the high tide line, followed by a narrow zone of the mollusc *Dendropoma gregaria*, and ending in a wetter habitat dominated by the reef phaeophyte *Padina sanctae-crucis* (TEC pers. obs.).

Tidal selection

Sampling for temperature determinations occurred on 20th Jul 2009 and 21st Jul 2009, 2 days with a negative low tide of -0.12 m occurring at 0744 and 0847 h (respectively). These times are typical for Hawaii spring tides in summer months and a -0.12 m tide is close to the maximum negative height for mean low low water for the island of O'ahu (max = -0.15 m for 2009, Honolulu Tidal Station, NOAA).

Habitat temperature ranges during low tides

On the two sampling days from the hours of ~ 0730 (an hour after dawn) to 1030 (when tidal inundation prevented

access to the shore) we used a Handy Thermo TVS-200 EX IR camera (NEC Avio IR Technologies, Tokyo, Japan) to capture digital images and video clips of the shore and resident biota. This camera captures temperature changes at 1/60 s from a distance range of 30 cm to infinity and has an accuracy of $\pm 2.0^\circ\text{C}$ with precision better than 0.08°C . All images were taken within a defined area of shore, from the terrestrial vegetation to the subtidal zone ($\sim 8\text{--}15\text{ m}$) and a horizontal area that was $\sim 20\text{ m}$ parallel to the water.

Image analyses for temperature determinations

Thermal analyses of photos were conducted using ImageJ software (www.nih.gov). The IR camera and its associated thermography software saved three images from each photo that were used in analyses: (1) color jpeg of the subject (2) thermal image in false color with a temperature scale bar and (3) a composite image of the normal jpeg and thermal image. Each thermal image or frame was in false color, thus images were converted with plugin script written and developed by William Winter (pers. comm.) to an indexed image so that each combination of red, blue, and green had one value from 0 to 364 that was linearly related to the thermal image scale bar. Using the linear option in the calibration function in ImageJ, it was then possible to determine the average, minimum, and maximum temperatures of the image or of a defined area within the image.

Ground-truthing of emissivity

Infrared energy is converted to temperature by the following equation:

$$\text{Infrared energy} = \sigma \times e \times T^4$$

where σ is the Stefan-Boltzmann constant ($\text{W}^{-1}\text{ m}^2\text{ K}^{-4}$), e is emissivity, and T is Temperature ($^\circ\text{K}$). For image analyses a value of 1.0 for emissivity was assumed yet, emissivity or the amount of infrared emitted by objects can vary with the composition of materials, temperature, and weathering. To measure biases that may have been introduced with this assumption, measurements of temperature and emissivity were collected in situ for commonly encountered molluscs, seaweeds, and rock surfaces. Emissivity was estimated by measuring temperature of an organism or surface with a small tipped probe (T_{org}) and FLIR BX320 IR camera (T_{ir}). Then following from the Stefan-Boltzmann equation, emissivity was estimated:

$$T_{\text{org}} = \text{the fourth root of } \left[\frac{(\sigma \times 1 \times T_{\text{ir}}^4)}{(\sigma \times e)} \right]$$

In situ measurements were collected at Diamond Head, on three consecutive days in May 2011 during hours

(0800–1400) with a negative tidal height (peak low tides ranged from -0.01 to -0.12 m). Surfaces were wet to damp at time of measurements. Due to limited duration of low tide, a few organisms and substrates were collected and emissivity measured in the laboratory. To estimate the introduced error when assuming an emissivity of 1.0 we calculated T_{org} with a T_{ir} of 30 and 35°C with the measured emissivity values. Then we subtracted the calculated T_{org} from 30 to 35°C (the T_{ir} with an emissivity of 1.0) and this was assumed to be the error that was likely to occur.

Organismal temperature ranges during low tides

To capture the temperature range that reef organisms experience during a typical diurnal low tide at Diamond Head, we periodically walked the defined area of shore and captured images ($<0.5\text{ m}^2$) of organisms in their habitats. These images were captured perpendicular to the substrate from a similar height to minimize any parallax error. An effort was made to not resample or take repetitive pictures of the same individuals. Images were analyzed as described above. Organisms were outlined in images to determine their average surface temperature. These reported temperatures reflect the temperatures that organisms endure in the field and do not necessarily reflect core body temperatures. In addition, we examined the conventional jpeg image to confirm species identifications. Composite images were used as a guide to determine surface temperature of the species in the photos.

Photos of organisms in their representative habitats and microhabitats were used to determine the typical range of temperatures encountered and were used to investigate if organisms differed in surface temperature from their surroundings. A grid of 56 randomly assigned points was generated and the point-intercept methodology used to determine the average temperature in a habitat. Points that fell upon organisms were excluded from the average to ensure independence. In images of invertebrate species, we also quantified the average temperature of the microhabitat (area directly next to the individuals). Differences in temperature were compared via paired t tests as data met normality requirements.

Within habitat temporal temperature variation

To determine the variation in temperature that occurs during these typical low tides, we took landscape photos of the exposed reef within the *Padina sanctae-crucis* habitat, taken from roughly the same location at a similar angle, and determined the temperature of six locations for 900 s intervals throughout the day. These images captured an area of shore that was approximately 3 m horizontal and

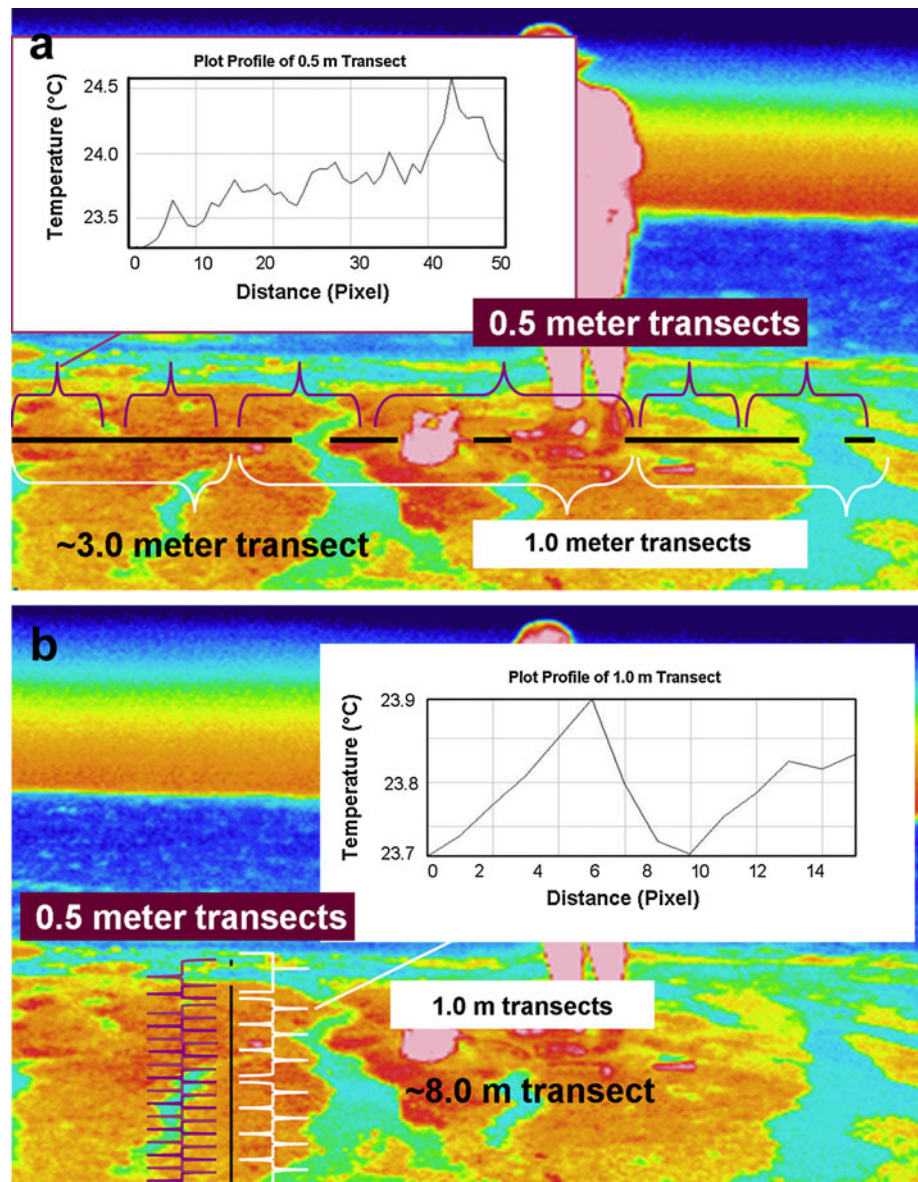
8 m vertical in distance, as determined from a known reference, making use of topographic and introduced landmarks to re-locate sites.

Separate analyses were conducted over the 2 days, thus a different set of six locations were used each day. The temperatures from each sampling were averaged together by 60 s intervals and then averaged over 900 s intervals. These data were regressed with tidal height to examine the relationship between temperature and tidal cycle.

To explore the effect of waves at low tide on the temperature of the shore, we captured the thermal consequences of two series of wave events (1 series of events day⁻¹). Images were captured from the same distance and angle, as described above. One wave series was captured at 08:20 h (less than an hour after peak low tide) on 20 July

2009 with video using the IR camera with a rate of 40 frames s⁻¹ and lasted for 75 s. The second wave series was documented with a series of digital stills on the 21 July 2009 at 09:02 h (less than an hour after peak low tide) and lasted for 63 s. The average temperature of the shore was determined using ImageJ (as described earlier) every 0.3 s throughout the filmed wave series (153 frames) and for each digital still ($\sim 1\text{--}5$ images s⁻¹ = 16 total images). Also, for each photo and frame, the total number of pixels exposed to air were measured with ImageJ by outlining the area of shore directly ahead of the water line and quantifying pixels. The pixels exposed to air were plotted with the temperature and cross correlation was used to statistically investigate the similarity between temperature and wave forms as a function of time lag.

Fig. 1 Method used to determine **a** horizontal and **b** vertical temperature variation within raised surfaces of *Padina sanctae-crucis* habitat. A horizontal transect of ~ 3.00 m (black) was sub-sampled into 1.00 (white), 0.50 (violet), 0.25 (not shown), 0.15 (not shown) distances while a vertical transect of ~ 8.00 m (black) was sub-sampled into 1.00 (white) and 0.50 m (violet) distances. Plots show the temperature sampled over the set number of pixels within the 0.50 or 1.00 m transect



Within habitat spatial temperature variation

To investigate spatial variation of temperature and to determine the number of temperature loggers needed to answer a specific research question, we investigated the horizontal (parallel to the shore) and vertical variation (perpendicular to the shore) in temperature across different distances within one habitat (Fig. 1). Five landscape photos captured from a similar location on day 1 during the low tide were haphazardly selected. Using a visible known distance in indexed images, the number of pixels to m was calibrated to create virtual transect lines. Initially two transect lines placed on raised surfaces (tidepools, cracks, and crevices were avoided) covered with the algae *P. sanctae-crucis*, were created to extend across the horizontal and vertical distance of the image. The lengths of the initial horizontal lines varied slightly among pictures (2.5–3.4 m), while the vertical transect distances were approximately 8 m from the landward edge of the *Padina* zone to the incoming tide. Temperatures along the transect lines were plotted and the interquartile distance among temperatures determined. The

interquartile distance provides an estimate of variation between the 25 and 75% quartile and it is robust to outliers thus it is a conservative measurement of overall variation. Then, using the known pixel to distance ratio, the transect lines were sub-sampled. Horizontal transect lines were sub-sampled into 1.00, 0.5, 0.25, and 0.15 m transects. Because of the limited number of pixels (fewer than 3 pixels for 0.25 meters transects), vertical transect lines were sampled into 1.00 and 0.50 m lengths. Mean interquartile distances were determined for each transect length on each image. Initial screening did not reveal statistical differences among images, thus these interquartile values were averaged across photos ($N = 5$). Because we sub-sampled the initial transect length, data lacked independence and 95% confidence intervals were used to compare means within horizontal and vertical lines. In addition, transect lines were subject to minor parallax error and for interpretation the pixel number per area of shore is reported.

Because spatial variation in temperature could be attributed to the bias introduced by assuming a value of 1.0 for emissivity; we further investigated spatial temperature

Table 1 Estimated emissivity (e) and the mean estimated error (\pm SE) at 30 and 35°C when assuming an e value of 1.0 for all surfaces

	n	Error at 30°C	Error at 35°C	e
Seaweeds				
<i>Acanthophora spicifera</i>	3	0.638 \pm 0.526	0.648 \pm 0.526	0.987 \pm 0.008
<i>Hydroclathrus clathratus</i>	2	0.266 \pm 0.262	0.271 \pm 0.266	0.999 \pm < 0.001
<i>Laurencia mcdermidiae</i>	3	0.541 \pm 0.438	0.550 \pm 0.445	0.993 \pm 0.008
<i>Liagora</i> spp.	6	0.753 \pm 0.155	0.766 \pm 0.158	0.995 \pm 0.002
<i>Padina sanctae-crucis</i>	7	0.904 \pm 0.305	0.919 \pm 0.309	0.988 \pm 0.005
<i>Sargassum echinocarpum</i>	2	0.790 \pm 0.902	0.803 \pm 0.917	0.990 \pm 0.014
Molluscs				
<i>Cypraea mauritiana</i>	1	0.236	0.240	1.000
<i>Drupa ricina</i> *	2	0.826 \pm 1.187	0.839 \pm 1.187	1.000 \pm < 0.001
<i>Morula</i> spp.	3	0.602 \pm 0.107	0.612 \pm 0.109	0.997 \pm 0.004
<i>Nerita picea</i>	2	0.233 \pm 0.094	0.237 \pm 0.096	1.000 \pm < 0.001
<i>Echinolittorina hawaiiensis</i>	6	0.599 \pm 0.213	0.609 \pm 0.217	0.997 \pm 0.002
<i>Siphonaria normalis</i>	4	0.232 \pm 0.198	0.235 \pm 0.202	1.000 \pm < 0.001
<i>Thais armigera</i>	–	–	–	–
<i>Dendropoma gregaria</i>	5	0.944 \pm 0.306	0.960 \pm 0.311	0.992 \pm 0.005
<i>Isognomon californicum</i> *	2	1.121 \pm 1.014	1.139 \pm 1.014	0.985 \pm 0.006
Other invertebrates				
<i>Anthopleura nigrescens</i>	1	1.096	1.114	0.990
<i>Actinopyga mauritiana</i>	1	0.764	0.776	1.000
<i>Echinometra oblonga</i>	1	0.142	0.144	1.000
Substrate types				
Basalt	2	0.242 \pm 0.013	0.246 \pm 0.013	1.000 \pm < 0.001
Limestone	1	<0.001	<0.001	1.000
Mix of Basalt & Limestone	1	1.099	1.117	1.000
Sand*	3	<0.001	<0.001	1.000 \pm < 0.001

* Indicates taxa measured for e in the laboratory

variation with a probe on the 18th and 19th May 2011 during hours with a negative tidal height (peak low tides ranged from -0.09 to -0.12 m). Temperature was measured on raised surfaces at every meter across a haphazardly placed 8 m horizontal transect for a total of 8 measurements/day. On May 19th the 8 m transect line was further sub-sampled into smaller 0.5 m transects. Five temperature measurements were taken with a probe at 4 haphazard meter locations. Each of the 5 measurements was spaced 0.1 m away from the previous measurement for a total distance of 0.5 m, 4 times. The interquartile distance was determined and averaged from the 8 measurements to determine the variation within the 8 m transects and from the 5 measurements to determine the variation within the 0.5 m distances.

Comparison of methodologies

To compare methodologies, we examined the temperatures determined from IR images to the temperature determined by HOBO[®] waterproof loggers. Loggers were placed in white rubber covers to mimic the white colored limestone shore. One logger was placed near shore, one mid shore,

and one close to the submerged reef on both days sampled. Between 0700 and 1030 h, photos of the temperature loggers were taken that included the nearby shore. An area of equal size to the logger was analyzed in photos for an average temperature. The temperature loggers recorded temperature every 900 s and temperature as determined via the analyzed images was compared to temperature from the nearest logger. Sample comparison between IR and loggers were never more than ± 300 s apart. Each location on the shore had 2–15 sampling intervals for comparison. An average temperature was calculated for each methodology, each day, at each location and pooled together for a total of six average comparisons (three per day). Data were initially screened for normality and homogeneity of variance and a paired *t* test was used to determine if there were any statistical differences between daily average temperatures determined from the two methods.

Results

Emissivity of reef organisms and substrates varied from 0.985 to 1.000. A value of 1.0 was assumed in image

Table 2 Average \pm SE, minimum, and maximum temperature ($^{\circ}$ C) of the surface of organisms and their habitats during low tides

Species	Authority	Zone (S,H,M,L)	# of ind. or area	# of pictures	Organism temp.	Min	Max	Habitat temp	Min	Max
Seaweeds										
<i>Acanthophora spicifera</i>	(Vahl) Borgesen	L	17076	4	25.3 ± 1.3	22.1	26.3	26.2 ± 1.7	22.1	28.1
<i>Hydroclathrus clathratus</i>	(C. Agardh) Howe	H,M,L	4383	1	25.5	–	–	26.4	–	–
<i>Laurencia mcdermidiae</i>	Abbott	L	2420	2	25.5 ± 0.5	25.2	25.9	25.9 ± 0.3	25.7	26.1
<i>Liagora</i> spp.		N/A	76125	5	26.5 ± 0.7	25.1	28.8	28.0 ± 0.9	25.3	29.5
<i>Padina sanctae-crucis</i>	Børgesen	L	65016	7	24.8 ± 0.3	22.5	26.2	25.4 ± 0.4	22.5	27.4
<i>Sargassum echinocarpum</i>	J. Agardh	L	9757	1	25.0	–	–	25.3	–	–
Molluscs										
<i>Cypraea mauritiana</i>	Linnaeus	M,L	2	1	23.2	–	–	22.5	–	–
<i>Drupa ricina</i>	Linnaeus	N/A	1	1	25.1	–	–	25.7	–	–
<i>Morula</i> spp.		N/A	4	3	27.4 ± 1.2	26.4	29.8	27.9 ± 0.9	27.9	29.3
<i>Nerita picea</i>	Recluz	S	51	5	23.3 ± 0.8	21.7	25.9	23.0 ± 0.6	21.7	24.4
<i>Echinolittorina hawaiiensis</i>	Rosewater and Kadolsky	S	192	8	25.2 ± 0.8	21.4	27.7	25.2 ± 0.7	21.1	26.9
<i>Siphonaria normalis</i>	Gould	S	81	9	28.5 ± 0.3	26.3	32.3	29.4 ± 0.5	26.4	33.2
<i>Thais armigera</i>	Link	L	1	1	24.3	–	–	24.1	–	–
<i>Dendropoma gregaria</i>	Hadfield and Kay	L	<200	3	28.6 ± 0.5	28.1	19.1	28.0	–	–
<i>Isognomon californicum</i>	Conrad	H	5	1	24.5	–	–	25.0	–	–
Other invertebrates										
<i>Anthopleura nigrescens</i>	Verrill	L	15	2	27.5 ± 0.2	27.3	27.7	27.6 ± 0.1	27.6	27.7
<i>Actinopyga mauritiana</i>	Quoy and Gaimard	N/A	1	3	25.4	24.3	26.0	25.4	24.2	26.2
<i>Echinometra oblonga</i>	De Blainville	L	4	2	25.3 ± 0.3	25.1	25.6	25.5 ± 0.9	24.9	26.1

Zone specifies the area of shore (Splash (S) > High (H) > Mid (M) > Low (L)) that organism is known to commonly occur based upon Kay (1979), Abbott (1999) and Abbott and Huisman (2004), Hoover (2002). Area is expressed as sampled pixels for seaweeds while # of individuals are expressed for invertebrates

analyses and some error in absolute temperature is likely. However based on the ground-truthing of e that was conducted in the field, this error does not exceed the $\pm 2.0^{\circ}\text{C}$ accuracy of the camera (Table 1). The error about IR determined temperatures is likely less than the average calculated error of 0.62°C which was determined for a temperature (35°C) above what was commonly encountered for organisms in the field. Furthermore, the error slightly increased (by 0.03°C) from calculations at 30 – 35°C (Table 1).

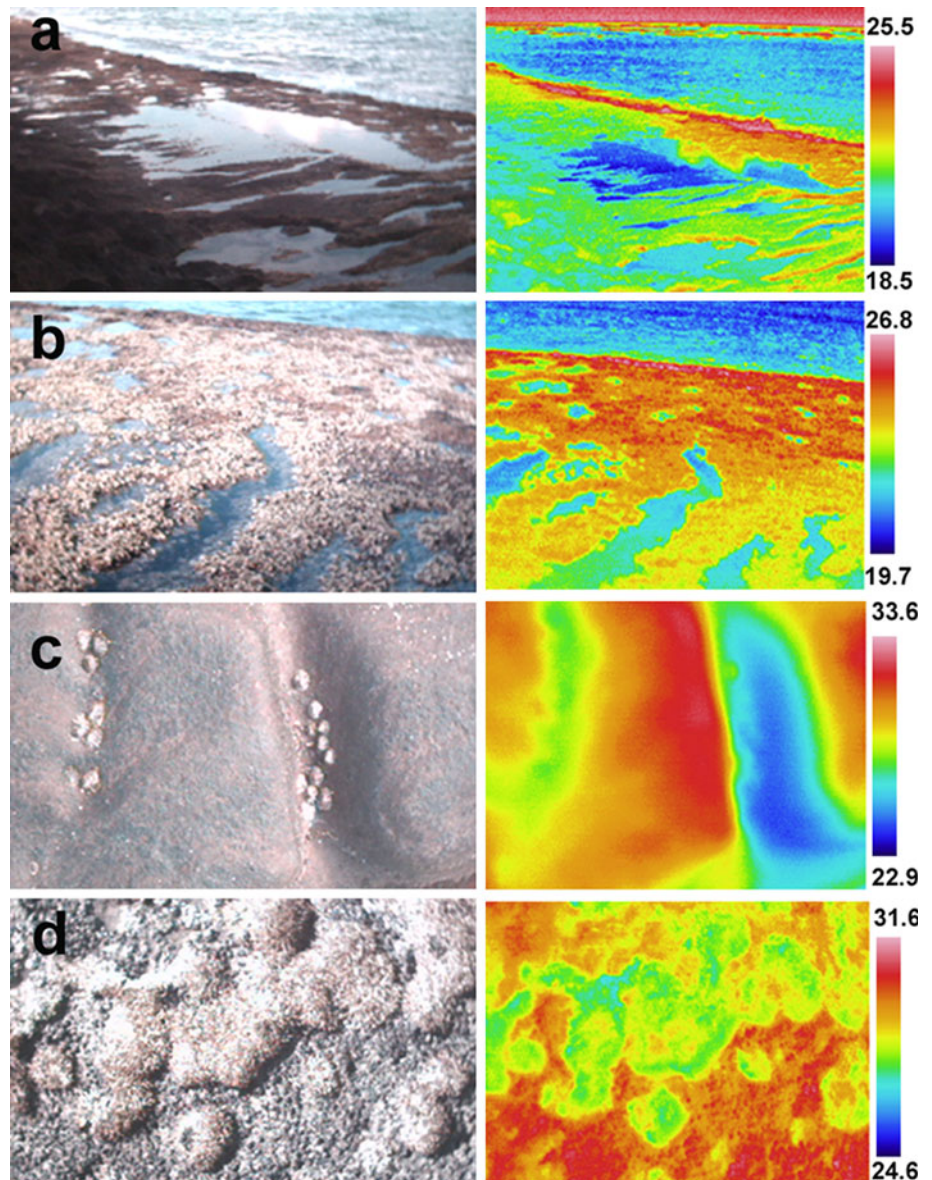
Over the 2 days in 2010, during the low tide events, 339 thermal images and three videos (4735 frames) of aerial exposed reef organisms and habitats were collected. Temperatures in these photos were determined to range from 18.3 to 38.3°C . However, the range of temperature that the organisms experienced (organism surface and

microhabitat temperature only) was narrower, 21.1 – 33.2°C (Table 2).

Organism surface and habitat temperatures did not correlate with distribution patterns. The gastropod, *Nerita picea*, which was distributed above the macroalgae and *Dendropoma gregaria* band (Kay 1979), had the lowest average surface temperature of any invertebrate or macroalgae examined despite being in the hottest zone. Similarly, *Siphonaria normalis*, a mollusk that commonly occurs close to the high tide line (Kay 1979), exhibited an outer shell temperature cooler than organisms from habitats closer to the low tide water line. Finally, the mollusk *Dendropoma gregaria* commonly occurred above the subtidal zone (Kay 1979), yet exhibited the hottest surface temperatures.

Surface temperatures of organisms were often different than their surrounding habitats (Figs. 2, 3, and 4).

Fig. 2 Select thermal images; **a** and **b** show the habitat thermal heterogeneity and **c** and **d** show the surface temperatures of reef organisms. *Siphonaria normalis* (2.0 cm in size) occurs in sunken depressions (green and blue color) that are $\sim 6^{\circ}\text{C}$ cooler than nearby raised surfaces and (bottom) *Liagora* sp. (individuals up to 5 cm in size) with cooler surface temperatures than the nearby habitat. Images on the left are taken instantaneously with the right images which are calibrated ($^{\circ}\text{C}$) in infrared



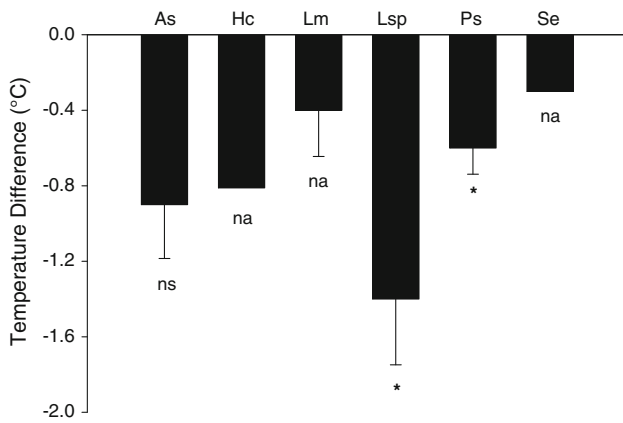


Fig. 3 Mean (\pm SE) difference in temperature ($^{\circ}$ C) between macroalgae and their overall reef habitat. Text below bars represents the results of paired *t* tests between organism and the overall habitat temperatures; na, not applicable due to small sample size; ns, not significant; * <0.05 . As, *Acanthophora spicifera*; Hc, *Hydroclathrus clathratus*; Lm, *Laurencia mcdermidiae*; Ps, *Padina sanctae-crucis*; Se, *Sargassum echinocarpum*

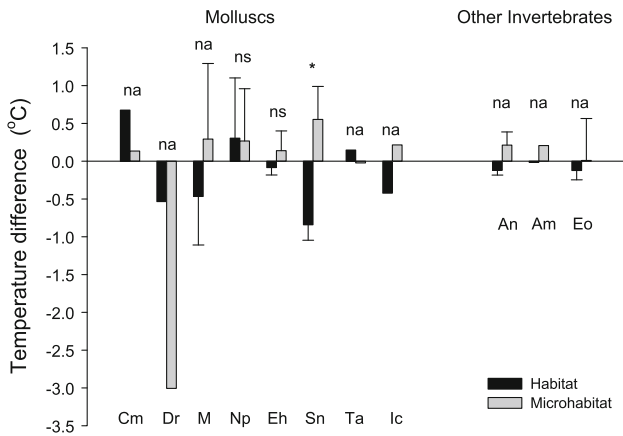


Fig. 4 Mean (\pm SE) difference in temperature ($^{\circ}$ C) between invertebrates and their habitat and microhabitat. Text above bars are the results of paired *t* tests: na, not applicable due to small sample size; ns, not significant; * <0.05 . Cm, *Cypraea mauritiana*; Dr, *Drupa ricina*; M, *Morula* spp.; Np, *Nerita picea*; Eh, *Echinolittorina hawaiiensis*; Sn, *Siphonaria normalis*; Ic, *Isognomon californicum*; An, *Anthopleura nigrescens*; Am, *Actinopyga mauritiana*; Eo, *Echinometra oblonga*

Macroalgae were found to be 0.4–1.8 $^{\circ}$ C cooler than the surrounding habitat, with species of the red alga *Liagora* (paired *t* test, $n = 5$, $P = 0.02$) and the brown alga *Padina sanctae-crucis* (paired *t* test, $n = 7$, $P = 0.03$) being significantly cooler than their habitats. Species of *Liagora* had the largest difference in temperature from the overall habitat, which was often bare of other macroalgae. Several molluscs were encountered with variable temperature differences from their overall habitat and their nearby microhabitat, suggesting movement or settlement preference to cooler microhabitats. Individuals of *Siphonaria*

normalis (paired *t* test, $n = 10$, $P = 0.03$) had cooler surface temperatures than their habitats, but their surfaces were warmer than the nearby microhabitat. Images of species of *Morula*, *Isognomon californicum* and *Echinolittorina hawaiiensis* (paired *t* test, $n = 8$, $P = 0.50$) exhibited a similar trend, but either had too few images taken for statistical comparison or no statistical differences were detected using the current sample size. The surface temperature of *Nerita picea* did not tend to differ from the overall habitat or nearby microhabitat (paired *t* test, $n = 4$, $P = 0.58$). Interestingly, *Drupa ricina* was 3.0 $^{\circ}$ C cooler than its microhabitat but was similar in temperature to the overall habitat. The echinoderms, *Actinopyga mauritiana* and *Echinometra oblonga*, and the anemone *Anthopleura nigrescens*, were found in sunken depressions or crevices but surprisingly, did not differ in temperature from their respective habitats.

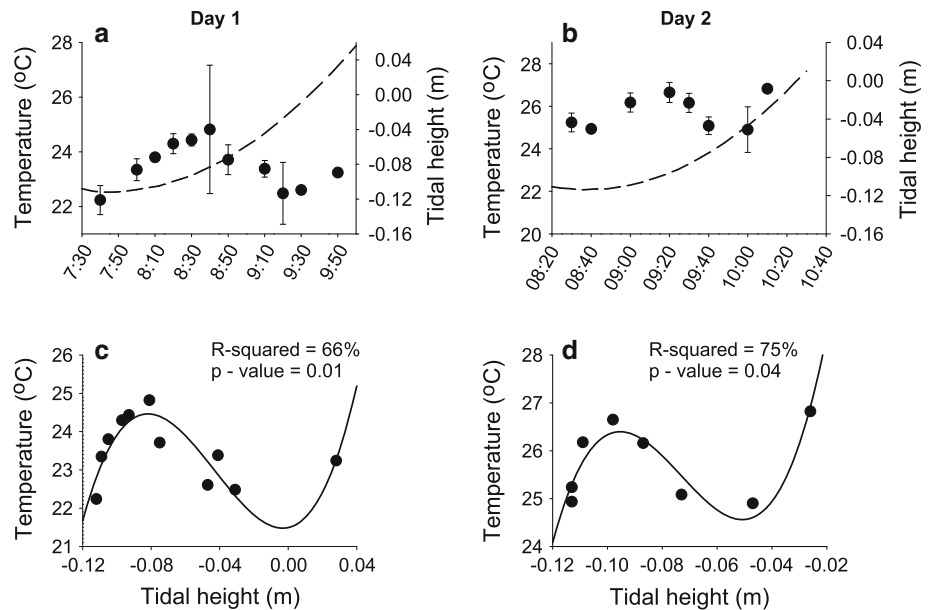
Probed determined temperatures of organisms and habitats collected during efforts to ground-truth emissivity in 2011 confirmed these findings. Species of *Liagora* on average were 5.0 $^{\circ}$ C cooler than their surrounding habitat; raised rock surfaces were hotter (mean range = 29.1–30.9 $^{\circ}$ C) than nearby seaweeds (mean = 26.2 \pm 0.8 SE $^{\circ}$ C), and similar or hotter than molluscs (mean range 26.7–30.0 $^{\circ}$ C); and, *S. normalis* occurred in cooler and more wetted depressions that occurred in basalt (on average 0.8 $^{\circ}$ C hotter).

Temperature varied temporally and was related to tidal cycles (Day 1, cubic relationship, $P = 0.01$, $R^2 = 66\%$; Day 2, cubic relationship, $P = 0.04$, $R^2 = 75\%$) (Fig. 5). On both days, the peak average temperature of the exposed reef occurred approximately \sim 40 min after mean low low water. Day 2, with a similar but later peak low tide, averaged warmer temperatures (21.4–27.3 $^{\circ}$ C) than Day 1 (19.4–28.4 $^{\circ}$ C). The difference between the minimum and maximum temperature recorded within this habitat over the low tide was determined to be 9 $^{\circ}$ C on Day 1 and 6 $^{\circ}$ C on Day 2.

Wave events lowered the temperature on the exposed intertidal reef (Figs. 6 and 7). A cross correlation between shore temperature and wave events revealed that temperature changes lag behind incoming waves by two seconds. Temperature was 66% correlated to wave events.

IR determined temperatures did not differ from those logged by conventional devices; however, spatial variation in temperature within the *Padina* habitat was detected with IR thermography (Figs. 2 and 8). Temperature varied in the horizontal direction over the varying transect lengths from mean interquartile distances of 0.29–0.35 $^{\circ}$ C. Horizontal and vertical variation tended to decrease with smaller sampled transect lengths and pixel number yet, the 95% confidence intervals around means often overlapped. Temperature varied in the vertical direction over varying transect lengths from mean interquartile distances of

Fig. 5 Relationship between temperature and tidal height for 2 days (Day 1, **a** and **c**; Day 2 = **b** and **d**), habitat temperature = circles \pm SE plotted with tidal height = long dashed line (**a** and **b**) and a fitted line plot showing the cubic relationship (**c** and **d**)



0.19–0.40°C. Variation was highest within the 8.0 meter vertical transect which had a similar pixel range as the 1.0 m horizontal transects. Yet the mean interquartile distance within the 1.0 m vertical transect was lower than the average value determined for 0.15 m horizontal transect and both of these transects had a similar sampled pixels.

A temperature probe also captured spatial variation in temperature across the horizontal distance of the shoreline. Probed temperature values on the 2011 sampled low tides revealed a mean interquartile distance of 1.2 ± 1.2 SE ($n = 2$ transects) within 8 m transect length and a lower mean interquartile distance of 0.6 ± 0.2 SE ($n = 4$) for the 0.5 m transects.

Discussion

For just two diurnal tidal events that represent typical low tides in mid day, IR thermography rapidly revealed surprisingly fine scale perspectives. Tidal species were associated with particular thermal habitats and exhibited thermal heating, thermal cooling and thermal neutral patterns. The range of temperatures that occur in intertidal reef habitats in O‘ahu, is surprisingly complex and dynamic for a shore that experiences small tidal ranges (Beach et al. 2006) and relatively warm constant air and water temperatures (Tewksbury et al. 2008). Habitat heterogeneity contributes to temperature variability, and IR images allowed for visualization and quantitative assessment of algae and invertebrates that occupy these hot and cold microhabitats. Thus, contrary to predictions, organisms living closest to the high tide line were not necessarily

hotter than those situated near the subtidal reef. Further, IR thermography indicated that temperature varies temporally and changes rapidly with the tidal height and wave events. These findings support the utility of IR thermography as a useful tool in exploring thermal ecology in a changing, heterogeneous environment and documenting baseline thermal stress levels with the realization of climate change.

Analyses of thermal images show that habitat temperature in the tropics can vary by as much as 20°C across a narrow intertidal reef yet, the difference in temperature that organisms experience at the microhabitat level may differ by as little as 12°C. This discrepancy is the result of the presence of cool and hot microhabitats. For instance, the calcified brown alga *Padina sanctae-crucis* is commonly intermixed with pockets of habitat-forming *Dendropoma gregaria* colonies, yet the alga maintain cooler surface temperatures than the molluscs. Similarly, the mollusc *Siphonaria normalis* was distributed in hot habitats near the high tide line but occurs in sunken depressions that were up to 6°C cooler than nearby raised rock surfaces. Garrity (1984) records similar findings for tropical gastropods in Panama, and Wethey (1984) also reports barnacles to favor cooler depressions. In Hawai‘i, habitat heterogeneity and other factors such as angle of the sun may have more of an impact on organism’s temperature and its thermal stress than distance from high tide line, a finding that would be difficult to determine with loggers or probes.

IR thermography captured rapid temperature fluctuations that are related to the tide and waves and it is likely greater variation would be observed with repeated temporal sampling. During diurnal low tides, temperature was related to tidal height with the hottest temperatures occurring after peak low tide but before high tide. Similar findings

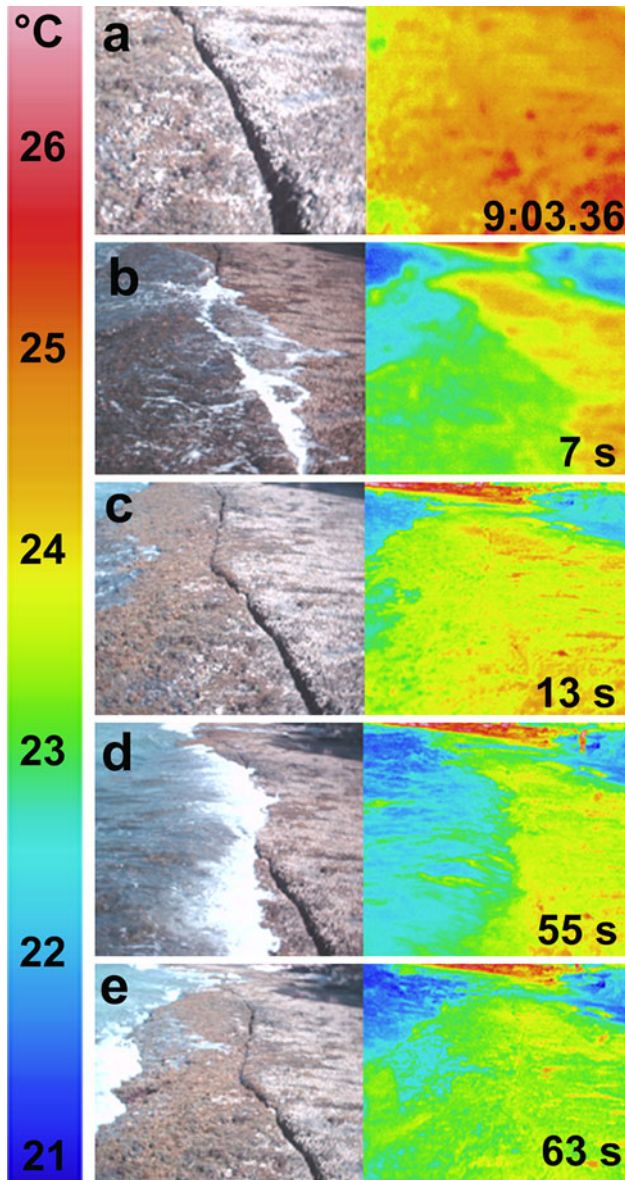


Fig. 6 Rapid temperature fluctuations during a series (a–e) of wave events captured with IR thermography (IR calibrated image on right simultaneously taken digital image on left). Coarse, pixel color calibrated to °C scale on right. Time stamp in corner of images is seconds that have elapsed from first image captured at 0903.36

are found along the Pacific coast of United States with loggers that mimic mussels. Shores with low tides that coincided with mid-day experience hotter temperatures (Helmuth et al. 2002) and shores with more wave action are cooler (Helmuth et al. 2006a). Daily temperatures in mussel beds in temperate areas fluctuate by ~11°C (Helmuth et al. 2006a), yet in Hawai'i, *P. sanctae-crucis* exposed reefs experience less temperature variation (up to 9°C). Further investigations that combine the rapid thermal assessment provided by IR thermography to the more long term conditions captured by mimic loggers could enhance

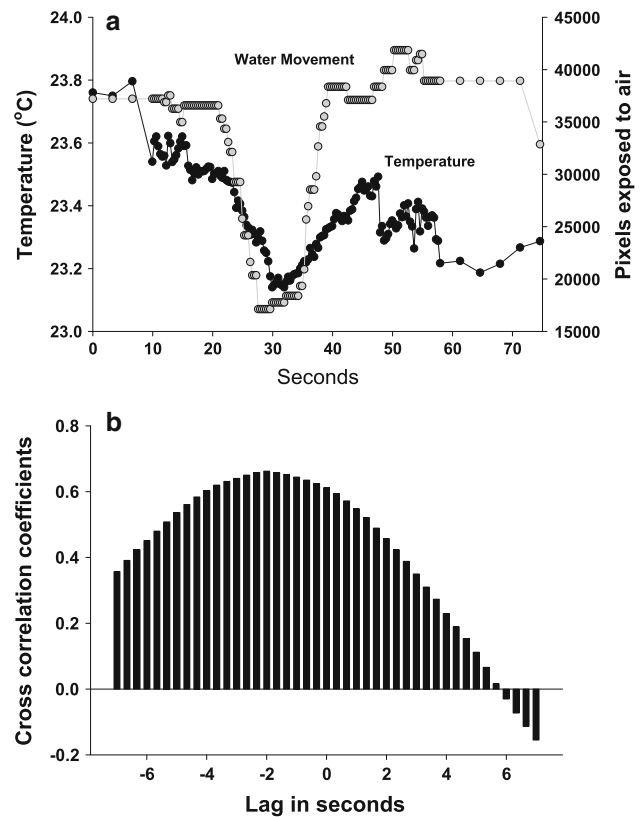


Fig. 7 Relationship between temperature and wave events. **a** is a plot of temperature with wave movement (measured as pixels exposed to air) in time. **b** shows the results of a cross correlation. Note temperature is 66% correlated to wave movement and lags behind the wave by 2 s

our predictions of thermal stress under hotter climates predicted to occur as a result of global climate change.

IR thermography reveals that, despite the hot conditions experienced by organisms on Hawaiian shores, select algal and invertebrate species occur in intertidal reefs, and either (1) tolerate excessive temperatures (e.g., *Echinolittorina hawaiiensis*), (2) possess physical characteristics that limit thermal stress (e.g., calcified species of *Liagora* spp. and *Padina sanctae-crucis*) that allow them to remain cooler than their immediate environment, or (3) occur in cooler microhabitats (e.g., *Siphonaria normalis*) that perhaps optimize performance. Macroalgae are commonly cooler than their habitats, possibly because of the retention of water and subsequent evaporative cooling of thalli. Two taxa that are consistently cooler than their habitats, *P. sanctae-crucis* and species of *Liagora*, possess whitish deposits of reflective calcium carbonate (Abbott 1999; Abbott and Huisman 2004; Beach et al. 2006) that may limit solar heating by increasing reflectance from calcified tissues. Alternately, the clumping morphology of species of *Liagora* and *Hydroclathrus clathratus* and the tightly growing monospecific stands of *P. sanctae-crucis* may limit desiccation and allow for evaporative cooling

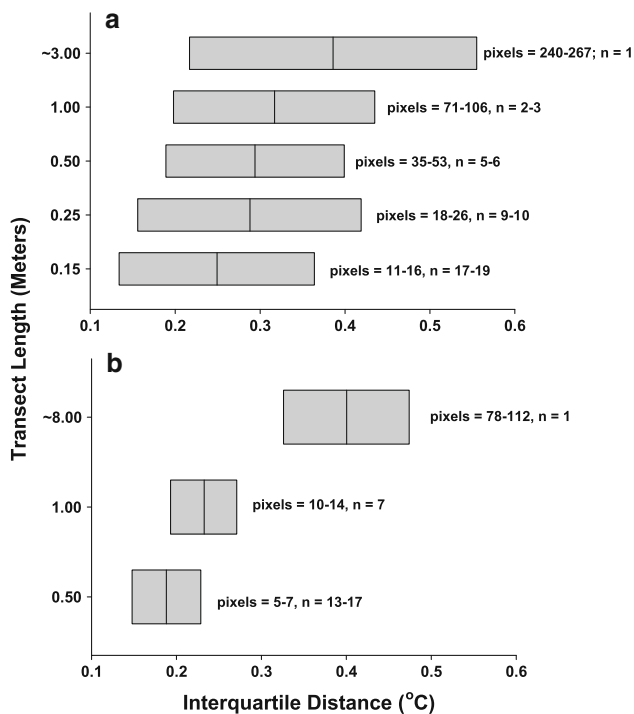


Fig. 8 Spatial variation in temperature found within *P. sanctaecrucis* habitat, expressed as interquartile distance, across **a** horizontal and **b** vertical transects of varying length on a low tide. Boxplots represent the 95% confidence interval around the mean determined from 5 photos. Note the number of pixels sampled vary with distance and due to parallax, pixel range varies between horizontal and vertical analyses. n, number of transects sampled per photo

(Bell 1995). Few studies have documented energy budget parameters for intertidal algae and morphological characteristics such as calcification can alter the amount of light absorbed by 23% lowering rates of maximum photosynthesis but defending against photoinhibition (Beach et al. 2006), and perhaps heat stress. Contrary to macroalgae and many other molluscs, it appears that the gastropods *Nerita picea* and *Cypraea mauritiana* and the echinoderms *Actinopyga mauritiana* and *Echinometra oblonga* endure tropical temperatures by favoring cooler habitats. Surface temperatures do not necessarily reflect the actual body temperatures of organisms (Lewis 1963), however, surface values provide insight into the types of temperatures these organisms must withstand. Further field and laboratory examinations with IR thermography at different shores combined with body temperatures may reveal more thermal specialists able to tolerate high temperatures or species with features that limit thermal stress.

Temperatures from IR thermography are similar to temperatures from waterproof sensors, yet data loggers are unable to match the spatial pixel scale detected by image based thermography. Additionally, numerous loggers and expense would be needed to replicate these thermography findings. Our spatial investigation into the variation over

set distances, within a habitat at this site, reveal that temperature can vary across the shore, and to conservatively reduce deviation to an approximate difference of ± 0.4 – 0.6°C , loggers should be placed 0.5–1.0 m apart. Therefore to precisely quantify temperature across a similar area as examined in this study ($20\text{ m} \times 8\text{ m} = 160\text{ m}^2$), at least 160 loggers ($160\text{ m}^2/1.0\text{ m} = 160$) are needed. Further quantitative sampling of aerial photos taken perpendicular to the shore with similar pixel to distance comparisons simultaneously correcting for emissivity are needed to clarify observed differences in temperature variation among horizontal and vertical areas of shore. Finally, thermography also allows for quick measurements of temperature over a vast area and the visualization of cooler and hotter microhabitats as wells as the co-occurrence of wave events without much effort. Previous studies interested in thermal “preferences” (Vermeij 1971; Garrity 1984; Wethey 1984) would physically measure the temperature with a probe across the habitat surrounding an organism, requiring more physical efforts. Our calculations and observations underscore the potential of IR thermography for rapid temperature assessments and the need to have an adequate number of loggers to precisely and accurately answer fine-scale to landscape scale research questions.

These data clearly demonstrate the potential of IR thermography as tool for ecologists. Not only can IR thermography document baseline conditions in the light of global climate change but it also could be used to investigate natural or other anthropogenic thermal disturbances. For instance, the rapidity and fine scale nature of this tool could allow scientists to assess the thermal impacts from wave altering jetties or piers, heating of habitats and organisms that result from oil spills, and the impacts to a community when cooling canopy is removed via herbivory, human harvest, or wave events.

IR thermography while useful does have some limitations. Emissivity of infrared energy is difficult to account for in a heterogenous environment like the intertidal zone. Measuring emissivity in situ requires considerable efforts. The use of thermocouples or probes in emissivity estimates is disadvantageous for the same reason IR thermography is preferred: (1) metal probes can heat and cool differently than their surroundings, (2) probing requires physical contact with organism and instrument, and (3) a probe senses the surfaces directly around it and thus a comparison of temperature from the two techniques is difficult given the pixel strength of IR thermography. IR thermography is best suited for rapid assessments and it is not ideal for long-term monitoring. Surface temperatures captured in images do not necessarily reflect body temperatures. In addition, while images are relatively easy to collect, parallax error needs to be accounted for and post

processing of images can be time-consuming. Despite these limitations, this tool provides exciting results. IR thermography allowed us to take a new look at thermal ecology on a tropical intertidal reef.

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