Satellite-derived SST data as a proxy for water temperature in nearshore benthic ecology

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ABSTRACT: Satellite-derived sea surface temperatures (SSTs) are increasingly being used as a proxy for water temperature in nearshore marine ecology, but there have been very few evaluations of how accurately SSTs reflect actual temperatures experienced by subtidal organisms. Here, we describe the benthic temperature climatology of 4 coastal locations along a ~1000 km latitudinal gradient in ocean temperature in Western Australia (WA), and compare temperature records from *in situ* loggers at 10 to 12 m depth with records from 2 independent satellite-derived SST datasets over 2 years. Satellite-derived SSTs were significantly correlated with *in situ* logger data at all locations, which demonstrate their overall ability to detect general patterns of ecological importance. However, SSTs were also significantly different from benthic water temperatures (usually 1 to 2°C higher), and they did not adequately detect ecologically important small-scale variability or provide reliable information on temperature extremes. Furthermore, rank orders of the study locations differed between the methodologies, especially in winter. We emphasize the need to carefully consider whether the accuracy and resolution of satellite-derived SSTs are appropriate for the specific ecological hypothesis being tested in nearshore subtidal habitats, and advocate the use of *in situ* loggers otherwise. We also highlight the suitability of the WA coastline for experimental work on the effects of temperature (and synergistic factors) on marine organisms.

KEY WORDS: Benthic climatology · Satellite-derived SST · Temperature gradient · Shallow water habitats

INTRODUCTION

Considerable advances in remote sensing technology over the past few decades have allowed researchers to map sea surface temperature (SST) across the globe at ever increasing spatial and temporal resolutions. Satellite-derived SST data have become a widely used tool for monitoring changes in ocean temperature driven by climate change and have been incorporated into a myriad of biological models and studies (e.g. Littaye et al. 2004, Zainuddin et al. 2006, Muhling et al. 2008). Temperature is a key factor controlling the distribution of species and physiological processes (Schils & Wilson 2006, O'Connor et al. 2007, Byrne et al. 2009, Staehr & Wernberg 2009), and easily accessible temperature data for the global ocean has facilitated considerable progress in our understanding of broad-scale biological patterns. As satellite-derived SSTs are now collected at high spatial and temporal resolutions and are readily available, their use as proxies for water temperature in nearshore benthic habitats has become increasingly popular (Donner et al. 2005, Broitman et al. 2008, Mauna et al. 2008). While this application of SSTs has been useful in explaining ecological patterns, there have been very few detailed comparisons of satellite-derived data and *in situ* temperature data collected from shallow subtidal habitats. Yet, this information is critical in linking ecological patterns and environmental variation in a mechanistic framework with predictive capacity.

Satellite-derived SST data are obtained by sensing ocean radiation in 2 or more wavelengths, usually in the infrared part of the electromagnetic spectrum, which can then be empirically related to SST. How-

ever, this measurement is derived from the top 'skin' of seawater (~0.01 mm thick) and may not be representative of seawater temperature further down in the water column ('bulk' temperature). The relationship between 'skin' and 'bulk' temperature is strongly influenced by sea state, weather conditions and local oceanography, and has been the focus of many ground-truthing studies (Barton & Pearce 2006, Pearce et al. 2006). It is clear that, under certain conditions, SST values may be representative of water temperatures to depths of a few meters in the open ocean (Katsaros 2003). Such observations may have prompted the use of satellite-derived SSTs in shallow-water ecological studies. However, in shallow coastal benthic habitats, factors such as tides, waves, water clarity and the thermal properties of the substratum, may influence temperature profiles and possibly reduce the correspondence between SSTs and the temperatures experienced by organisms living near the bottom. Given the severity of likely impacts, there is an increasing need to understand how organisms would respond to the current rate of global change, including ocean warming, and such an understanding is only possible if coupled with accurate environmental data. Here, we compare temperatures measured *in situ* on subtidal reefs with 2 types of satellite-derived SSTs, with particular reference to variability over space and time, and within the context of nearshore marine ecology. We emphasize that we did not aim to assess the accuracy or precision of satellite-derived SSTs; this would have required *in situ* measurements of temperature from the sea surface, and such studies are numerous in the literature (Yokoyama & Tanba 1991, Pearce et al. 2006). Rather, this study evaluated the usefulness of SST as a proxy for actual temperature in shallow subtidal habitats at water depths of ~10 m.

The coastal environment of Western Australia (WA) is unique in many ways. The west coast is very extensive (ranging from 15° to 35° S) but sparsely populated, so that most marine habitats can be considered relatively pristine and largely shaped by natural forces. The coastline is heavily influenced by the Leeuwin Current (LC) (Cresswell & Golding 1980, Pattiaratchi & Buchan 1991, Pearce 1991) which, along with latitudinal factors, drives a well-defined temperature gradient. Many temperate marine species are at their northern (warm) distribution limit (Wernberg et al. 2003a, Tuya et al. 2008, Wernberg et al. 2008) and tropical species at their southern (cool) distribution limit (Babcock et al. 1994, Greenstein & Pandolfi 2008) along this temperate–tropical transition zone. The region therefore has great potential for the conduct of field studies on the effects of temperature on the ecology and physiology of marine organisms. Despite numerous investigations of the offshore oceanographic conditions, envi-

ronmental data from the nearshore habitats of the region remain scarce. Our concurrent aim for this study was, therefore, to quantify the climatology and temperature gradient in nearshore subtidal habitats along the coastline of temperate WA.

MATERIALS AND METHODS

Study site. The study covered 4 locations evenly distributed across ~6° latitude (~1000 km of coastline) of temperate coastline in WA (Fig. 1). Despite considerable distance (~300 km) between them, these locations are broadly comparable with submerged rocky reefs that run parallel to the coast at distances of <1 to 12 km from the shore (Searle & Semeniuk 1985). These reefs are all exposed to heavy swells and persistent wind-induced waves (Lemm et al. 1999), and all support similar benthic communities dominated by a low standing canopy of the kelp *Ecklonia radiata* (Wernberg et al. 2003b, Tuya et al. 2008, Wernberg et al. 2008).

***In situ* logger data.** At each location, a 'TidbiT' self-recording temperature logger (Onset Stowaway logger, model TBI32-05+37, accuracy ± 0.2°C) was mounted on a stake ~5 cm above the bottom at 10
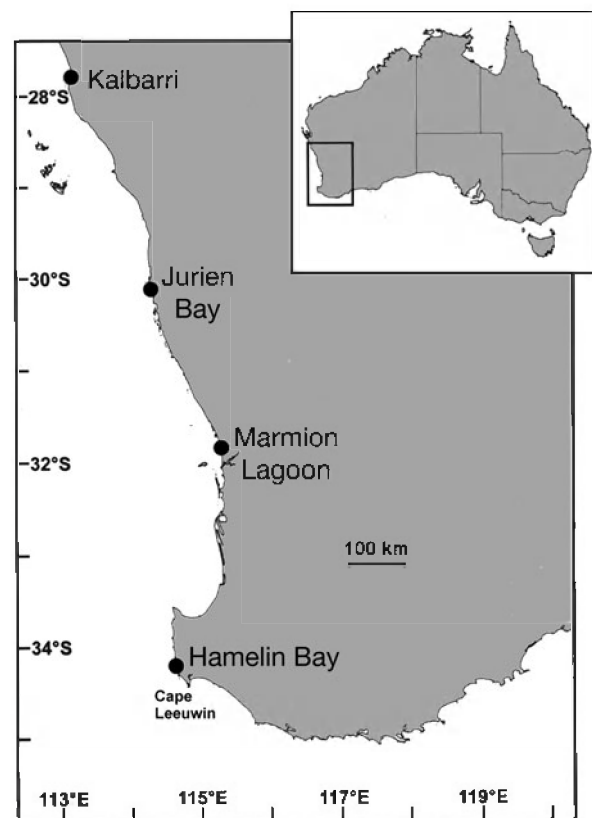

Fig. 1. Map of the 4 study locations along the southwest coastline of Western Australia

to 12 m depth at each of 3 reefs separated by >1 km in a north–south direction. All 12 loggers were installed by 24 April 2006 and from then on continuously recorded temperature measurements at hourly intervals for 2 yr.

Satellite-derived SST data. Two satellite-derived SST datasets were compared with the logger data. The first dataset was obtained by the advanced very high resolution radiometer (AVHRR) aboard the NOAA series of satellites. SSTs derived by AVHRR have been archived by the Australian Bureau of Meteorology since the 1970s and are now freely available on their website (www.bom.gov.au), which also includes details on the methodologies used to calculate SSTs (www.bom.gov.au/sat/SST/sst.shtml). Daily SST maps of Australian waters were used to manually generate a dataset for each of the 4 study locations. A single pixel (representing ~20 × 20 km) was selected for each study location and, using a simple calibration curve, the colour intensity of the pixel was converted to a temperature value in °C. The same pixel for each location was selected from all images.

The second dataset was obtained from the moderate-resolution imaging spectroradiometer (MODIS) installed on the Terra and Aqua NASA-operated satellites. This is a relatively new instrument which provides highly accurate SSTs at spatial resolutions of <1 km. MODIS data were supplied as maximum SSTs within 4 d periods (bins) for each reef; in contrast to the AVHRR data, a value for SST above each reef was possible with MODIS due to the increased resolution of the data. The mean maximum SST (±SD) for each location was calculated from the 3 replicate reefs within each location. Data were again supplied by the Australian Bureau of Meteorology.

It is not possible to obtain satellite-derived SSTs during periods of thick cloud cover. Consequently, there were no data for some days in the AVHRR datasets and for some 4 d bins in the MODIS dataset. This problem was most prevalent at Hamelin Bay, but even here data were available for >90% of all sampling occasions (pairwise tests were not conducted for days when satellite-derived SSTs were unavailable). The use of 2 distinct satellite-derived SST datasets allowed us to compare the 2 different instruments (AVHRR and MODIS) and 2 different data types (daily mean temperatures and maximum values from 4 d bins).

Data analysis. Logger data were initially used to characterize the thermal environment of our study locations and general patterns across seasons, years and the study region as a whole. Differences in daily mean temperatures, maxima and minima among locations (fixed) and reefs (random and nested within locations) were tested with ANOVAs on untransformed logger data for each year of study. Subsequently, for

comparisons with AVHRR-derived data, daily means from the *in situ* loggers were calculated and then averaged across the 3 replicate reefs at each location. This generated a single value for each location and day of study. For comparisons with the MODIS-derived data, logger data were arranged into corresponding 4 d bins and the maximum values recorded by each logger were extracted. Means (±SD) of the 3 loggers at each location were then compared with the MODIS data. Pearson's r values were used to indicate the strength of the correlation between logger and satellite-derived data, while differences were tested with paired *t*-tests.

Seasonal comparisons were conducted by averaging daily mean temperatures across the 4 seasons for both *in situ* and satellite-derived data. Finally, periods of temperature maxima, which are thought to be of particular ecological importance, were analyzed from the logger data collected at each location. The proportion of the daily means that were greater than the upper range of temperatures recorded in the study region (i.e. 18–25°C) were also calculated and plotted for each location.

RESULTS

General climatology of study locations

Our 4 study locations ranged in mean annual temperature by ~2°C (Table 1). Generally, sea temperature on the subtidal reefs, as described by daily means, maxima and minima, increased with decreasing latitude; hence, the study locations were arranged along a latitudinal/temperature gradient (Fig. 2). As would be expected for a mid-latitude temperate study region, patterns in sea temperature were highly seasonal (Fig. 2). The daily mean temperature ranged by 6.9, 7.8, 7.1 and 5.8°C at Kalbarri, Jurien Bay, Marmion Lagoon and Hamelin Bay, respectively. Overall, sea temperatures ranged by >10°C, from a winter minimum of 15.7°C at Jurien Bay to a summer maximum of 26.9°C at Kalbarri.

Interestingly, while the latitudinal/temperature gradient persisted for annual daily mean temperatures, maximum daily means and annual maxima, it was not as clear for minimum daily mean temperatures or annual minima. For instance, the minimum daily mean recorded at Marmion Lagoon was lower than that at Hamelin Bay, and the absolute minimum reading obtained in 2006/2007 was lower at Jurien than at either Marmion Lagoon or Hamelin Bay (Table 1). Nevertheless, overall daily mean temperatures, maxima and minima were strongly significantly different among locations, while no differences were observed among replicate reefs within each location during both

Table 1. Summary of temperature data recorded by loggers at each of the 4 locations for each year of study. Mean values are averages of 3 replicate loggers at each location (±SD). Maxima and minima represent the highest and lowest temperatures recorded at any logger at each location during each year of study. Variability among hourly and daily logger readings are shown as CVs

| | Temperature (°C) | | | | | Max. CV between loggers (%) | |
| | Daily mean | | | Annual | | | |
	Annual	Max.	Min.	Max.	Min.	Hourly	Daily
Apr 2006–Apr 2007							
Kalbarri	21.88±0.05	24.16±0.03	19.26±0.07	24.32	18.51	9.1	1.8
Jurien	20.73±0.04	23.71±0.07	17.13±0.82	24.31	15.67	6.3	6.0
Marmion	20.27±0.02	23.30±0.10	16.57±0.41	23.72	15.73	6.4	4.8
Hamelin	19.49±0.03	21.62±0.07	16.81±0.07	21.97	16.48	4.8	2.8
Apr 2007–Apr 2008							
Kalbarri	21.89±0.01	26.13±0.03	19.69±0.03	26.91	19.30	3.4	0.7
Jurien	20.93±0.12	24.94±0.19	17.45±0.62	26.17	16.21	9.9	4.9
Marmion	20.14±0.10	23.73±0.14	16.81±0.16	24.10	15.89	5.7	4.2
Hamelin	19.45±0.04	22.61±0.10	16.78±0.17	23.13	16.50	4.0	3.2
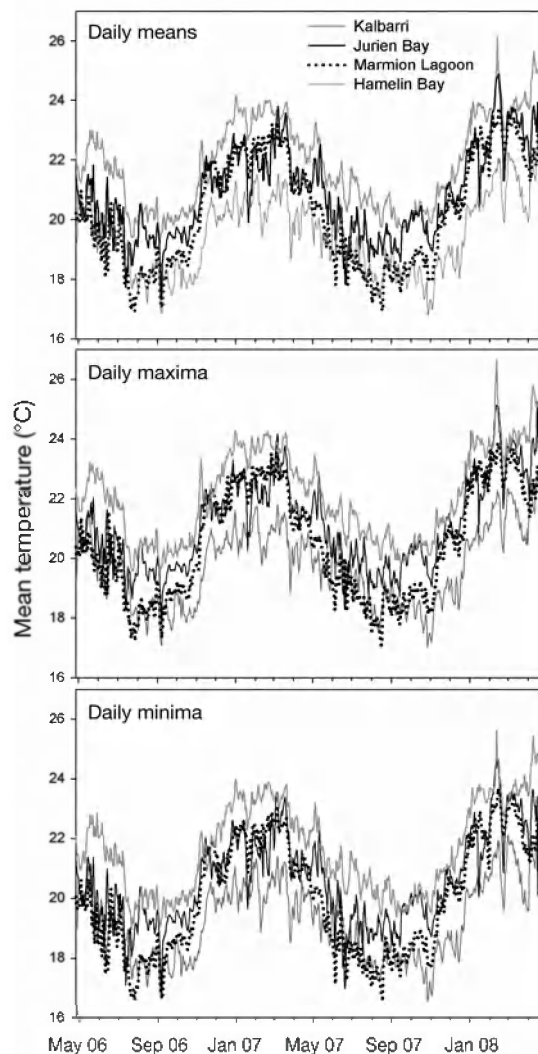
Fig. 2. Daily mean, maximum and minimum temperatures for each study location throughout the period of data collection (2006–2008). Values are means of 3 replicate loggers at each site

years of study (Table 2). Subsequent post-hoc testing (Tukey's pairwise tests) indicated that Kalbarri > Jurien Bay > Marmion Lagoon > Hamelin Bay with respect to daily mean temperatures, maxima and minima.

All locations showed strong and similar seasonal variation, as annual minimum temperatures were consistently recorded during the austral winter (June–August) and annual maxima were observed during the austral summer (December–February) (Fig. 2). Seasonal mean temperatures (both years combined) were considerably lower in winter and spring than in summer and autumn at all sites, as would be expected (Table 3). Within each site, maximum and minimum seasonal mean temperatures differed by 2.8, 2.5, 3.8 and 2.1°C at Kalbarri, Jurien Bay, Marmion Lagoon and Hamelin Bay, respectively. The latitudinal/temperature gradient was apparent from the rank orders of seasonal means for spring (September–November) and autumn (March–May), but not for winter or summer (Table 3). During winter, Hamelin Bay was slightly warmer than Marmion Lagoon, while Marmion Lagoon was warmer than Jurien Bay during summer, despite the latter being ~300 km further north.

Variation among loggers at replicate reefs within locations was generally minimal, as evidenced by low maximum coefficients of variation (CVs) (Tables 1 & 3). However, comparisons among locations showed that variability among replicate reefs (i.e. across daily or hourly measurements) was consistently greatest at Jurien Bay and consistently lowest at Kalbarri. Small-scale temporal variability was also generally low. For example, diurnal variability was typically <1°C and variation in daily means for consecutive days was minimal (Table 1). However, we observed occasional short-term spikes in temperature, which considerably increased temporal variation. For example, in Febru-

Table 2. Results of nested ANOVA for differences in daily mean, minimum and maximum temperatures (untransformed) among locations and reefs within locations, for each year of study. KAL: Kalbarri; JUR: Jurren; MAR: Marmion; HAM: Hamelin

Source	df	MS	F	p
Year 1 (Apr 06–Apr 07)				
Daily mean				
Location	3	1099	1303	<0.001
Reef(location)	8	0.84	0.42	0.908
Error	4368	1.99		
Post-hoc comparison of locations (p < 0.05):				
KAL> JUR > MAR > HAM				
Daily max.				
Location	3	1072	1667	<0.001
Reef(location)	8	0.64	0.32	0.958
Error	4368	2.00		
Post-hoc comparison of locations (p < 0.05):				
KAL> JUR > MAR > HAM				
Daily min.				
Location	3	1098	903	<0.001
Reef(location)	8	1.22	0.59	0.787
Error	4368	2.06		
Post-hoc comparison of locations (p < 0.05):				
KAL> JUR > MAR > HAM				
Year 2 (Apr 07–Apr 08)				
Daily mean				
Location	3	1211	464	<0.001
Reef(location)	8	2.60	0.97	0.454
Error	4368	2.67		
Post-hoc comparison of locations (p < 0.05):				
KAL> JUR > MAR > HAM				
Daily max.				
Location	3	1190	477	<0.001
Reef(location)	8	2.49	0.92	0.497
Error	4368	2.71		
Post-hoc comparison of locations (p < 0.05):				
KAL> JUR > MAR > HAM				
Daily min.				
Location	3	1236	408	<0.001
Reef(location)	8	3.02	1.11	0.355
Error	4368	2.73		
Post-hoc comparison of locations (p < 0.05):				
KAL> JUR > MAR > HAM				

2006, mean daily temperatures increased by ~2°C at all study locations, representing a temperature increase of ca. one-third of the total annual variation.

Measures of extreme upper temperatures also changed along the latitudinal gradient. For example,
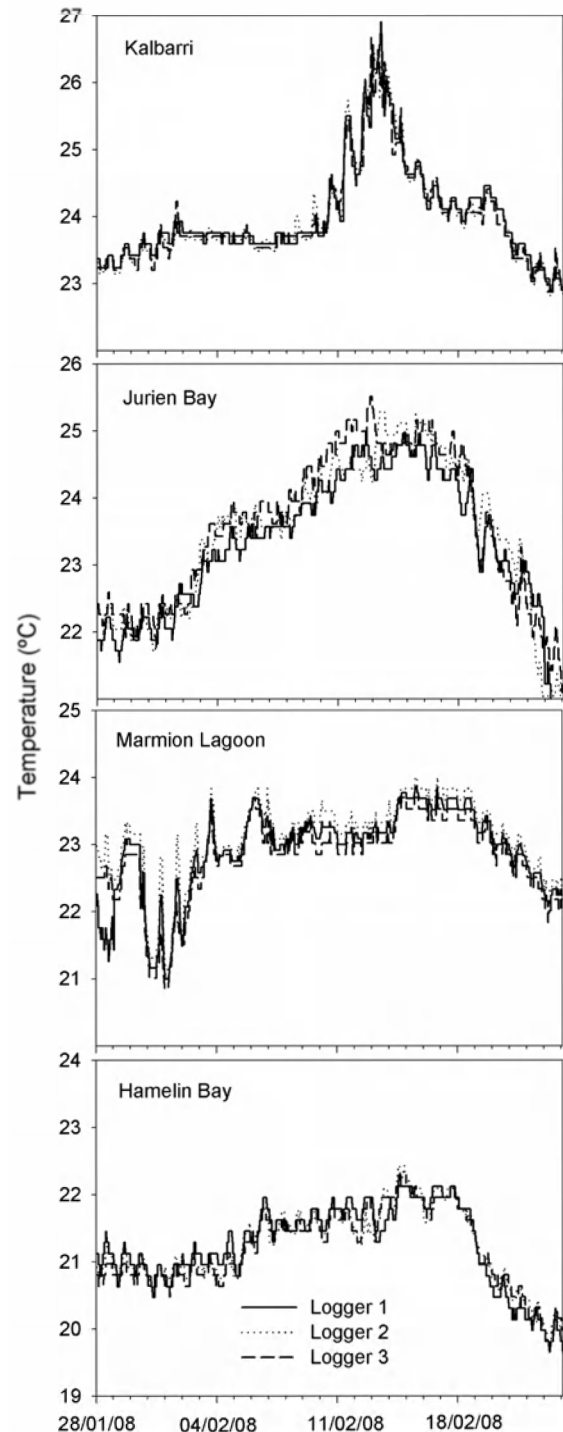

Fig. 3. Short-term temperature spikes recorded at all locations in February 2008. Plots are hourly measurements collected by each logger during the thermal event

ary 2008, a noteworthy temperature spike was recorded at all 4 locations, to varying extents (Fig. 3). The signal was strongest at Kalbarri, as during a 3 d period, the temperature at all 3 reefs increased by almost 3°C to >26.5°C, before returning and stabilizing at a more 'usual' temperature of ~24°C (Fig 3). Occasionally, discrete thermal events were detected at all study locations, and these often occurred simultaneously at all locations, perhaps suggesting that the same broad-scale drivers, such as storm events or sustained solar radiation on surface waters, affect the entire study region. For instance, over a 20 d period in December

Table 3. Daily mean, maximum and minimum temperatures, and maximum SDs among loggers and between consecutive days for each season (2 yr combined) at each of the study locations. Mean values are averages of 3 replicate loggers at each location (±SD). Maxima and minima represent the highest and lowest temperatures recorded at any logger at each location during each season. Variability among loggers and between consecutive days are shown as CVs

	Temperature (°C)			Max. CV between loggers (%)	
	Seasonal daily mean (rank)	Seasonal max.	Seasonal min.	Hourly	Daily
Winter (Jun–Aug)					
Kalbarri	20.84 ± 0.04 (1)	22.98	18.92	0.9	1.6
Jurien	19.51 ± 0.18 (2)	21.93	16.21	5.8	5.2
Marmion	18.40 ± 0.06 (4)	21.61	15.73	4.5	4.1
Hamelin	18.75 ± 0.11 (3)	20.85	16.96	3.0	4.4
Spring (Sep–Nov)					
Kalbarri	20.48 ± 0.03 (1)	23.41	18.99	0.7	2.4
Jurien	19.89 ± 0.06 (2)	22.73	15.67	6.1	2.7
Marmion	19.08 ± 0.06 (3)	22.62	16.21	2.8	3.4
Hamelin	18.32 ± 0.07 (4)	21.11	16.48	1.6	3.0
Summer (Dec–Feb)					
Kalbarri	23.23 ± 0.04 (1)	26.91	20.72	0.9	2.6
Jurien	22.00 ± 0.13 (3)	25.51	19.22	3.4	3.7
Marmion	22.07 ± 0.20 (2)	24.01	19.80	4.3	3.4
Hamelin	20.34 ± 0.03 (4)	22.43	17.73	2.1	2.5
Autumn (Mar–May)					
Kalbarri	22.98 ± 0.04 (1)	25.85	18.51	1.7	1.5
Jurien	21.94 ± 0.13 (2)	26.17	18.26	4.6	4.2
Marmion	21.28 ± 0.04 (3)	23.84	18.34	2.5	2.8
Hamelin	20.44 ± 0.13 (4)	23.13	18.08	3.3	5.1

~45% of daily mean temperatures were >22°C at Kalbarri, compared with ~23% at Jurien Bay and Marmion Lagoon and only 2% at Hamelin Bay (Fig. 4). Interestingly, a clear north–south divide was evident in the number of daily mean temperatures >19°C (>90% of daily means at Kalbarri and Jurien, compared with ~60% of daily means at Marmion Lagoon and Hamelin Bay), which may be of ecological importance (see 'Discussion').

Satellite-derived vs. logger-derived data

The satellite-derived SST data gathered by the AVHRR instrument was significantly correlated with the *in situ* logger data at all locations, with the minimum correlation (Pearson's) of r = 0.85 being observed at Hamelin Bay (Fig. 5, Table 4). However, the datasets were also significantly different: the AVHRR-derived temperatures were generally greater than those recorded by the loggers (Table 4), as evidenced by AVHRR-derived annual means, which were 1–2°C greater at each location. However, the rank of locations by annual mean temperature did not vary between the remote and the *in situ* methodologies (Table 4).

Seasonal means derived by the AVHRR instrument were, overall, also slightly higher than those derived by the loggers, although the rank of locations based on temperature did not differ between the 2 datasets for spring or autumn. However, differences in the rank order were observed for summer and winter seasonal mean temperatures. While the satellite-derived SST data suggested that Jurien Bay was the coolest location during winter, the logger data showed that the shallow subtidal Marmion Lagoon was marginally the coolest location. Similarly, Marmion Lagoon was ranked second based on summer seasonal mean temperatures in the logger-derived dataset but ranked third in the AVHRR-derived dataset (Tables 3 & 4).

Compared with the AVHRR data, data collected by the MODIS instrument, analyzed as maximum temperatures within 4 d bins, were less well correlated with *in situ* logger data (Fig. 6, Table 4). Nevertheless, correlations were significant and ranged from 0.90 at Marmion Lagoon to 0.53 at Hamelin Bay. As with the AVHRR-derived temperatures, MODIS data were significantly different from the logger data, and were higher at Kalbarri, Jurien Bay and Marmion but lower at Hamelin Bay (Table 4). Furthermore, SSTs were more variable in space than logger-derived temperatures, as evidenced by significantly greater SDs among replicate measurements (~1 km apart) within each location
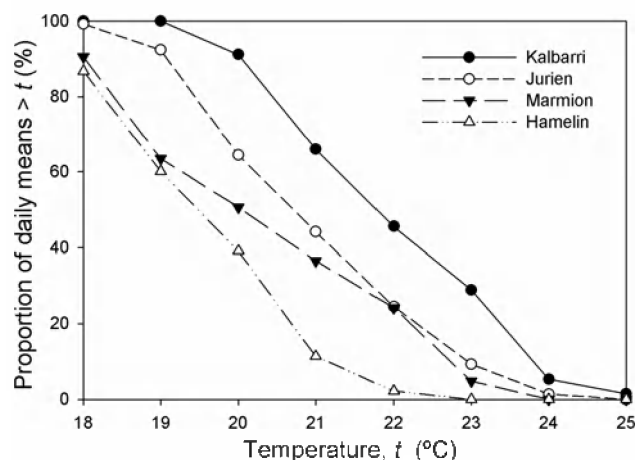

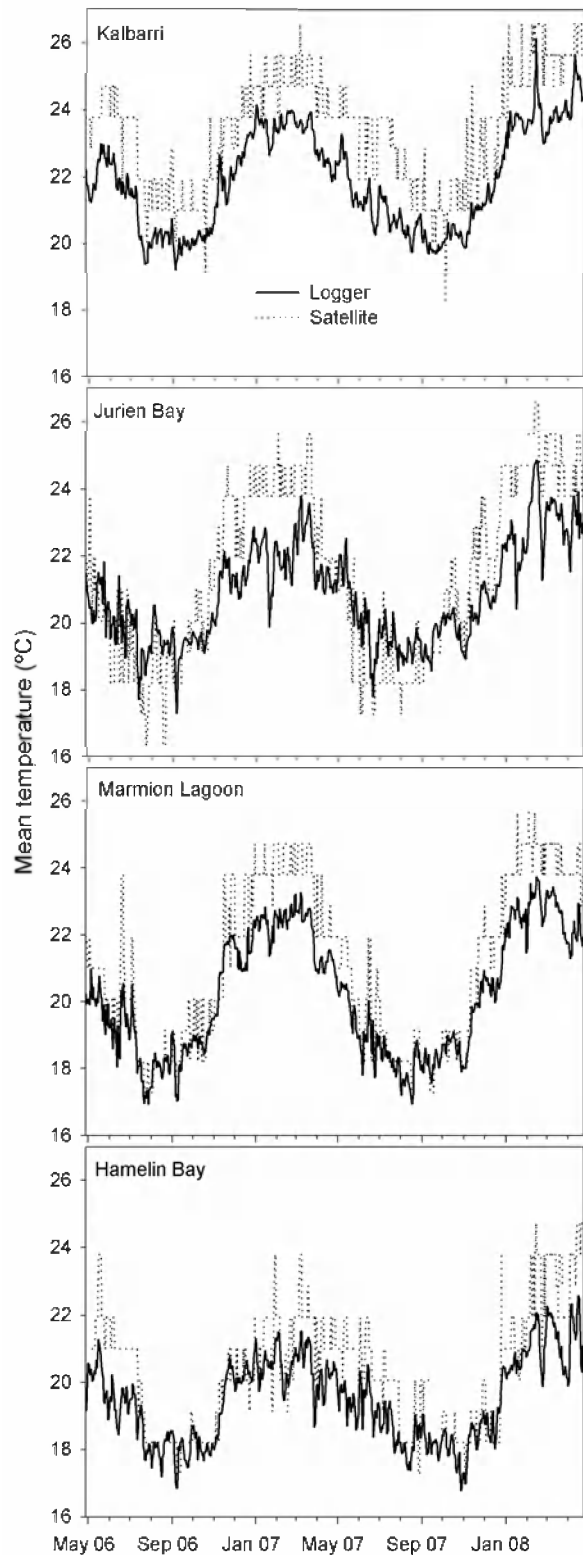Fig 4. Percentage of daily mean temperatures >18 to 25°C (whole integers) for each location

Fig. 5. Sea temperatures recorded by *in situ* loggers (daily means) and satellite-derived sea surface temperatures (SSTs) obtained by the advanced very high resolution radiometer (AVHRR) (daily means) at each study location throughout the study (2006–2008)

Table 4. Summary of satellite-derived sea surface temperature (SST) data from the 4 study locations [mean ± SD (rank)]. The relationships between logger-derived and satellite-derived data were tested using Pearson's correlation. Differences between the 2 datasets were tested using paired *t*-tests. For tests between logger data and the advanced very high resolution radiometry (AVHRR) dataset, 712 pairs of data (i.e. 711 df for *t*-tests) were used for Kalbarri, Jurien Bay and Marmion Lagoon, while 704 pairs were used for Hamelin Bay. For tests between logger data and the moderate-resolution imaging spectroradiometer (MODIS) dataset, 179, 174 and 163 pairs were used for Kalbarri, Jurien Bay and Marmion Lagoon, and Hamelin Bay, respectively. (*) p-value <0.001 (for all tests)

| | Temperature (°C) | | | | | | Pearson's correlation | Paired *t*-test (loggers vs. sat) | |
| | Annual mean (rank) | | Seasonal mean (rank) | | | | | | |
	2006–07 (Apr–Apr)	2007–08 (Apr–Apr)	Winter (Jun–Aug)	Spring (Sept–Nov)	Summer (Dec–Feb)	Autumn (Mar–May)		Mean	SD
AVHRR satellite data									
Kalbarri	23.37±1.52 (1)	23.45±1.78 (1)	22.73±1.11 (1)	21.69±1.06 (1)	24.64±1.08 (1)	24.69±0.93 (1)	0.91*	−59.33*	—
Jurien	21.41±2.42 (2)	21.47±2.68 (2)	18.56±0.99 (4)	20.61±1.67 (2)	24.08±1.14 (2)	22.73±1.81 (2)	0.89*	−11.92*	—
Marmion	21.17±2.29 (3)	20.98±2.51 (3)	18.93±1.23 (3)	19.47±1.52 (3)	23.58±1.13 (3)	22.53±1.57 (3)	0.96*	−29.71*	—
Hamelin	20.16±1.63 (4)	20.53±1.97 (4)	19.69±1.29 (2)	18.75±0.92 (4)	21.09±1.54 (4)	21.90±1.53 (4)	0.85*	−23.60*	—
MODIS satellite data									
Kalbarri	25.60±3.12 (1)	25.52±3.39 (1)	22.69±2.39 (1)	24.61±2.81 (1)	28.18±2.41 (1)	26.82±2.44 (1)	0.65*	−18.33*	−18.70*
Jurien	22.09±2.25 (2)	22.16±2.77 (2)	19.59±1.41 (2)	21.42±2.00 (2)	24.35±1.59 (2)	23.14±1.99 (2)	0.72*	−7.62*	−10.94*
Marmion	21.36±2.21 (3)	21.31±2.11 (3)	19.25±1.18 (3)	20.14±1.27 (3)	23.55±1.32 (3)	22.24±1.55 (3)	0.90*	−11.80*	−5.68*
Hamelin	19.02±3.00 (4)	19.03±3.04 (4)	17.13±2.61 (4)	17.43±2.56 (4)	20.73±2.13 (4)	20.50±2.81 (4)	0.53*	3.62*	−12.03*
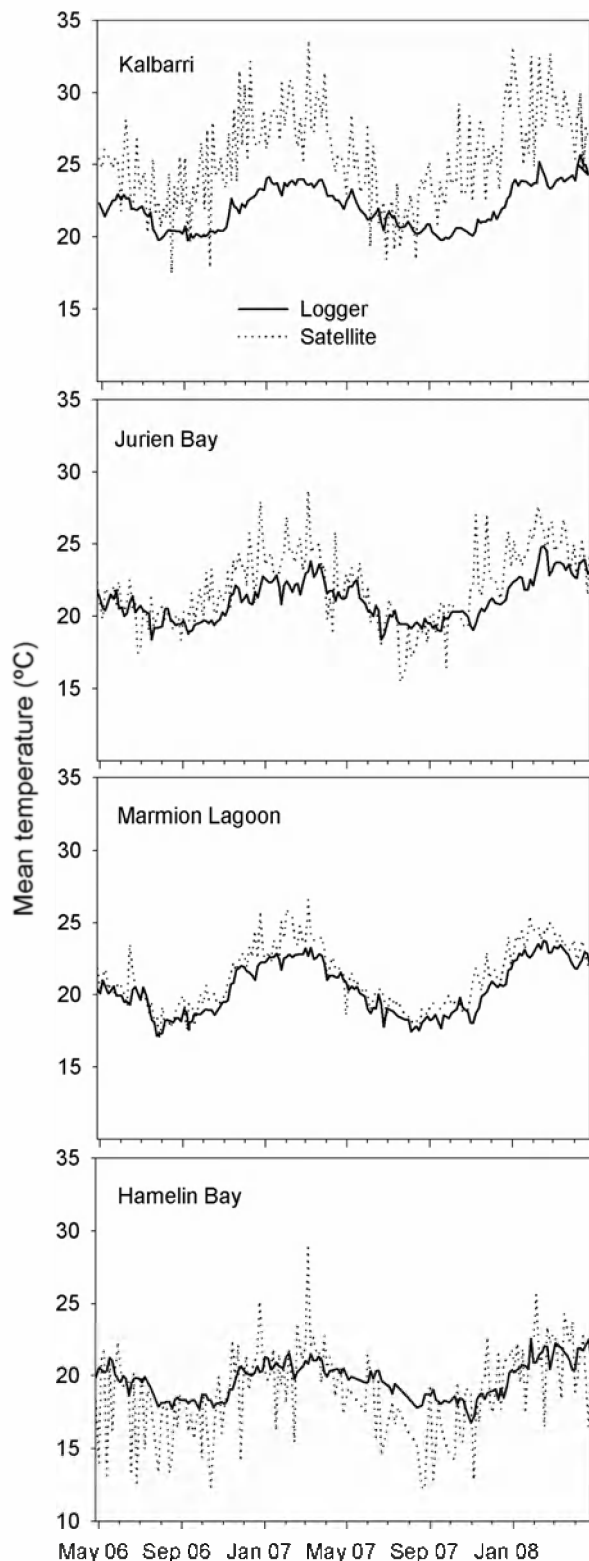
Fig. 6. Sea temperatures recorded by *in situ* loggers (maxima from 4 d bins) and satellite-derived sea surface temperatures (SSTs) obtained by the moderate resolution imaging spectroradiometer (MODIS) (maxima from 4 d bins) at each study location throughout the study (2006–2008)

(Tables 3 & 4). Despite these differences in actual mean temperatures and in variability, there were no differences between the 2 methodologies in terms of the rank of locations based on annual daily mean temperatures (Table 4).

Seasonal mean temperatures derived by the MODIS instrument were again slightly higher than those derived from the loggers, with the exception of the Hamelin Bay location. Here, MODIS-derived means were ~1°C lower than the logger values during winter and spring (Table 4). Interestingly, the rank of the locations based on seasonal mean temperature remained constant through the seasons in the MODIS dataset, in contrast to both the AVHRR and logger datasets.

DISCUSSION

General climatology of study locations

The study region is strongly influenced by the Leeuwin Current (LC), which is a unique poleward flowing eastern boundary current that carries warm water along the coast of WA (Pearce 1991). As a result, the coastal waters off WA are warmer in winter than eastern boundary waters at comparable latitudes off South Africa and South America. Moreover, the LC suppresses wind-driven upwelling (Pearce 1991), so that surface waters remain clear and comparatively nutrient-poor (Waite et al. 2007, Koslow et al. 2008).

This unique oceanography was evidenced in the current study in 2 ways. First, as a result of elevated winter temperatures, seasonal variation in mean daily temperatures was low at all study locations, with differences between summer and winter averages of ~2°C. For instance, winter temperatures at Hamelin Bay (34° S) were 6 to 9°C warmer than those recorded at the Cape of Good Hope (also at 34° S) on the west coast of South Africa (McQuaid & Branch 1984), again highlighting the considerable effect of the LC on the coastal system of WA.

Second, annual and seasonal temperature minima did not vary along the latitudinal cline as predictably as the mean temperatures or the maxima. The lowest temperature in the first year of study was recorded at Jurien Bay and the absolute minimum for the second year of study was observed at Marmion Lagoon, rather than Hamelin Bay. Although the daily minima still generally significantly decreased with latitude, the unintuitive pattern of extreme minima with latitude may be of ecological importance and should be considered in future ecological studies conducted in the region, particularly for species with tropical affinity. We observed a relative lack of depression in minimum temperatures at Hamelin Bay, which was almost cer-

tainly driven by the LC. The main flow of the LC runs some 18 km offshore from the Perth metropolitan area (~12 km west of Marmion Lagoon), which increases offshore winter sea temperatures by up to 3 to 4°C (Pearce et al. 2006). Further south, the LC tracks closer inshore before deviating eastwards along the Southern Australian coastline (Pearce 1991, Smith et al. 1991, Waite et al. 2007). Therefore, the LC may have had greater influence at Hamelin Bay than at Marmion Lagoon, as evidenced by relatively elevated winter sea temperatures. What remains unclear, however, is the degree of inter-annual variability in these patterns and to what extent these observations were driven by small-scale eddies of the LC. The oceanographic and biological importance of such deviations from the main flow of the LC has gained recognition in recent years (Koslow et al. 2008, Meuleners et al. 2008).

Nonetheless, benthic climatology clearly shifted along the latitudinal gradient, in terms of both mean water temperature and extremes of upper and (to a lesser degree) lower temperatures. Periods of extreme temperatures (i.e. winter minima and summer maxima) are of great ecological importance. For example, the kelp *Ecklonia radiata*, which is a key habitat-forming species within the warm-temperate ecosystem, is at the northern limit of its range at Kalbarri. Its growth and productivity are known to be adversely affected at temperatures >19°C (Kirkman 1984, Hatcher et al. 1987), yet >90% of daily means at both Jurien Bay and Kalbarri were above this threshold. In addition, we observed short-lived spikes in temperature of ~3°C at both locations, which raised water temperatures on the subtidal reefs to >25°C. This suggests that the population is thermally stressed during extreme events, and any increase in the frequency and/or duration of such events could affect the population's ability to grow, reproduce, and undergo post-disturbance recovery.

Similarly, minimum winter temperature may be a controlling factor in the poleward range expansion of warm-water species. For example, in Eastern Australia, a recent range expansion of the habitat-altering sea urchin *Centrostephanus rodgersii* into Tasmanian waters has been partly driven by winter sea temperatures exceeding the cold threshold for its larval development (Ling 2008, Ling et al. 2008). More locally, studies on the physiology and historical distributions of warm-water reef-building corals suggest that any poleward migrations along the WA coastline would be largely driven by increased winter sea temperatures and a strengthening of the LC (Greenstein & Pandolfi 2008). Even today, there are many warm-water reef corals found at high latitudes in WA (Greenstein & Pandolfi 2008), perhaps partly due to the relatively 'warm' winter temperatures experienced along the coastline. Therefore, the latitudinal cline in both

means and extremes of temperature in our study region will provide a valuable framework for detecting and investigating the effects of a warming climate.

The 4 study locations were broadly distributed along a latitudinal/temperature gradient, which ranged by ~2°C in terms of mean daily temperatures. Crucially, other environmental factors that may influence benthic assemblages at these locations, such as nutrient levels (Pearce 1991, Lourey et al. 2006), light (Staehr & Wernberg 2009), grazing pressure (Vanderklift & Kendrick 2004, Wernberg et al. 2008), discrete thermal events (present study), the availability of hard substrata and exposure to oceanic swells (Wernberg & Thomsen 2005), do not co-vary substantially with latitude and temperature. In addition, the locations are broadly similar in their ecology; they are characterized by patches of *Ecklonia radiata* and many dominant species span the entire latitudinal cline (Tuya et al. 2008, Staehr & Wernberg 2009). Therefore, with the absence of confounding factors and the presence of key taxa throughout the region, the warm temperate coastline of WA represents an ideal natural laboratory for investigating the interactive effects of temperature on complex ecological processes.

Satellite-derived vs. logger-derived data

Satellite-derived SSTs are undoubtedly a useful tool for modern marine ecologists. While they have been used to model and predict biological processes in the open ocean for many years, only recently have they been applied as proxies for temperatures influencing benthic organisms in subtidal habitats. In our study, both satellite-derived datasets were significantly correlated with logger data collected from hard substrata at ~10 m depth. Therefore, for broad-scale ecological studies, it may be acceptable to infer benthic climatology from SSTs.

However, satellite-derived SSTs are collected from a thin boundary layer at the air–sea interface, and increasingly deviate from actual sea temperatures with increasing water depth (Katsaros 2003). Therefore, as our study showed, satellite-derived SSTs are likely to be significantly different from actual water temperatures influencing shallow subtidal habitats. Within the context of our study, the rank order of our study locations was not consistent between the logger data and the satellite-derived datasets. Such deviations could have important implications for interpreting the results of comparative experiments on the effects of ambient temperature on the physiology or ecology of marine organisms in the region. For instance, if benthic climatology were described with satellite-derived data alone, the importance of warmer winter temperatures

at Hamelin Bay would be under-appreciated and a certain degree of explanatory power would be lost.

In addition, linking physiology with ecology within a changing climate will require accurate records of temperature minima and maxima, and of the duration of extreme events, which are likely to be at least as important as mean temperature values. Describing benthic climatology solely with satellite-derived SST data negates an understanding of small-scale variability in temperature across both time and space. As discussed above, we detected short-term fluctuations in water temperatures surrounding subtidal reefs that may have important ecological implications, but such fine-resolution information is only obtainable with *in situ* recorders, not with remote sensing technology.

To conclude, there is a current lack of experimental field studies on the effects of temperature and other climate change-related variables on the structure of marine communities (Harley et al. 2006). Extensive, relatively homogenous coastlines with clearly defined temperature gradients, such as in WA, provide excellent opportunities for *in situ* ecological manipulations that will improve our understandings of temperature-related processes. Our results highlight the usefulness of satellite-derived SSTs as proxies for water temperature in shallow benthic habitats, but also demonstrate the importance of the additional information gained from *in situ* temperature loggers particularly in relation to short-term peak events. We recommend that, rather than employing remote-sensing technology as a matter of course, benthic ecologists consider whether the accuracy of the information is actually appropriate for, and commensurable with, the ecological questions they ask.

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