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Rocky intertidal temperature variability along the southeast coast of Australia: comparing data from *in situ* loggers, satellite-derived SST and terrestrial weather stations

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ABSTRACT: Predicting how both spatial and temporal variation in sea and air temperature influence the distribution of intertidal organisms is a pressing issue. We used data from satellites, weather stations and *in situ* loggers to test the hypothesis that satellite-derived sea surface temperatures (SSTs) and weather station air temperatures provide accurate estimates of ambient temperature variability on rocky intertidal shores for temporal (hourly for 1 yr) and spatial (10 m to 400 km) variation along the southeast coast of Australia. We also tested whether satellites and weather stations accurately detect the duration, frequency and number of extreme temperature events. Daily mean satellite SSTs and weather station air temperatures were significantly and strongly correlated with intertidal water and air temperatures, respectively (water: $r^2 = 0.62$, air: $r^2 = 0.63$). Nevertheless, depending on location, daily satellite SSTs were up to 6.7°C, and on average 1°C, higher than *in situ* water temperatures, while daily maximum air temperatures measured by weather stations were up to 23.2°C, and on average 4.2°C, lower than *in situ* air temperatures. At all locations, the frequency, duration and number of days greater than 30°C, as well as rates of temperature change, were all significantly lower when measured by weather stations. These differences suggest that satellite SSTs and weather stations are ineffective at capturing extremes in intertidal water and air temperature variability. We reinforce the argument that *in situ* measurements that focus on biologically relevant variation are the only legitimate means of predicting the effects of temperature change on intertidal taxa.

KEY WORDS: Temperature data logger · Intertidal invertebrate · Remote sensing · Climate change · Extreme temperature events

INTRODUCTION

As air and sea temperatures continue to rise, remote sensing techniques, such as satellite-derived sea surface temperatures (SSTs), are becoming increasingly important tools in assessing how changes in temperature will influence the geographic distributions of species (Gilman et al. 2006, Helmuth 2009). It is well known, for example, that large-scale ocean temperature variability significantly influences physiological and demographic processes of many marine invertebrates, fish and primary producers, with shifts in species range limits associated with increased sea temperatures (Zacherl et al. 2003, Gilman 2006, Lima et al. 2006, Herbert et al. 2007, Last et al. 2011). Invertebrates living in intertidal habitats may be particularly vulnerable to fluctuating temperatures as they have to adapt to temperature extremes in both the terrestrial and marine environment (Fields et al. 1993). However, at relatively small spatial scales, such as across the vertical extent of a rocky intertidal shore, body temperatures of sessile and sedentary invertebrates can be determined by the timing and duration of aerial exposure (Helmuth et al. 2002), and studies have shown that air temperatures during low tide have greater effects on the physiological processes of both intertidal

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mussels and barnacles compared to water temperatures during high tide (Hofmann & Somero 1995, Somero 2002). Therefore, both air and water measurements are required to characterise the thermal environment of rocky intertidal shores.

Several ecological studies have previously used satellite-derived SSTs to characterise the thermal environment of intertidal habitats (Barry et al. 1995, Broitman et al. 2001, 2005, 2008, Lagos et al. 2005, Herbert et al. 2007, Blanchette et al. 2008). Studies have shown that satellite-derived SSTs are highly correlated with daily *in situ* measurements of SST (Keogh et al. 1999, Barton & Pearce 2006, Smale & Wernberg 2009); nevertheless, satellite-derived SSTs are unlikely to reflect the variability of the temperature regimes experienced by the vast majority of rocky intertidal organisms (Helmuth & Hofmann 2001, Gilman et al. 2006). Indeed, Helmuth & Hofmann (2001) found that aerial body temperatures of the mussel *Mytilus californianus* varied independently of water temperatures and suggested that water temperatures by themselves should not be used as a measure of temperature stress for intertidal organisms.

Numerous factors operating across both large and small spatial scales pose difficulties when using remote sensing to estimate *in situ* temperatures on rocky intertidal shores. These include tidal dynamics and their variability among geographic locations (Helmuth et al. 2002, 2006, Harley 2008), degree of wave exposure and height on shore (Harley & Helmuth 2003), as well as topographic orientation and slope of substratum (Helmuth & Hofmann 2001, Harley 2008). As a result of this natural variability, even hourly temperature measurements commonly recorded by terrestrial weather stations and daily composite SST produced by satellite images are unlikely to detect acute (extreme) or chronic (continually stressful) temperature events, which are more likely to influence the mortality, growth and reproduction of intertidal organisms (Denny et al. 2006, 2009, Harley & Paine 2009, Helmuth et al. 2010).

Southeast Australia has been identified as being particularly vulnerable to climate change and hosts many subtropical, warm-temperate and cold-temperate species (Hughes 2003, Poloczanska et al. 2007, Edgar 2008). SSTs along the southeast coast of Australia are largely influenced by the East Australian Current (EAC), which flows most strongly in the summer months and weakens during winter, usually deflecting offshore around Laurieton (31° 39′ S, 152° 48′ E) in northern New South Wales (NSW), producing large warm-core eddies that penetrate the coastal waters of southern NSW and eastern Victoria (Huyer et al. 1988, Roughan & Middleton 2004). These southward-flowing warm-core eddies produce latitudinal temperature gradients and are expected to increase in strength, penetrating further south, under future climate change scenarios (Roughan & Middleton 2004, Lough 2009, Ridgway & Hill 2009). Many species have their northern or southern geographical range limits within this region (Knox 1963, O'Hara & Poore 2000, Hidas et al. 2007, 2010, see also Ayre et al. 2009, Lathlean et al. 2010), and therefore, we might expect many of these species' range limits to shift with response to climate change. However, there is a significant gap in our understanding of the typical spatial and temporal temperature regimes experienced by intertidal organisms along the southeast coast of Australia, and researchers in the past have simply used satellite- or buoy-derived SST as a measure of large-scale temperature variability.

This study provides a detailed assessment of both large and small-scale *in situ* rocky intertidal temperature variability along the southeast coast of Australia. We first determined the extent to which nearshore SSTs derived from satellites and air temperatures derived from terrestrial weather stations can be used as appropriate surrogates of rocky intertidal water and air temperatures, respectively. We expected that water and air temperatures sensed remotely would be strongly correlated with values estimated using *in situ* loggers, but that absolute values would likely differ. We then show that small-scale (i.e. local) variability in air and water temperature, measured by *in situ* data loggers, better characterises the thermal environment experienced by intertidal organisms. Our objective here was to test whether temperature variability measured over both fine spatial (pairs of loggers separated by metres at 3 tidal heights) and fine temporal scales (10 min intervals) can reveal demographically important temperature variation that cannot be estimated using remote sensing.

MATERIALS AND METHODS

Study region

The study region spanned more than 400 km and included 4 rocky intertidal shores along the southeast coast of Australia: Garie Beach (34° 10′ 38.05″ S, 151° 03′ 57.77″ E), Kiama (34° 40′ 07.47″ S, 150° 51′ 25.66″ E), Bermagui (36° 25′ 35.64″ S, 150° 05′ 01.84″ E) and Mallacoota (37° 34′ 39.87″ S, 149° 46′ 01.58″ E; Fig. 1). Garie Beach and Bermagui had slightly sloping platforms

(10 to 20°), while Kiama and Mallacoota had steeper gradients (20 to 30°). All locations experience a mixed semi-diurnal tidal regime with a tidal range of approximately 2 m. Previous studies have shown that the degree of wave exposure can significantly influence temperature variability at a site (Harley & Helmuth 2003, Fitzhenry et al. 2004, Denny et al. 2006); therefore, locations were chosen which have a north to northeast orientation, and all 4 experience similar levels of wave exposure (J. Lathlean pers. obs.). All locations support similar benthic communities within the mid-shore region largely dominated by the barnacles *Tesseropora rosea* and *Catomerus polymerus*, the gastropods *Bembicium nanum, Nerita melanotragus* and *Morula marginalba*, the limpets *Cellana tramoserica* and *Patelloida latistrigata*, and the macroalgae *Hormosira banksii*, *Porphyra lucasii*, *P. columbina* and *Corallina officinalis* (Underwood et al. 1983).

In situ logger data

To determine large-scale spatial variability in air and water temperatures among the 4 rocky shore locations, TidbiT® v2 Temp data loggers (Onset Stowaway logger, model UTBI-001, accuracy ±0.2°C) were deployed within the mid-intertidal zone (0.8 to 1 m above mean low water mark and 25 to 50 cm away from biota) at each of Garie Beach, Kiama, Bermagui and Mallacoota and continuously recorded both air and water temperatures at 10 min intervals from mid-April 2008 until June 2009. Loggers accurately recorded temperatures within ±0.2°C. To assess temperature variability within a single location, additional loggers were deployed at 2 sites separated by approximately 50 m and across 3 intertidal heights within Garie Beach in February 2010. Air and sea surface temperature profiles between loggers at equivalent tidal heights were significantly correlated and produced average differences in air and water temperatures no greater than 2.6°C and 0.6°C, respectively, over an extended period from February to September 2010 (see Fig. S1 and Table S1 in the Supplement at www.int-res.com/articles/suppl/m439p083_supp.pdf). Denny et al. (2006) showed that intertidal temperatures can vary with differences in substrate aspect and orientation. Therefore, we took a conservative approach to estimating temperature variability by attaching all loggers to horizontal or slightly sloping rock surfaces with a north to northeast orientation.

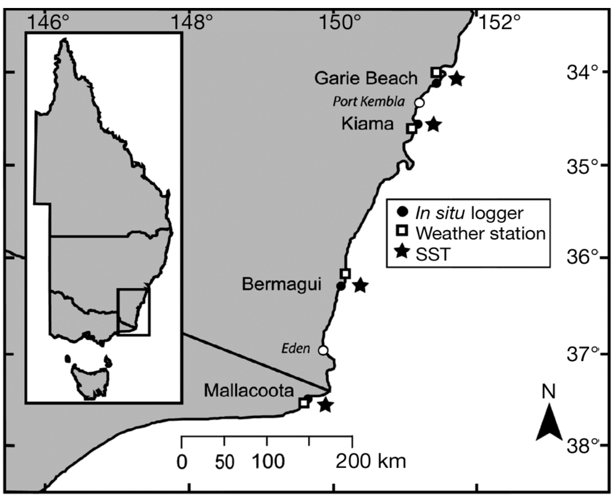

Fig. 1. Four rocky intertidal shores along the southeast coast of Australia showing approximate locations of *in situ* logger, weather station and satellite sea surface temperature (SST) collection points. Port Kembla and Eden represent locations where tidal data were obtained

To separate data logger temperatures into air and water temperatures, we used methods of estimating 'effective shore level' (ESL) similar to those of Harley & Helmuth (2003). Here, a sudden drop in temperature by at least 3°C within 20 min during the daytime indicates when the logger is first inundated with the incoming tide. The time of this sudden drop is then matched with tidal heights recorded by buoys to give an ESL for each logger. Tidal data were obtained from either the Australian Bureau of Meteorology's National Tidal Centre (www.bom.gov.au/oceanography/projects/ntc/ntc.shtml) or Manly Hydraulics Laboratory for buoys at Port Kembla (34° 29′ S, 150° 55′ E), Bermagui (36° 25′ S, 150° 4′ E) or Eden (37° 4′ S, 149° 54′ E), and hourly temperature data recorded by loggers were compared with hourly tidal data recorded by the closest of these buoys (see Fig. 1). Temperatures that were recorded when the tidal height was below ESL values were deemed to be air temperatures, whereas temperatures recorded when the tidal height was above these values were deemed to be water temperatures. We applied a 0.3 m buffer zone above and below the ESL for each logger and excluded data that were obtained within this buffer zone because wave splash may also significantly influence whether a logger is submerged. This approach ensured that temperatures recorded during the changing of the tides accurately represent air or water temperatures. Once logger data were separated into air and water temperatures, daily mean, maxima and minima were calculated for both air and water temperatures at each of the 4 locations to characterise temporal and spatial temperature variability. Additionally, air and water temperature frequency distributions were used to specifically compare temperature variability across the 4 locations.

Satellite SST and terrestrial weather station data

Comparisons were made between logger-derived *in situ* intertidal water temperatures and satellite-derived SSTs at all 4 locations from 16 April 2008 to 6 June 2009. Satellite SST readings recorded twice every 24 h were obtained from the advanced very high resolution radiometer (AVHRR) taken from the NOAA series of polar orbiting satellites through the Integrated Marine Observing System web portal (www.marine.csiro.au/remotesensing/imos/aggregator.html). To standardise comparisons between *in situ* loggers and satellite-derived SSTs across the 4 locations, daily SST was acquired for single fixed pixels (representing an area of ~2 × 2 km) approximately 7 km offshore for each of the 4 locations (Fig. 1). Choosing pixels 7 km offshore allowed standardised SST measurements among locations and maintained an equivalent offshore distance throughout the sampling region. Several single-day composites of SST were missing due to cloud cover at the time images were being taken by satellites, and therefore no comparisons could be made with *in situ* loggers on these days. Using these data, we correlated daily SST composites with daily mean water temperatures recorded by *in situ* temperature loggers within the mid-intertidal zone. Monthly maximum, minimum and mean satellite temperatures were also correlated with monthly maximum, minimum and mean logger temperatures to determine whether satellite SSTs were capable of detecting extreme temperature events that are often more biologically relevant than daily means (Denny et al. 2009).

Comparisons between air temperatures derived from *in situ* intertidal data loggers and terrestrial weather stations were also done for all 4 locations. Terrestrial weather station data were obtained from the Australian Bureau of Meteorology for coastal stations closest to the 4 study locations. Consequently, logger air temperatures recorded at Garie Beach, Kiama, Bermagui and Mallacoota were correlated with weather station air temperatures at Sydney Airport (27.8 km), Kiama Headland (<0.5 km), Narooma (24.3 km) and Mallacoota (<0.5 km), respectively (distances between loggers and weather stations shown in brackets). Each weather station recorded air temperatures every 3 h, which allowed daily maximum, minimum and mean temperatures to be calculated and correlated with daily maximum, minimum and mean logger air temperatures.

Biologically relevant temperature variation

Demographic patterns of rocky intertidal invertebrates can often be significantly influenced by extreme temperature events, and invertebrates respond depending on the thermal characteristics leading up to and during the extreme temperature event (Denny et al. 2009, Mislan et al. 2009). Therefore, to further assess the ability of terrestrial weather stations to record biologically relevant estimates of rocky intertidal temperature, the number, duration and frequency of extreme temperature events recorded by *in situ* loggers at all 4 locations were compared with the same parameters recorded by nearby weather stations during the summer of 2008/09. Here, number refers to the number of days where air temperatures reached 30°C, duration refers to the total time temperatures stayed at or above 30°C, similar to degree heating hours (DHH) used by Helmuth et al. (2010), and frequency (expressed as its inverse) refers to the average time between 30°C events. These parameters were chosen based on findings of Denny et al. (2006, 2009), which showed that the number, duration and frequency of extreme temperature events are just as important as absolute temperatures when assessing how intertidal invertebrates respond to increased temperatures. Temperatures over 30°C were classified as extreme because previous studies have shown this temperature to be the approximate threshold for heat shock protein (Hsp) production in *Mytilus* spp. found at similar latitudes as in the present study (Halpin et al. 2004).

The rates at which temperatures rise and fall are also important parameters that can influence an organism's ability to respond to thermal stress. For intertidal organisms, the most rapid change in temperature is most likely to occur during the changing of the tides (Helmuth & Hofmann 2001, Harley & Helmuth 2003). Therefore, we used continuous *in situ* logger data (i.e. not separated into air and water temperatures) with 10 min sampling intervals to compare the frequency of rapid heating events measured by *in situ* loggers and the remote sensing methods at Garie Beach, Kiama and Bermagui during the summer of 2008/09. For *in situ* data, a rapid heating event was defined as either a rise of 15°C or more within 4 h, 10°C or more within 3 h, or 5°C or more within 3 h. For equivalent comparisons to be made using remote sensing methods, a rapid heating event was defined as differences of 15, 10 or 5°C between daily satellite SSTs and daily maximum air temperatures recorded by weather stations. These rates were somewhat arbitrarily defined based on the most extreme rate of heating (i.e. 18°C within 4 h) being recorded by a logger at Garie Beach during the time of interest.

Data analysis

Pearson's r values were used to indicate the strength of the correlation between (1) logger water temperature and satellite SST, (2) logger air temperature and weather station air temperature and (3) loggers at 2 sites within Garie Beach across the 3 different intertidal heights with differences being tested with paired *t*-tests. Correlations and paired *t*-tests could only be undertaken for approximately 9 mo at Mallacoota because the logger was damaged.

A 2-way ANOVA using log (x+1) transformed data was used to test for statistically significant differences in daily means, maxima and minima of air and water temperatures across 3 of the rocky shore locations (from June 2008 to May 2009; Mallacoota was excluded from ANOVA due to incomplete data), and time. Where significant differences were found, Student-Neuman-Keuls (SNK) tests were used to determine which locations or seasons had significantly different temperatures. Due to natural variability in weather and the tidal cycle, some loggers appeared to remain either emerged or submerged for more than 24 h. Consequently, several days during the sampling period did not record either air and water temperatures and were therefore excluded from analysis.

RESULTS

Comparisons of temperature variability at geographic scales

Air temperatures generally declined with increasing latitude (Tables 1 & 2). For example, mean ± SD daily maximum *in situ* air temperatures, averaged

Table 1. Seasonal and annual variation in daily mean, maximum and minimum air and water temperatures (± SD) from *in situ* temperature data loggers within the mid-intertidal zone at the 4 study locations between June 2008 and May 2009. Max/Min represents the highest and lowest temperatures recorded at each location during a specific season

	2008				2009				Annual	
	Winter (June–Aug)		Spring (Sept–Nov)		Summer (Dec–Feb)		Autumn (Mar–May)		2008/09	
	Mean	Max/Min	Mean	Max/Min	Mean	Max/Min	Mean	Max/Min	Mean	Max/Min
Air temperature										
Daily mean										
Garie Beach	15.4 ± 1.8		18.2 ± 2.8		22.3 ± 2.7		20.4 ± 2.5		19.1 ± 3.6	
Kiama	14.6 ± 1.8		17.8 ± 2.5		21.7 ± 2.4		20.3 ± 2.4		18.6 ± 3.5	
Bermagui	13.0 ± 2.0		15.9 ± 2.6		20.2 ± 2.3		19.0 ± 2.6		17.0 ± 3.7	
Mallacoota	11.6 ± 1.9		15.8 ± 3.7							
Daily maximum										
Garie Beach	18.6 ± 3.0	30.3	24.4 ± 7.8	45.5	29.4 ± 7.7	50.8	25.9 ± 6.8	47.9	24.5 ± 7.7	50.8
Kiama	19.1 ± 2.9	28.7	25.1 ± 6.4	40.1	27.8 ± 5.5	42.0	25.3 ± 5.4	42.3	24.3 ± 6.1	42.3
Bermagui	16.8 ± 3.1	27.9	20.4 ± 4.9	32.5	24.2 ± 4.4	37.0	22.6 ± 3.5	32.6	21.0 ± 4.9	37.0
Mallacoota	16.3 ± 3.6	29.4	23.8 ± 7.1	40.8						
Daily minimum										
Garie Beach	12.3 ± 2.6	7.6	14.5 ± 2.2	8.2	18.0 ± 1.4	14.1	17.0 ± 2.5	10.4	15.4 ± 3.2	7.6
Kiama	10.2 ± 2.6	5.3	13.2 ± 2.5	7.1	17.7 ± 1.6	14.2	16.7 ± 2.7	9.5	14.4 ± 3.8	5.3
Bermagui	10.0 ± 2.5	5.5	12.5 ± 2.6	6.2	17.2 ± 1.9	12.5	16.1 ± 2.9	8.8	13.9 ± 3.8	5.5
Mallacoota	8.4 ± 2.1	3.8	10.6 ± 2.7	5.8						
Water temperature										
Daily mean										
Garie Beach	16.8 ± 1.5		16.7 ± 1.3		20.2 ± 1.5		20.9 ± 1.5		18.6 ± 2.4	
Kiama	16.9 ± 2.1		16.3 ± 1.4		19.5 ± 1.5		21.4 ± 2.0		18.7 ± 2.8	
Bermagui	15.1 ± 1.2		16.1 ± 1.2		19.2 ± 1.1		19.4 ± 1.1		17.4 ± 2.2	
Mallacoota	13.8 ± 0.9		15.7 ± 1.4							
Daily maximum										
Garie Beach	17.5 ± 1.8	23.1	17.3 ± 1.4	21.1	20.9 ± 1.6	25.3	21.7 ± 1.9	29.6	19.4 ± 2.6	29.6
Kiama	17.9 ± 2.4	22.6	17.1 ± 1.6	22.5	20.1 ± 1.6	27.0	22.4 ± 2.4	29.6	19.5 ± 2.9	29.6
Bermagui	15.2 ± 1.2	17.5	16.3 ± 1.2	19.4	19.5 ± 1.1	21.5	19.6 ± 1.1	21.8	17.6 ± 2.3	21.8
Mallacoota	13.9 ± 1.0	15.9	15.9 ± 1.6	18.7						
Daily minimum										
Garie Beach	16.2 ± 1.6	13.5	16.2 ± 1.4	12.7	19.4 ± 1.6	16.1	20.3 ± 1.4	17.2	18.1 ± 2.4	12.7
Kiama	16.0 ± 2.1	11.2	15.4 ± 1.9	10.3	18.8 ± 1.7	15.1	20.5 ± 2.0	13.6	17.8 ± 2.8	10.3
Bermagui	14.9 ± 1.3	13.3	15.9 ± 1.3	13.5	18.8 ± 1.2	14.1	19.1 ± 1.2	16.6	17.2 ± 2.2	13.3
Mallacoota	13.7 ± 0.9	12.3	15.4 ± 1.3	13.3						

Table 2. Results of ANOVA for the differences in daily mean, maximum and minimum air and water temperatures (log [x+1] transformed) among 3 locations across 4 seasons. Data from Mallacoota were only available until 10 December 2008 and therefore not included in the analysis

Source	df	SS	*F*	p
Air temperature				
Daily mean				
Location	2	2.65	85.01	<0.0001
Season	3	23.28	497.91	<0.0001
Location × Season	6	0.24	2.59	0.0170
Error	1068	16.65		
Daily maximum				
Location	2	4.57	55.20	<0.0001
Season	3	20.92	168.28	<0.0001
Location × Season	6	0.35	1.40	0.2108
Error	1068	44.25		
Daily minimum				
Location	2	2.35	40.17	<0.0001
Season	3	38.39	433.42	<0.0001
Location × Season	6	0.96	5.46	<0.0001
Error	1068	31.21		
Water temperature				
Daily mean				
Location	2	0.66	53.17	<0.0001
Season	3	9.89	442.87	<0.0001
Location × Season	6	0.29	7.09	<0.0001
Error	805	4.97		
Daily maximum				
Location	2	1.40	99.29	<0.0001
Season	3	7.73	364.93	<0.0001
Location × Season	6	0.35	8.36	<0.0001
Error	805	5.69		
Daily minimum				
Location	2	0.21	13.88	<0.0001
Season	3	8.55	368.83	<0.0001
Location × Season	6	0.23	4.88	<0.0001
Error	805	6.22		

over the 12 mo sampling period, were 24.5 ± 7.7, 24.3 ± 6.1 and 21.0 ± 4.9°C at Garie Beach, Kiama and Bermagui, respectively (Table 1), with maximum air temperatures of 50.0, 42.3 and 37.0°C at Garie Beach, Kiama and Bermagui, respectively (Table 1). Air temperatures recorded by *in situ* loggers also varied consistently with latitude when seasons were analyzed separately (SNK test for interactions, see Table 2). Daily maximum air temperatures recorded by weather stations averaged for the 12 mo sampling period were 21.5 ± 4.9, 20.0 ± 3.9, 18.4 ± 3.4 and 18.1 ± 4.5°C at Garie Beach, Kiama, Bermagui and Mallacoota, respectively, with maximum air temperatures of 38.3, 37.5, 33 and 38.4°C, respectively. *In situ* logger air temperatures were highly variable across all 4 locations from June to November 2008, suggesting that air temperature variability does not vary with latitude (Fig. 2).

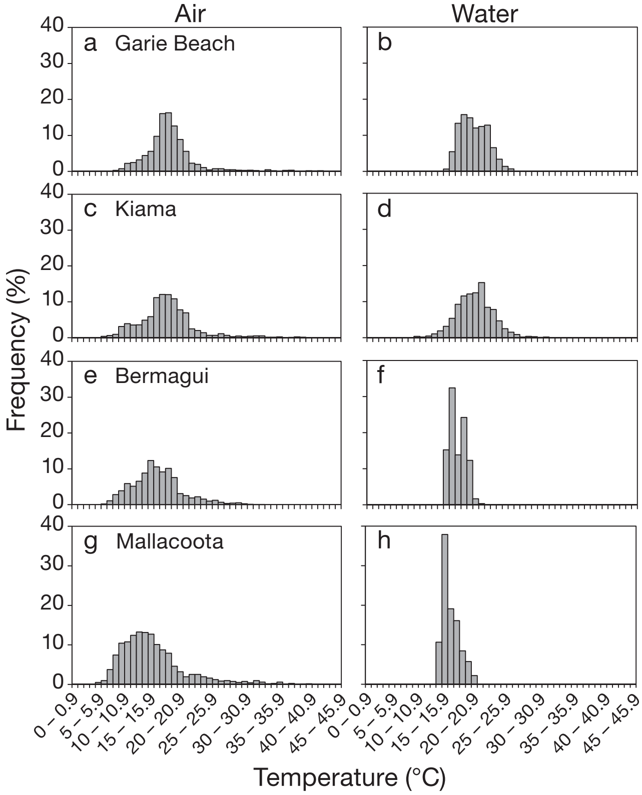

Fig. 2. *In situ* logger air and water temperature frequency distributions at the 4 study locations from 1 June to 30 November 2008. Locations are arranged from north to south

In contrast to air temperatures, *in situ* loggers only recorded a weak latitudinal decline in water temperatures, with loggers at Garie Beach and Kiama, separated by approximately 60 km, recording similar intertidal water temperatures that were both significantly different from intertidal water temperatures recorded at Bermagui, which is approximately 210 km south of Kiama (Fig. 3, Table 2). For example, the annual daily mean water temperatures recorded by *in situ* data loggers at Garie Beach, Kiama and Bermagui were 18.7 ± 2.4, 18.7 ± 2.8 and 17.4 ± 2.2°C, respectively (Table 2). However, intertidal water temperatures appeared to be consistently more variable at Garie Beach and Kiama than they were at Bermagui and Mallacoota, and this was not detected by satellite SST data (Figs. 2 & 3).

Satellite versus *in situ* logger water temperatures

Comparison of SST and *in situ* logger estimates of water temperature revealed that although the 2 sets of measures were always significantly correlated, they typically produced significantly different esti-

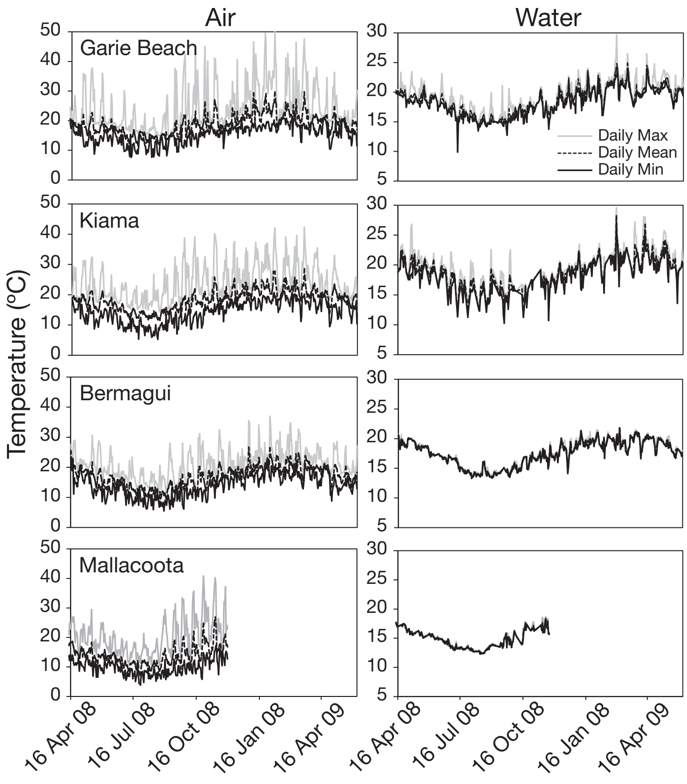

Fig. 3. Daily mean, maximum and minimum air and water temperatures recorded by *in situ* data loggers at the 4 study locations from 16 April 2008 to 6 June 2009 (Mallacoota data were only available until 10 December 2008). Note different scales on *y*-axes

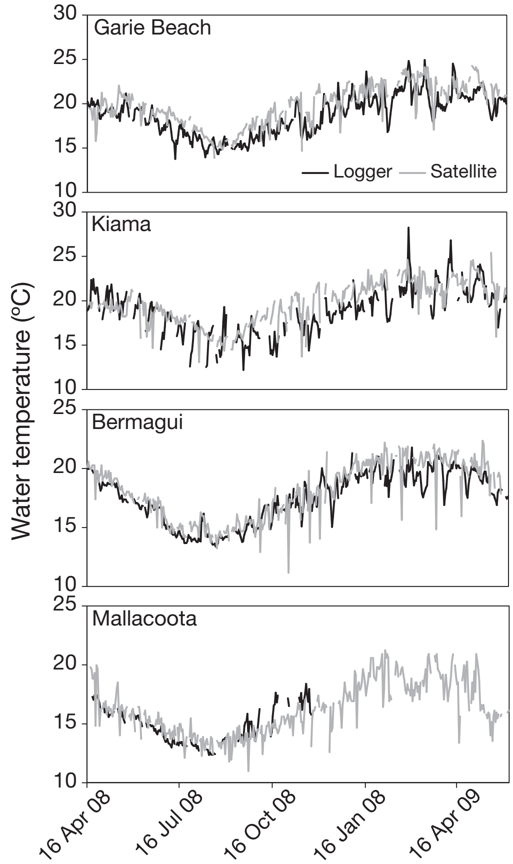

Fig. 4. Daily mean water temperatures from *in situ* loggers within the mid-intertidal zone at each of the 4 study locations and satellite-derived SSTs approximately 7 km offshore of each of the 4 study locations from 16 April 2008 to 6 June 2009 (Mallacoota data were only available until 10 December 2008). Note different scales on *y*-axes for Bermagui and Mallacoota

mates of absolute temperatures. For example, at all 4 study locations, daily satellite SSTs 7 km offshore were significantly correlated with daily mean water temperatures recorded by *in situ* loggers within the mid-intertidal zone, although the correlation coefficient varied substantially among locations, ranging from 0.50 at Kiama to 0.77 at Bermagui (Fig. 4, Table 3). Similarly, means, maxima and minima of monthly satellite SSTs were significantly correlated with water temperatures estimated by intertidal loggers, except for the most southerly location, Mallacoota (Fig. 4, Table 3). The strength of correlations between monthly measurements varied considerably more among locations than correlations between daily means (Table 3).

Although daily satellite SSTs and daily logger water temperatures were strongly correlated, absolute estimates of water temperature were significantly different from each other, with the exception of temperatures recorded at Mallacoota (Table 3). Daily satellite SSTs were generally greater than logger water temperatures, with maximum differences at times reaching 6.7°C, but on average these differences were less than ~1°C across all 4 locations and decreased with increasing latitude (Fig. 4, Table 3). Paired *t*-tests also revealed that loggers often recorded significantly higher monthly mean, maximum and minimum temperatures compared to satellites, with maximum and mean differences reaching 6°C and 1.3°C, respectively (Table 1).

Weather station versus *in situ* logger air temperature

At all 4 locations, daily means, maxima and minima of air temperature recorded by *in situ* loggers and weather stations were all significantly correlated (Fig. 5, Table 4), although these correlations were substantially weaker than those between daily satellite SSTs and intertidal water temperatures

Table 3. Outcome summary of paired *t*-tests and Pearson correlations comparing daily means and monthly means, maxima and minima of water temperatures, derived from *in situ* loggers within the mid-intertidal zone at the 4 study locations with satellite-derived SSTs approximately 7 km offshore of each location from 16 April 2008 to 6 June 2009 (see Fig. 3). Mallacoota data were only available until 10 December 2008. Mean and max. difference refers to the average and maximum differences between water temperatures measured by *in situ* loggers and satellites. *$p < 0.001$, **$p < 0.05$

	df	Difference (°C) Mean	Max.	*t*	p	Pearson's correlation (r)
Daily means						
Garie Beach	363	1.03	4.98	13.55	<0.001	0.64*
Kiama	266	0.81	6.67	6.75	<0.001	0.50*
Bermagui	341	0.64	6.24	10.07	<0.001	0.77*
Mallacoota	147	0.04	3.20	0.40	0.655	0.58*
Monthly means						
Garie Beach	12	1.19	1.80	10.95	<0.001	0.97*
Kiama	12	1.05	2.68	3.61	0.004	0.80*
Bermagui	12	0.59	1.28	5.50	<0.001	0.98*
Mallacoota	6	0.20	1.31	0.59	0.578	0.63*
Monthly maxima						
Garie Beach	12	0.49	1.90	1.73	0.110	0.89*
Kiama	12	0.05	4.44	0.08	0.941	0.55**
Bermagui	12	0.78	2.20	4.44	0.001	0.93*
Mallacoota	6	0.06	1.90	1.06	0.919	0.41
Monthly minima						
Garie Beach	12	0.63	3.15	1.94	0.077	0.68*
Kiama	12	1.29	6.03	2.51	0.027	0.53**
Bermagui	12	1.02	2.72	2.68	0.020	0.52**
Mallacoota	6	1.26	2.70	3.33	0.016	0.36

Table 4. Outcome summary of paired *t*-tests and Pearson correlations comparing daily means, maxima and minima of air temperatures derived from *in situ* loggers within the mid-intertidal zone at the 4 study locations with air temperatures obtained by terrestrial weather stations no more than 28 km away from 16 April 2008 to 6 June 2009 (see Fig. 4). Mallacoota data were only available until 10 December 2008. Mean and max. difference refers to the average and maximum differences between air temperatures measured by *in situ* loggers and weather stations. *$p < 0.001$

	df	Difference (°C) Mean	Max.	*t*	p	Pearson's correlation (r)
Daily means						
Garie Beach	416	1.02	9.56	7.84	<0.0001	0.60*
Kiama	416	1.47	7.44	13.69	<0.0001	0.62*
Bermagui	410	0.08	19.20	0.73	0.4671	0.60*
Mallacoota	228	1.53	7.71	12.41	<0.0001	0.69*
Daily maximum						
Garie Beach	416	2.98	23.19	10.34	<0.0001	0.39*
Kiama	416	4.23	18.77	16.70	<0.0001	0.27*
Bermagui	410	2.59	21.00	12.46	<0.0001	0.26*
Mallacoota	228	3.90	18.17	12.82	<0.0001	0.49*
Daily minimum						
Garie Beach	416	0.73	10.32	5.02	<0.0001	0.54*
Kiama	416	0.10	7.42	1.11	0.2688	0.73*
Bermagui	410	1.50	18.40	12.53	<0.0001	0.61*
Mallacoota	228	1.03	8.30	10.72	<0.0001	0.76*

(cf. Tables 3 & 4). With the exception of minimum and mean air temperatures at Kiama and Bermagui, respectively, *in situ* loggers consistently recorded significantly higher daily air temperatures than weather stations (Fig. 5), with differences most pronounced for daily maximum air temperatures (Table 4). For example, across the 4 locations, daily maximum air temperatures recorded by *in situ* loggers were on average 2.6 to 4.2°C higher than daily maximum air temperatures recorded by weather stations (Fig. 5, Table 4). In contrast, daily minimum air temperatures recorded by *in situ* loggers were on average only 0.1 to 1.5°C higher than daily minimum air temperatures recorded by weather stations. Maximum differences in mean, maximum,and minimum air temperatures recorded by *in situ* loggers and weather stations were 19.2, 23.2 and 18.4°C, respectively, which are considerably greater than similar comparisons of *in situ* logger water temperatures and satellite SSTs (cf. Tables 3 & 4).

Biologically relevant temperature variation

Regardless of latitude, *in situ* loggers recorded a considerably greater number, frequency and duration of extreme temperature events compared to nearby weather stations (Table 5). For example, the *in situ* logger at Garie Beach recorded 29 and 44 days where temperatures reached 35 and 30°C, respectively; in comparison, weather stations detected only 2 and 19 days reaching 35 and 30°C, respectively. The number, frequency and duration of extreme temperature events also increased with decreasing latitude, indicating that northern locations may be more thermally stressful for intertidal invertebrates. For example, the number of days where temperatures reached 35°C decreased

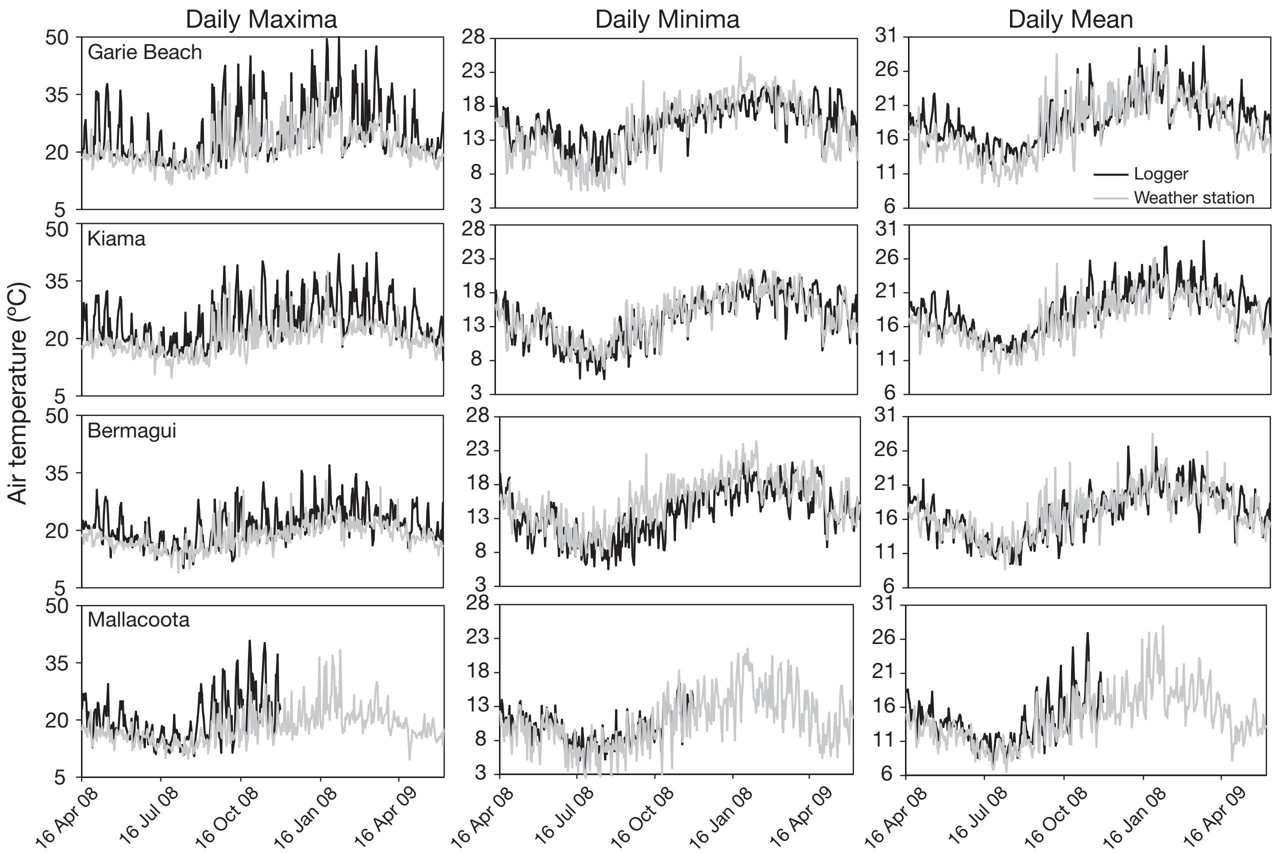

Fig. 5. Daily air temperatures from *in situ* loggers within the mid-intertidal zone and weather station temperatures at each of the 4 study locations from 16 April 2008 to 6 June 2009 (Mallacoota data were only available until 10 December 2008). Note different scales on *y*-axes

Table 5. Comparison of biologically important temperature parameters measured by an *in situ* data logger within the mid-intertidal zone at Garie Beach, Kiama and Bermagui with nearby terrestrial weather stations during the summer of 2008/09. 30°C temperature events were classified as any day where air temperatures reached 30°C. Data from Mallacoota were only available until 10 December 2008 and therefore not included in the analysis

	No. days max. temp >35°C	No. days max. temp >30°C	Duration (h above 30°C)	Frequency (average time between 30°C events, h ± SD)
Garie Beach				
In situ data logger	29	44	111	42.8 ± 55.7
Weather station	2	19	105	86.3 ± 99.6
Kiama				
In situ data logger	15	44	95	43.2 ± 45.9
Weather station	1	6	24	255 ± 206.6
Bermagui				
In situ data logger	3	17	29	123.1 ± 105
Weather station	0	1	3	–

from 29 to 15 to 3 and the total number of hours spent above 30°C decreased from 111 to 95 to 29 at Garie Beach, Kiama and Bermagui, respectively. *In situ* loggers also recorded a considerably greater number of rapid heating events compared to those recorded by weather stations and satellites across all locations (Table 6). For example, at Garie Beach the *in situ* logger recorded 24 days where temperatures increased by over 15°C within 4 h, whereas weather stations and satellites only recorded 2. Logger data revealed that heating rates also varied with latitude (Table 6). For example, the number of days where temperatures increased by more than 15°C within 4 h decreased from 24 to 10 to 5 at Garie Beach, Kiama and Bermagui, respectively.

Table 6. Number of rapid heating events recorded by *in situ* data loggers and remote sensing devices among 3 of the study locations during the summer of 2008/09. Heating rates were determined by the difference in daily SSTs and daily maximum air temperatures recorded by weather stations. Data from Mallacoota were only available until 10 December 2008 and therefore were not included in the analysis

	No. days when temp. increased by more than		
	15°C within 4 h	10°C within 3 h	5°C within 3 h
Garie Beach			
In situ data logger	24	40	62
Weather station and satellite	2	15	45
Kiama			
In situ data logger	10	34	74
Weather station and satellite	1	5	12
Bermagui			
In situ data logger	5	16	50
Weather station and satellite	0	2	11

DISCUSSION

The strong correlations that we detected between daily or monthly temporal variation in temperatures estimated by both satellite and weather station data and *in situ* intertidal temperature loggers provides superficial validation of the use of remote sensing to characterise the intertidal environment. However, even estimating variation at these coarse scales, remotely sensed and *in situ* estimates of air and water temperature at times differed by up to 23.2 and 6.7°C, respectively. Our results also show that the use of satellites and weather stations as proxies of intertidal temperatures significantly underestimate biologically important extreme temperature events.

Temperature variability at geographic scales

Excluding the most southern location, *in situ* temperature variability among locations was shown to be highly variable, with average air and water temperatures generally declining with latitude. However, *in situ* air temperatures recorded at Mallacoota, the most southern location, appeared greater and more variable than temperatures recorded at Bermagui, suggesting that intertidal air temperatures along the southeast coast of Australia may not necessarily decline with increasing latitude.

Helmuth et al. (2006) similarly reported that among-site variation in the body temperatures of mussels were not well correlated with latitude. This unexpected lack of correlation with latitude most likely reflects differences among sites with respect to wave exposure (Harley & Helmuth 2003, Fitzhenry et al. 2004, Davenport & Davenport 2005), even though wave exposure was subjectively quantified and standardised by choosing locations with similar aspects. Indeed, Jackson (2010) demonstrated that the degree of wave exposure on rocky intertidal shores influences air temperatures within crevices. However, further research is needed to understand the role of wave exposure on latitudinal patterns of intertidal air temperature within this region.

Satellite and weather station data versus logger data

The results of this study show that, although strongly correlated, *in situ* intertidal water temperatures are significantly different than those estimated by satellites, with *in situ* loggers generally recording lower water temperatures than satellites. This strong correlation between satellite SST and intertidal water temperature supports an equivalent study undertaken within the subtidal, where nearshore benthic water temperatures and satellite-derived SSTs were highly correlated to, yet 1 to 2°C lower than, satellite SSTs within temperate regions of Western Australia (Smale & Wernberg 2009). As we observed when comparing *in situ* and satellite water temperatures, air temperatures recorded by *in situ* loggers and weather stations were both strongly correlated and significantly different. Nonetheless, correlations between weather stations and loggers were considerably weaker than correlations between satellites and loggers, and *in situ* air temperatures were generally warmer than weather station air temperatures. The consistently higher air temperatures recorded by *in situ* loggers may reflect differences in microclimates. For example, *in situ* loggers in the present study were exposed to full UV light, while weather station temperature readings were taken within shaded housings (information from the Australian Bureau of Meteorology, www.bom.gov.au).

Importantly, our study showed that the effectiveness of satellite-derived SSTs and weather station air temperatures as proxies of intertidal water and air temperatures varied across geographic locations.

This geographic variation in the accuracy of satellite SSTs in estimating intertidal water temperatures may reflect differences in nearshore water circulation across the 4 study locations. For instance, at large spatial scales, SSTs in this region are mostly influenced by large warm-core eddies that move in a counter-clockwise direction from north to south (Huyer et al. 1988, Roughan & Middleton 2002, 2004). However, at relatively small spatial scales, the movement of nearshore water may also be influenced by subtidal topography, including islands (see Mace & Morgan 2006), and localised atmospheric conditions. Therefore, the association between intertidal and offshore water temperatures may vary among locations because offshore water may not always move shoreward.

The effectiveness of weather stations as estimates of intertidal air temperatures also varied among locations. Surprisingly, however, correlations between weather stations and *in situ* loggers at Kiama and Mallacoota, where loggers were located within several hundred metres of weather stations, were no stronger than correlations for Garie Beach and Bermagui, where loggers were up to 28 km from weather stations. This suggests that the value of weather station data as surrogates for values estimated by *in situ* loggers could not be improved by standardised usage of weather stations in close proximity to rocky shores of interest.

Biologically relevant temperature variability

The physiological performance of many marine and terrestrial organisms has long been understood to be strongly influenced by short-term extremes and rapid fluctuations in temperature. Consequently, thermal limits are often used to estimate the vulnerability of a particular species to *in situ* heat stress (Denny et al. 2006, Dong et al. 2008). Our results show that weather station data are unlikely to detect acute changes in intertidal air temperatures or accurately characterise temperature extremes relevant to organisms. Since air temperatures are believed to play a significant role in the physiological processes of intertidal organisms (Schiel et al. 2004), this is a major discrepancy that may have important implications when using weather station data to model past and future effects of temperature variability on species distributions and range limits. For instance, Denny et al. (2006) used weather station data to create a model of predicted body temperatures for the intertidal limpet *Lottia gigantea* and found that over a 5 yr period, body temperatures only reached lethal limits (34–38°C) on 3 days. Our results would suggest that this might be a serious underestimation of extreme intertidal temperature events.

Mortality caused by heat stress depends not only on the frequency of high temperature events but also on the rate of heating and cooling experienced by organisms (Denny et al. 2006), which in the absence of behavioural avoidance will be determined by the timing of low tides, the degree of wave exposure and weather (Harley & Helmuth 2003, Harley 2008, Mislan et al. 2009). In the present study, we have shown that satellite SSTs and weather station air temperatures are unlikely to detect the majority of rapid heating events within the mid-intertidal zone. Therefore, we argue that attempts to predict the effect of temperature change on intertidal taxa require *in situ* measurements and should focus on biologically relevant variation.

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