

# **Physical mechanisms influencing localized patterns of temperature variability and coral bleaching within a system of reef atolls**

Rebecca Green<sup>1,2,3</sup>, Ryan Lowe<sup>1,2,3</sup>, Mark Buckley<sup>3,4</sup>, Taryn Foster<sup>5</sup>, James Gilmour<sup>5</sup>

<sup>1</sup> The Oceans Institute and School of Earth Sciences, University of Western Australia, Crawley, WA, Australia

<sup>2</sup> ARC Centre of Excellence for Coral Reef Studies, University of Western Australia, Crawley, WA, Australia

<sup>3</sup> Oceans Graduate School, University of Western Australia, Crawley, WA, Australia

<sup>4</sup> Pacific Coastal and Marine Science Center, U.S. Geological Survey, Santa Cruz, CA, USA

<sup>5</sup> Australian Institute of Marine Science, Indian Ocean Marine Research Center, Crawley, WA, Australia

Corresponding author: [rebecca.green@uwa.edu.au](mailto:rebecca.green@uwa.edu.au)

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## **Abstract**

Interactions between oceanic and atmospheric processes within coral reefs can significantly alter local scale (< kilometers) water temperatures, and consequently drive variations in heat stress and bleaching severity. The Scott Reef atoll system was one of many reefs affected by the 2015-2016 mass coral bleaching event across tropical Australia, and specifically experienced sea surface temperature anomalies of 2°C that caused severe mass bleaching (61-90%) over most of this system; however, the bleaching patterns were not uniform. Little is known about the processes governing thermodynamic variability within atolls, particularly those that are dominated by large amplitude tides. Here we identify three mechanisms at Scott Reef that alleviated heat stress during the marine heatwave in 2016: 1) the cool wake of a tropical cyclone that induced temperature drops of 1.3°C over a period of 10 days; 2) air-sea heat fluxes that interacted with the reef morphology during neap tides at one of the atolls to reduce water temperatures by up to 2.9°C; 3) internal tidal processes that forced deeper and cooler water (up to 2.7°C) into some sections of the shallow reefs. The latter two processes created localized areas of reduced temperatures that led to lower incidences of coral bleaching for parts of the reef. We predict these processes are likely to occur in other similar tide-dominated reef environments worldwide. Identifying locations where physical processes reduce heat stress will likely be critical for coral reefs in the future, by maintaining communities that can help facilitate local recovery of reefs following bleaching events that are expected to increase in frequency and severity in the coming decades.

## 23 **Introduction**

24 Coral reefs are recognized as one of the most sensitive ecosystems to climate change,  
25 existing under a specific range of chemical, physical and biological conditions (Hoegh-  
26 Guldborg 2005). The limits of this environmental envelope are being increasingly exceeded  
27 under the effects of global climate change, with rising frequency and severity of prolonged  
28 and/or intense heat stress events that have induced large-scale bleaching over the past three  
29 decades (Heron et al. 2016; Hughes et al. 2017). Marine heatwaves (MHW) often occur over  
30 large geographical scales, but water temperatures in a reef system can also differ substantially  
31 from the open ocean (Jokiel and Brown 2004; Falter et al. 2014), and at fine-scales within the  
32 individual reefs (Davis et al. 2011; Pineda et al. 2013).

33 Atmospheric conditions such as solar radiation, air temperature, cloud cover and wind  
34 speed can warm or cool waters by altering air-sea heat fluxes (McGowan et al. 2010). Heat lost  
35 or gained from atmospheric exchange causes local temperature variations within shallow coral  
36 reefs (McCabe et al. 2010; MacKellar et al. 2013; Zhang et al. 2013). The intensity of heating  
37 or cooling depends on the water depth; shallow sites will heat faster during the day and cool  
38 faster at night than deeper sites (Davis et al. 2011). Oceanic processes that drive reef  
39 circulation, and hence the residence times that influence local temperature variability, include  
40 waves (Falter et al. 2014; Rogers et al. 2016) and tides (Lowe et al. 2016). Reef morphology  
41 further influences water circulation patterns and can create extremely heterogeneous residence  
42 times that may facilitate local heating (Lowe et al. 2009). These processes all act synergistically  
43 to either amplify (DeCarlo et al. 2017) or mitigate (Schmidt et al. 2016) thermal stress, resulting  
44 in local reef temperatures that can substantially deviate from the surrounding ocean. This can  
45 lead to spatial heterogeneity in bleaching patterns within a reef system at scales finer than  
46 satellite-based measurements can resolve.

47 The majority of reef thermodynamic studies have focused on reefs where waves play a  
48 dominant role in circulation and transport (Falter et al. 2014; Rogers et al. 2016). However,  
49 one-third of the world's reefs are 'tide-dominated', where wave forcing is small but tides are  
50 large, and therefore experience very different hydrodynamic regimes (Lowe and Falter 2015).  
51 In these reefs the offshore tidal amplitude can often exceed the depth of the reef rim, and as a  
52 consequence, at low tide the reef becomes exposed (Lowe et al. 2016). These topographic  
53 constrictions and/or increased bottom friction slows the outflow of water from the system, and  
54 can result in 'tidal truncation,' where the falling (ebb) tide duration is substantially longer than  
55 the rising (flood) tide duration (Lowe et al. 2015). The extended residence times caused by this  
56 tidal truncation have been associated with large variations in water quality parameters such as  
57 temperature, pH, oxygen, and particulate nutrients (Lowe et al. 2016; Pedersen et al. 2016;  
58 Gruber et al. 2017,2018).

59 Atoll reefs rise steeply from the deep ocean to a shallow reef crest that surrounds a lagoon,  
60 which is generally connected to the ocean via channels. The outer reef slopes and deeper  
61 lagoons of reefs also can be exposed to internal waves and internal tidal bores (Wang et al.  
62 2007; Leichter et al. 2012), which are generated by tidal forcing in density-stratified  
63 environments and transport cooler water from below the thermocline. Although the exterior  
64 slopes are exposed to oceanic flows, restricted water exchange between the lagoons and open  
65 ocean mean atolls are considered the most hydrodynamically closed reef formation  
66 (Andréfouët et al. 2015). As a result, the thermal regime over a typical atoll system can be  
67 highly variable, but there are limited studies of the thermodynamics of atoll reefs, particularly  
68 in atolls where tides play a much more dominant role than waves.

69 In this study we explore the mechanisms responsible for spatial variability in temperature  
70 in a tide-dominated coral reef atoll in northwestern Australia in 2016 during the longest global  
71 mass bleaching event on record (Eakin et al. 2017). The Scott Reef system of three atolls (North

72 Reef, South Reef and Seringapatam Reef) rise from depths of over 1000 m on the edge of the  
73 continental shelf in northwestern Australia, located >300 km from the mainland coast (Figure  
74 1a). The closest reefs are Ashmore 240 km to the north and the Rowley Shoals 400 km to the  
75 south, thus the Scott Reef system is isolated and the coral communities are largely self-seeded  
76 (Gilmour et al. 2009; Underwood et al. 2009). South Reef has a deep lagoon (~50 m) that is  
77 open on its entire northern flank to a 2 km wide, 500 m deep channel (Figure 1b). The lagoons  
78 of North Reef and Seringapatam Reef are considerably shallower (~15 m), and almost  
79 completely enclosed by a shallow reef rim (Figure 2a). North Reef has two narrow, shallow  
80 channels that connect its lagoon to the open ocean in the northeast and south; whereas  
81 Seringapatam Reef has just one channel in the northeast (Figure 2b). At low tide, the only  
82 exchange between these lagoons and the open-ocean occurs through these channels, because  
83 the spring tidal range in the region reaches 4 m, but the reef rim is only ~0.3–1.2 m below mean  
84 sea level. Internal waves of semi-diurnal tidal frequency (‘internal tides’) have been detected  
85 on the outer flanks of Scott Reef and the surrounding continental shelf (Rayson et al. 2011),  
86 which cause vertical displacement of isotherms (Rayson et al. 2018) to transport cooler water  
87 from depth onto shallower reef slopes (Green et al. 2018b).

88 The aims of the study are: 1) to assess local (km) scale temperature variability at a coral  
89 reef atoll during the marine heatwave; 2) to understand the physical mechanisms driving  
90 temperature variation; 3) to identify locations where heat stress and the incidences of coral  
91 bleaching were reduced, and thus potential refugia during marine heatwaves.

## 92 **Methods**

### 93 **Field measurements**

94 In January 2016, temperature loggers (HOBO U22 Pro-v2) were deployed with 15-minute  
95 logging intervals at sites within the lagoons and on the reef slopes of the atolls (Figure 3). We

96 focus on data from 12 representative sites in a water depth of 6-9 m, and one shallower 3 m  
97 site (site 3a). The temperature loggers were calibrated in a room temperature water bath before  
98 and after the deployment (Lentz et al. 2013), ensuring they read to within 0.1°C of each other.  
99 In addition, four RBR Solo pressure sensors (tide gauges) continuously recorded pressure at 1  
100 Hz and were deployed inside and on the outer slope of North Reef and Seringapatam Reef at  
101 ~6 m depth. The tide gauges were recovered in April 2016, after recording 185 tidal cycles.

102 At 12 long term monitoring (LTM) sites, benthic communities were sampled every 1 m  
103 along 5 x 50 m permanent transects, with 10 m intervals between each transect. Sites were  
104 surveyed in January 2016, during the mass bleaching in April, and again in October 2016.  
105 During each survey, a tape was laid along the permanent transect and a camera used to capture  
106 an image of the benthic community at 30 - 50 cm from the substrata. In April, visual  
107 assessments of the severity of coral bleaching were made at 13 sites by estimating the  
108 percentage of bleached corals according to the following categories: >91%, 61-90%, 31-60%,  
109 11-30%, 1-10% or <1%. The percentage of bleached corals included those that had bleached  
110 but whose fluorescent pigments remain, those that had bleached white without fluorescent  
111 pigments, and those that had recently died, i.e., intact coral skeletons covered in turf algae  
112 (Depczynski et al. 2013).

### 113 **Satellite temperature and atmospheric data**

114 Sea surface temperature (SST) was obtained from NOAA Coral Reef Watch daily  
115 nighttime global 5 km satellite coral bleaching heat stress monitoring product v3.1 between  
116 1985 and 2017 (NOAA Coral Reef Watch 2018). Daily sea surface temperature anomalies  
117 (SSTA), degree heating weeks (DHW) and bleaching alert areas (BAA) were also obtained  
118 from this dataset between 2015-2016. Hourly atmospheric data (including air temperature and  
119 pressure, wind vectors, cloud cover, humidity, longwave radiation, shortwave radiation) were

120 extracted at ~25 km resolution from the National Centers for Environmental Prediction's  
121 (NCEP's) Climate Forecast System Version 2 (CFSv2, <http://cfs.ncep.noaa.gov/>, Saha et al.  
122 (2011)).

123 Following a similar approach to Zhang et al. (2013), we used the CFSv2 data to calculate  
124 the net flux of heat across the air-sea interface ( $Q_{net}$ ,  $W m^{-2}$ ), i.e.

$$Q_{net} = Q_{SWR} + Q_{LWR} + Q_{lt} + Q_{sb}. \quad (1)$$

125 The short-wave radiation flux ( $Q_{SWR}$ ) represents the net input of solar energy to the ocean, and  
126 depends on factors such as the length of the day (which varies with season and latitude), and  
127 absorption or reflection in the atmosphere (e.g. by clouds). The outgoing long-wave radiation  
128 flux ( $Q_{LWR}$ ) is the infrared radiation emanating from the ocean surface back to the atmosphere  
129 and thus represents a heat loss from the ocean. Latent heat flux ( $Q_{lt}$ ) is the heat lost due to  
130 evaporation and is primarily influenced by wind speed and relative humidity. Sensible heat  
131 flux ( $Q_{sb}$ ) represents the convective heat exchange and is therefore related to the wind speed  
132 and the difference in temperature between the ocean and air. The latent and sensible terms were  
133 calculated using bulk atmospheric heat flux parametrizations, as described in Zhang et al.  
134 (2013).

135 The influence of strong winds and waves generated by tropical storms and cyclones on the  
136 temperature regimes at Scott Reef were investigated during the 2016 heatwave event and for a  
137 historical cyclone event in 2004. Hindcast predictions of the significant wave height ( $H_s$ ) and  
138 wind conditions (speed and direction) were output from the NOAA Wavewatch III model,  
139 (<http://polar.ncep.noaa.gov/waves/>, Tolman (2008)). Using output from these various datasets  
140 we calculated spatially-averaged values within the region bounded by longitudes [121.6°E  
141 122.1°E] and latitudes [13.6°S 14.2°S].

## 142 **Data analysis**

143 Daily mean temperatures were calculated for each logger by averaging over 24 h starting  
144 at midnight. Local measurements of water level were averaged at 15-minute intervals and put  
145 into a common vertical reference datum, by assuming at high tide the sea surface was flat across  
146 each atoll. The data were subsequently adjusted so that  $z = 0$  m corresponded to the mean water  
147 level of the experiment (Lowe et al. 2015).

148 Images collected at the long term monitoring sites were analysed using point sampling  
149 technique and benthic groups identified to the lowest taxonomic resolution achievable by each  
150 observer (Jonker et al. 2008). Monitoring sites vary in their taxonomic composition, but  
151 *Acropora* dominates in the shallow lagoons (Gilmour et al. 2013). The effects of heat stress on  
152 rates of bleaching and mortality among sites was therefore standardised by comparing the two  
153 most common coral groups at Scott Reef that have contrasting susceptibility to coral bleaching,  
154 and are also the most widely distributed across habitats and study sites over the system.  
155 *Acropora* were used as the most susceptible group to heat stress (we include here branching,  
156 corymbose, digitate and tabulate growth forms), while massive *Porites* is among the least  
157 susceptible (Gilmour et al. 2013; Hoey et al. 2016). Variation in coral mortality among sites,  
158 was calculated as the percentage change in coral cover before (January 2016) and after (October  
159 2016) the mass-bleaching. Sites were included only when the pre-bleaching cover of each coral  
160 groups was  $>2\%$ , as inferring mortality from relative changes in cover is unreliable when initial  
161 cover is low. The *Acropora* were found in high ( $>2\%$ ) abundance at all sites, whereas the  
162 massive *Porites* were rare ( $<2\%$ ) at some lagoon sites (10, 13, 14, 15).

163 We adopted the definition of Marine Heatwaves (MHW) developed by Hobday et al. (2016)  
164 as a discrete (i.e. clear start/end dates), prolonged (a duration of at least 5 consecutive days)  
165 anomalously warm water (relative to a baseline climatology) event. The baseline climatology  
166 was derived from daily SST between 1985-2014 using an 11-day window centered on the day,  
167 using codes available in R (<https://CRAN.R-project.org/package=RmarineHeatWaves>). Any

168 MHW was defined relative to a 90<sup>th</sup> percentile threshold, and for each event calculated, its  
169 duration (time between start and end dates), mean and maximum intensity (mean and highest  
170 temperature anomaly) were considered, as described in more detail in Hobday et al. (2016).  
171 We applied the climatology to the SST from the beginning of 2015 to investigate the 2015-  
172 2016 heatwave event in the Scott Reef region. In addition, we identified and quantified MHWs  
173 from daily *in situ* temperature logger measurements, using a climatology calculated using the  
174 average temperature for all records over the Scott Reef system, where data had been collected  
175 intermittently over 7 long term monitoring sites since 2006 (denoted by unfilled symbols in  
176 Figure 3).

## 177 **Results**

### 178 **Thermal conditions**

179 During the austral summer of 2015-2016, the ocean off northwestern Australia began to  
180 experience a marine heatwave. The waters surrounding Scott Reef had large positive SST  
181 anomalies of 2°C during the hottest month of March 2016 (Figure 4a). The other oceanic reefs  
182 of Ashmore and the Rowley Shoals experienced anomalies of 1.5°C and 1.2°C, respectively.  
183 A comparison of the mean temperature obtained by averaging over all of the *in situ* sites at  
184 Scott Reef against the SST shows close agreement between the two data sources ( $R^2 = 0.91$ ,  
185 root mean squared deviation = 0.24°C for the time period shown in Figure 5a).

186 The October 2015 to October 2016 SST record for the waters surrounding Scott Reef  
187 revealed several periods above the threshold to be classified as a MHW, initially starting in  
188 October 2015 (Figure 4b). The longest continuous MHW (237 d) occurred from 19 March to  
189 10 November 2016 with a mean temperature anomaly of 1.4°C, and a maximum temperature  
190 anomaly of 2.5°C on 2 March 2016. There were two notable decreases over the period shown,  
191 in which the SSTs fell outside of MHW conditions: in mid-December 2015 (where the SST

192 dropped by 2.5°C over 16 d) and late January 2016 (where the SST dropped by 1.3°C over 8  
193 d). The 2.5°C temperature decrease in SST mid-December 2015 corresponds to the onset of  
194 the Australian summer monsoon, which creates negative air-sea heat fluxes (i.e., ocean  
195 cooling) due to increased cloud cover, wind and rainfall (see Benthuisen et al. 2018 for more  
196 detail). For the second event, moderate wind speeds of up to 10.5 m s<sup>-1</sup> and low pressure of  
197 1006 hPa at the end of January (Figure 5b,c) coincided with the passage of Tropical Cyclone  
198 (TC) Stan, a category 3 cyclone that traversed southwards ~300 km to the west of Scott Reef  
199 on 27 January 2016 (Figure 1a). Cyclone Stan caused a 1.3°C temperature decrease at Scott  
200 Reef that alleviated the MHW conditions across the region for the following 25 days. The  
201 summer MHW corresponded with coral bleaching heat stress that peaked at 16.6°C-weeks in  
202 early May, experienced 4°C-weeks (i.e., significant coral bleaching) for 173 d, and reached  
203 NOAA’s CRW alert level 2 (i.e., mortality likely) for 58 d.

#### 204 **Air-sea heat exchange**

205 We investigated how the air-sea heat flux terms in Equation 1 varied over the annual cycle  
206 to understand how differences in atmospheric forcing contribute to the heating or cooling of  
207 ocean temperatures (Figure 6a). During the continuous MHW months of February – September  
208 2016, there was net heating (positive  $Q_{net}$ ) in all months apart from May through July, when  
209 there was net cooling (negative  $Q_{net}$ ). The air-sea heat flux variability was predominantly driven  
210 by variations in the positive solar energy input (short-wave radiation) and the heat loss due to  
211 evaporation (latent heat flux), which contributed to a mean total heat flux value of +104 W m<sup>-2</sup>  
212 during March 2016.

213 The ‘exposed’ reef temperature sites (sites 1-6 and 11 in Figure 3), defined as those not  
214 bounded by a near-continuous reef rim, had similar in situ temperatures to the offshore SST,  
215 i.e., the difference in temperature relative to offshore SST ( $\Delta T$ ) was ~0°C (shown for sites 2, 4

216 and 11 in Figure 6b). In contrast, at sites within the enclosed lagoons of North Scott and  
217 Seringapatam Reef (i.e., sites 9, 10, 13-15), the difference between in situ temperatures and  
218 those offshore generally followed a similar pattern to the variation of the net air-sea heat flux  
219 ( $Q_{net}$ ), whereby lagoon temperatures were warmer than offshore ( $\Delta T > 0^\circ\text{C}$ ) in all months apart  
220 from May through July (shown for sites 10 and 13 in Figure 6c). The exception was one site in  
221 the southern Seringapatam lagoon (site 15), where the temperature difference did not correlate  
222 with the variation in the net heat flux. Temperatures here were cooler than those offshore ( $\Delta T$   
223  $< 0^\circ\text{C}$ ) for  $\sim 75\%$  of the time, compared to  $\sim 30\%$  of time for the next closest lagoon site (site  
224 14,  $\sim 2$  km away).

225 To investigate how the large tides interact with the atoll morphology to explain the  
226 temperature variability observed in southern Seringapatam lagoon (site 15), we examined the  
227 water levels and in situ temperature over the whole study period, and display here one  
228 representative cycle in March 2016 (Figure 7). During this spring-neap cycle the lagoon water  
229 level ( $\eta$ ) closely followed the offshore water level on only one day (18 March), during the  
230 minimum neap tide. For the remainder of the spring-neap cycle there were significant  
231 differences in tidal height (due to tidal truncation, where the offshore water level falls below  
232 the reef rim), particularly during spring tide; as a consequence, at spring low tide the lagoon  
233 water level was up to 1.3 m higher than offshore, and took up to 9 h to transition from high to  
234 low tide (Figure 7a). For the duration of the field observations we calculated the mean range  
235 and duration of the tidal rise and fall for Seringapatam lagoon (site 13) and outer reef (site 12).  
236 Outside of the lagoon, the mean tidal range was 2.2 m, with comparable mean tidal rise and  
237 fall durations of 6.3 and 6.1 h. In contrast, within the lagoon the mean tidal range was only 1.5  
238 m, with a shorter mean tidal rise duration of 3.9 h and an extended tidal fall duration of 8.5 h.

239 These tidal characteristics worked together with local net air-sea heat fluxes to drive the  
240 temperature variability observed in southern Seringapatam. The central lagoon and outer reef

241 temperatures generally increased during the day and cooled at night (reflecting the diurnal  
242 variability in the net air-sea heat flux), with the outer reef daily temperature on average 0.4°C  
243 cooler than in the lagoon (Figure 7b). The temperature difference between the central and  
244 southern lagoon sites was affected by both the tidal range and the location of the lagoon sites.  
245 When the tidal range was large (>2.5 m), the temperature in the southern lagoon was similar to  
246 the central lagoon. However, as the tidal range decreased towards neap tide, night-time  
247 temperatures in the southern lagoon (site 15) fell when the tide flooded (e.g. by 2.1°C over 6 h  
248 on the 18 March). The daily temperature range in the southern lagoon increased as the tidal  
249 range fell up until 19 March, at which point temperatures remained significantly cooler than at  
250 the central lagoon and outer reef sites. The greatest concurrent temperature difference for the  
251 two lagoon sites shown reached 2.9°C, despite being only 3.5 km apart and at a similar depth.  
252 This neap tide cooling at the southern site was recurrent over multiple spring-neap cycles  
253 throughout the observation period.

#### 254 **Cool water influence and bleaching observations**

255 For each site, we calculated the mean daily temperature and mean daily temperature range  
256 from in situ loggers for the deployment period between January and April (Figure 8a,b).  
257 Generally, cooler mean daily temperatures (30.7 - 31°C) were observed at sites located on the  
258 reef slope sites exposed to offshore waters and those in the South Reef lagoon. Within the  
259 shallow enclosed lagoons of North Reef and Seringapatam, there were three sites with warmer  
260 mean temperatures (31.3 – 31.5°C, sites 10, 15 and 16), but also sites where the mean  
261 temperatures were similar to the exposed sites (30.8 – 30.9°C sites 9 and 14). With the  
262 exception of the cooler site (site 15) within the Seringapatam lagoon (with the largest mean  
263 daily range of 1.6°C), small mean daily temperature ranges <0.4°C were observed in the semi-  
264 enclosed lagoons, increasing to a maximum of 0.7°C on the eastern reef slopes and within  
265 South Reef. The three sites that are more exposed to deeper oceanic water on the western reef

266 slopes and in the channel experienced larger mean ranges of  $>0.9^{\circ}\text{C}$ . At site 3, temperature  
267 drops of up to  $2.7^{\circ}\text{C}$  as the tide flooded were sometimes detected. Bleaching scores revealed  
268 severe bleaching across the study area, with 92% of sites being  $>61\%$  bleached (Figure 8c).  
269 The only site with less severe bleaching (between 31–60%) was in southern Seringapatam (site  
270 15). Generally, lower incidences of bleaching were found at sites where the daily mean  
271 temperature range was larger. We show the relative change in coral cover of the two most  
272 widely distributed species with contrasting susceptibilities to bleaching (Figure 8d,e). Overall,  
273 mortality that occurred following bleaching was lower for the massive *Porites* than for  
274 *Acropora*. The maximum reduction in cover of massive *Porites* was 55%, whereas *Acropora*  
275 cover decreased by  $>85\%$  at all sites not subject to cooling, and there were five sites where the  
276 decrease was 100%. For both coral groups, mortality was far lower at sites 3, 4 and 15,  
277 reflecting the role of local mechanisms of cooling in reducing mortality rates of corals with  
278 contrasting susceptibilities.

279 In situ MHW metrics give an indication of the heat stress experienced at individual sites  
280 (Table 1). With the exception of the cooler Seringapatam lagoon site (site 15), the highest  
281 temperature anomalies (greatest maximum intensity) were observed in the semi-enclosed  
282 lagoons and all occurred within a four day period (3-6 March) that surrounded neap tide on 4  
283 March. The total duration of MHWs over the period in situ data were available for these sites  
284 (1 February – 30 September) varied substantially between 92 (site 15) and 215 days (site 11)  
285 but had an almost uniform mean intensity of  $1.2$  or  $1.3^{\circ}\text{C}$  (Table 1).

## 286 **Discussion**

287 During the austral summer of 2015-2016, an extreme and prolonged MHW was observed  
288 across tropical northwestern Australia, which caused severe coral bleaching and mortality at  
289 the three atolls of the Scott Reef system. The extended MHW through the winter months likely

290 compounded the effects of the summer MHW by decreasing the potential for corals to recover.  
291 Persistent thermal anomalies can cause disease outbreak (Miller et al. 2009) and also inhibit  
292 reproduction; typically coral spawning would be expected in both autumn and spring on these  
293 reefs, but neither spawning nor visible eggs were observed around the predicted spawning dates  
294 in 2016 (Foster et al. 2018). In this region, MHWs are typically related to El Niño conditions,  
295 whereas for the subtropical reefs further south along the Western Australia (WA) coast (i.e.  
296 south of 22°S), MHWs are associated with La Niña conditions (Zhang et al. 2017; Xu et al.  
297 2018). During El Niño, the Australian Monsoon tends to weaken, resulting in reduced cloud  
298 cover and winds, which increases the net air-sea heat flux input at regional scales (Zhang et al.  
299 2017; Benthuyesen et al. 2018). During La Niña years, the intensification of the Leeuwin  
300 Current, a poleward flowing eastward boundary current, transports anomalously warm tropical  
301 water southwards along the subtropical coast of WA that can result in large temperature  
302 anomalies (Feng et al. 2013), which in turn can severely impact coastal ecosystems throughout  
303 southwestern Australia (Wernberg et al. 2013). Latitudinal differences in temperature  
304 anomalies during the peak period of the MHW in 2016 revealed minimal heat stress along the  
305 southern Pilbara and Midwest-Gascoyne coasts, while positive anomalies were sustained at  
306 Christmas Island, the oceanic atolls and inshore Kimberly, consistent with regional warming  
307 patterns expected during El Niño conditions (Figure 4a).

308 The study focused on the tide-dominated reefs of the Scott Reef atoll system, which have  
309 previously demonstrated remarkable recovery (over decadal timescales) from severe  
310 disturbances, including bleaching events and tropical cyclone damage (Gilmour et al. 2013).  
311 The Scott Reef system is geographically isolated from other reef systems, and consequently is  
312 thought to receive a negligible supply of larvae from external sources, relying primarily on  
313 local brood stock to replenish the reef over ecological time scales (Gilmour et al. 2009;  
314 Underwood et al. 2009; Underwood et al. 2018). It is therefore important to determine how the

315 local oceanography can help to alleviate heat stress and subsequent coral bleaching within  
316 specific areas within the reefs, given that any remnant populations surviving a mass beaching  
317 event could help to facilitate future reef recovery. Based on the patterns of the temperature  
318 variability and the bleaching response across the three atolls, we can identify three different  
319 cooling mechanisms observed at Scott Reef that acted to reduce heat stress during the 2015-  
320 2016 MHW.

### 321 **Cooling mechanism 1: Tropical Cyclone Stan**

322 Tropical cyclones are able to induce SST cooling at ocean scales of over 100s of  
323 kilometers, and alleviate heat stress in coral reef regions sufficiently enough to mitigate  
324 impending bleaching during a MHW (Carrigan and Puotinen 2014). Negative net air-sea heat  
325 fluxes during tropical cyclones, due to factors such as increased wind, cloud cover and reduced  
326 solar insolation cause heat loss from the upper ocean (see Equation 1 and Figure 6a).  
327 Furthermore, vigorous mixing of the upper ocean from the strong winds associated with  
328 tropical cyclones entrains colder water from beneath the thermocline, which deepens the mixed  
329 layer to cool surface temperatures (Rayson et al. 2015). This ocean mixing mechanism usually  
330 dominates the SST response to cyclonic conditions, with air-sea heat fluxes playing a  
331 secondary role (Price 1981). For the Great Barrier Reef located off the opposite side of the  
332 Australian continent, which also experienced severe heat stress in 2016, atmospheric cooling  
333 and ocean mixing from ex-Tropical Cyclone Winston potentially prevented widespread  
334 bleaching in its vicinity over the southern regions (Hughes et al. 2017). Previous studies have  
335 highlighted how frequently tropical cyclones influence reefs in northwestern Australia (Zinke  
336 et al. 2018) and that they can readily induce vertical mixing to 80-120 m depth (Rayson et al.  
337 2015) causing deeper, cooler water to be entrained into the surface.

338 In northwestern Australia, the trajectory of Tropical Cyclone Stan at the end of January  
339 2016 resulted in a 1.3°C drop in SST in the ocean surrounding Scott Reef, which halted MHW  
340 conditions for 25 days and likely slowed the onset of bleaching. Whilst the effect of tropical  
341 cyclones may be beneficial to coral reefs by reducing temperatures in a cool wake, strong wind  
342 and waves can also cause catastrophic damage. For example, Cyclone Fay (category 5) passed  
343 directly over Scott Reef in 2004, with significant wave heights ( $H_s$ ) incident to the reef reaching  
344 5.6 m (estimated from Wavewatch III), which caused extensive damage to reef communities,  
345 including thousands of massive corals dislodged and pushed up onto the reef flat (Gilmour and  
346 Smith 2006). Tropical Cyclone Stan in 2016 instead had a positive effect on Scott Reef, as it  
347 passed sufficiently far enough away from the system (~300 km) for coral colonies to experience  
348 cooling but not to be affected by the damaging effect of strong waves. Despite  $H_s$  reaching 2.8  
349 m on 30 January 2016 (estimated from Wavewatch III), no evidence of any new cyclone  
350 damage was observed in our surveys.

### 351 **Cooling mechanism 2: large tides with local air-sea heat exchange**

352 At Scott Reef the large tidal amplitude exceeds the depth of the reef rim relative to  
353 mean sea level, and as a result the reef rim becomes exposed on each tidal cycle, which creates  
354 a highly asymmetric tide in the semi-enclosed lagoons (Figure 7a). In Seringapatam the mean  
355 falling period of the tide (8.5 h) occupies most of the full 12.4 h duration of the semi-diurnal  
356 tide, and at low tide the water level can be 1.3 m higher than offshore at low tide. During the  
357 low phases of the tide, water can only exchange between the lagoon and open-ocean through  
358 one narrow channel in the northeast (Figure 2b). Reduced exchange (and hence enhanced  
359 residence times) associated with this tidal truncation can drive temperature extremes, as air-sea  
360 heat exchange can act longer on reef waters at low tide to alter temperatures (Lowe et al. 2016).

361 During the 2015-2016 MHW, positive air-sea heat flux anomalies intensified oceanic  
362 heating to increase SST anomalies at regional scales across tropical northern Australia  
363 (Benthuisen et al. 2018). In shallow and semi-enclosed reef systems local air-sea heat fluxes  
364 can then further regulate warming responses within reef systems to enhance or alleviate any  
365 pre-existing regional warming (MacKellar et al. 2013; Zhang et al. 2013). At Scott Reef, sites  
366 within shallow enclosed lagoons were generally warmer than offshore during the summer and  
367 cooler during winter months, reflecting a seasonal reversal in the net air-sea heat fluxes ( $Q_{net}$ )  
368 from net heat input in summer and heat loss in the winter; whereas sites exposed to the  
369 surrounding ocean had similar temperatures to offshore waters (Figure 6). The mean daily  
370 temperature in the enclosed lagoons (between January and April) was generally higher than at  
371 exposed sites, given that the time it takes for lagoon water to be replaced with oceanic water  
372 can be lengthy (order of days, see Green et al. (2018a)). This implies that in the summer (when  
373  $Q_{net}$  is positive), these lagoon sites are likely to heat up more quickly and remain warmer for  
374 longer periods; therefore, reef communities living within these reefs would be susceptible to  
375 greater levels of heat stress than at the exposed sites (Figure 8).

376 The largest temperature range was, however, observed inside the southern lagoon of  
377 Seringapatam, where water was cooled over the shallow reef rim at night-time (consistent with  
378 a negative hourly  $Q_{net}$ , not shown). As the tide began to flood, this cooled water was transported  
379 into the lagoon and caused large decreases in night-time temperatures at the adjacent lagoon  
380 site during neap tide (Figure 7). At North Reef, flushing through channels is generally spatially-  
381 limited to those areas adjacent to the channels (Green et al. 2018a), and it is therefore unlikely  
382 that this site is influenced by any exchange through the northeastern channel. This mechanism  
383 was only observed at neap tide as during spring tide when the flows are strong, the tides would  
384 contribute to mixing of lagoon and oceanic waters, and also decrease the lagoon residence time.  
385 During neap tide, higher residence times combined with low tidal energetics and enhanced

386 nocturnal cooling due to the shallower depths over the reef rim allowed cooler, denser water  
387 from the reef rim to sink to the lagoon floor. This resulted in concurrent temperature differences  
388 of up to 2.9°C with a central lagoon site. The temperature remained cooler until the tidal range  
389 increased, which likely promoted mixing with warmer lagoon surface and offshore waters,  
390 causing temperatures to return to similar values as the other sites during spring tide. As a result  
391 of the extended period of cooler temperatures which halved the MHW duration compared to  
392 other sites (Table 1), considerably less bleaching (31-60%) and mortality was observed (the  
393 relative decrease in cover of *Acropora* was 11% despite being the dominant species, compared  
394 to 100% at other lagoon sites of Seringapatam). Therefore survivors from this site will be  
395 important in the recovery of the broader reef that experienced severe bleaching.

396 Over the rest of the Scott Reef system, the maximum intensity of heat stress detected  
397 in situ occurred within a 3-day period coinciding with neap tide in March (Table 1), indicating  
398 that reduced tidal flows and shallower depths generally strengthen the temperature anomalies.  
399 The reef rim cooling mechanism was not detected at other enclosed lagoon sites we studied  
400 because either they were too far from the reef rim to benefit from the cooling (sites 10, 13 and  
401 14), or rapid flushing of the lagoon prevented cooler temperatures from persisting (site 9, see  
402 Green et al. (2018a)). However, we anticipate that other locations adjacent to the reef rim in  
403 southern Seringapatam are likely to experience the benefits of the tide-induced night-time  
404 cooling.

### 405 **Cooling Mechanism 3: internal tides**

406 The final cooling mechanism is related to the presence of internal tides, which occur  
407 due to the combination of steeply sloping bathymetry, large tidal range and stratified water  
408 column surrounding Scott Reef. In the channel separating North and South Reef, internal tides  
409 cause isotherm displacements of up to 100 m during spring tide, allowing cooler water to mix

410 with surface waters (Rayson et al. 2018). In the western entrance to South Reef, cool water  
411 intrusions of up to 4.5°C have been detected at 40 m depth as cooler, deeper offshore water is  
412 advected upslope as the tide floods into the lagoon (Green et al. 2018b). In the shallower  
413 environments these intrusions are intermittently observed, but temperature drops of up to 2.7°C  
414 concurrent with flooding tide were sometimes detected at site 3. As the reef lies on the edge of  
415 the continental shelf, depths plummet more rapidly on the west side (~1000 m) than on the east  
416 (~500 m). The internal tide processes that originate in the deeper ocean on the west are reflected  
417 in the higher daily temperature range and the comparatively moderate bleaching observed in  
418 the west and channel sites during 2016, consistent with studies showing that large diurnal  
419 temperature variability can mitigate the risk of bleaching at the reef-scale (Safaie et al. 2018).  
420 Such thermocline shoaling delivers cooler, deeper water into shallow reef environments, and  
421 has previously been demonstrated to reduce thermal warming sufficiently enough to reduce  
422 bleaching (Wall et al. 2015; Schmidt et al. 2016). At the sites exposed to cooler water at Scott  
423 Reef (3, 3a and 4) 61–90% of communities were bleached, compared to >91% in the eastern  
424 sites (1 and 5), and a similar pattern of variation was evident following the 1998 bleaching  
425 event at Scott Reef (Smith et al. 2008; Gilmour et al. 2013), creating an additional area in the  
426 atoll system where temperature anomalies can be reduced by the oceanic processes.

427         In summary, in this study we have identified three physical mechanisms that acted to  
428 locally alleviate heat stress and/or bleaching severity within different parts of the Scott Reef  
429 system of atolls during the MHW. Both the cool water intrusions and air-sea heat flux  
430 mechanisms described created local areas where bleaching severity was reduced. These  
431 processes are dependent on the relatively large tides present around these reefs, and thus similar  
432 processes may occur in other tide-dominated reefs worldwide. Although sites exposed to the  
433 cooling mechanisms experienced lower incidences of bleaching, percentages of affected corals  
434 were still substantial (>31%), highlighting that exposure to these processes will not guarantee

435 the necessary relief from stressful or lethal temperatures on coral reefs, and may not be  
436 sufficient to prevent bleaching in the future. Marine heatwaves are occurring globally with  
437 increased frequency and severity, and the world's oceans will further warm into this century  
438 (Oliver et al. 2018). Therefore, understanding the physical processes that promote reef  
439 resilience is critical to identifying local areas of refugia, to help determine potential future  
440 patterns of survival and recovery, and focus management strategies on locations that merit  
441 strong conservation action.

442

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## **Figure Legends**

Figure 1. Study area. (a) Regional context of the Scott Reef system and nearby reefs in northwestern Australia. Tropical Cyclone Stan track marked with dates, which passed ~300 km to the west of the system in late January 2016. (b) The three atolls of South Reef, North Reef and Seringapatam Reef, area bounded by box in (a).

Figure 2. Aerial photographs of Seringapatam Reef. (a) Photo showing the wide reef rim on the east of the atoll, which is similar to that enclosing North Reef. (b) Photo of the channel in the northeast, at low tide this is the only conduit through which lagoon water can exchange with open ocean water. Photo credit: Nick Thake Photography.

Figure 3. Site locations for (a) North and South Reef, with bathymetry <65 m displayed as a colormap and depths >65 m shown as contours. (b) Seringapatam (using ESRI satellite World Imagery, as no detailed bathymetry was available). Specific observations at each site indicated by the legend in (b), where  $\eta$  is water level and LTM is a long term benthic monitoring site.

Figure 4. Thermal conditions surrounding the bleaching event. (a) Regional scale pattern of satellite sea surface temperature anomalies (SSTA), monthly averaged for the hottest month of March 2016. (b) Satellite sea surface temperature (SST) spatially averaged over the Scott Reef area, with the climatological mean (blue) and 90<sup>th</sup> percentile threshold (green), calculated using a climatology derived between the years 1985 – 2014. The shaded red area indicates the periods during which marine heatwaves were detected, using methods described in Hobday et al. (2016). Corresponding NOAA CRW degree heating weeks (DHW) displayed in red on the right axis, with bleaching alert levels superimposed (warning - possible bleaching, alert level 1 - bleaching likely, alert level 2 - mortality likely)

Figure 5. Effect of Tropical Cyclone Stan. (a) Mean daily in situ (red) temperature for all instruments, and mean satellite sea surface temperature (black) for pixels surrounding Scott Reef. The lightly shaded regions represent the standard deviation of the mean. (b) Wind speed and (c) atmospheric pressure, derived from the Climate Forecast System Version 2 (CFSv2) hourly product, averaged over 1 day. Vertical dashed line indicates the arrival of TC Stan in the region.

Figure 6. Heat flux variables and their effect on temperature. (a) Seasonal snapshot of terms that comprise the net air-sea heat fluxes  $Q_{net}$  surrounding Scott Reef for the period of temperature logger deployment, including the net short- and long-wave radiation ( $Q_{SWR}$  and

$Q_{LWR}$ ), the latent ( $Q_l$ ) and sensible ( $Q_{sb}$ ) heat flux contributions. Refer to methods for descriptions of terms. Note that positive values represent heat input to the ocean. Vertical dashed line indicates the arrival of TC Stan. (b) Differences ( $\Delta T$ ) in daily mean temperature at exposed lagoon or slope sites, relative to offshore SST. The dashed line ( $\Delta T = 0$ ) indicates no difference in temperature. (c) as (b) but for shallow semi-enclosed lagoon sites. All data are smoothed with a 7 day moving average.

Figure 7. Snapshot of a spring-neap cycle at Seringapatam. (a) Outer slope (black) and lagoon (red) water level ( $\eta$ ) relative to mean sea level. (b) In situ temperature for sites on the outer reef (11, black), central (13, red) and south (15, green) lagoon. Night-time indicated by gray shaded areas.

Figure 8. Spatial overview of bleaching event. (a) Mean daily temperature between 16 January and 13 April 2016. (b) Mean daily temperature range for the same time period. (c) Bleaching categories observed in April 2016. Relative change (mortality) in percentage cover before (January 2016) and after (October 2016) mass-bleaching for the dominant (d) massive *Porites* and (e) *Acropora* coral groups. \*s indicate sites where cooling occurs.