

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

Rebecca Green^{1,2,3}, Ryan Lowe^{1,2,3}, Mark Buckley^{3,4}, Taryn Foster⁵, James Gilmour⁵

¹ The Oceans Institute and School of Earth Sciences, University of Western Australia, Crawley, WA, Australia

² ARC Centre of Excellence for Coral Reef Studies, University of Western Australia, Crawley, WA, Australia

³ Oceans Graduate School, University of Western Australia, Crawley, WA, Australia

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

⁵ Australian Institute of Marine Science, Indian Ocean Marine Research Center, Crawley, WA, Australia

Corresponding author: rebecca.green@uwa.edu.au

Keywords: tide-dominated, atoll, hydrodynamics, temperature variability, coral bleaching, northwestern Australia

1 Abstract

2 Interactions between oceanic and atmospheric processes within coral reefs can significantly
3 alter local scale (< kilometers) water temperatures, and consequently drive variations in
4 heat stress and bleaching severity. The Scott Reef atoll system was one of many reefs
5 affected by the 2015-2016 mass coral bleaching event across tropical Australia, and
6 specifically experienced sea surface temperature anomalies of 2°C that caused severe mass
7 bleaching (61-90%) over most of this system; however, the bleaching patterns were not
8 uniform. Little is known about the processes governing thermodynamic variability within
9 atolls, particularly those that are dominated by large amplitude tides. Here we identify three
10 mechanisms at Scott Reef that alleviated heat stress during the marine heatwave in 2016:
11 1) the cool wake of a tropical cyclone that induced temperature drops of 1.3°C over a period
12 of 10 days; 2) air-sea heat fluxes that interacted with the reef morphology during neap tides
13 at one of the atolls to reduce water temperatures by up to 2.9°C; 3) internal tidal processes
14 that forced deeper and cooler water (up to 2.7°C) into some sections of the shallow reefs.
15 The latter two processes created localized areas of reduced temperatures that led to lower
16 incidences of coral bleaching for parts of the reef. We predict these processes are likely to
17 occur in other similar tide-dominated reef environments worldwide. Identifying locations
18 where physical processes reduce heat stress will likely be critical for coral reefs in the
19 future, by maintaining communities that can help facilitate local recovery of reefs following
20 bleaching events that are expected to increase in frequency and severity in the coming
21 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 90th 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⁻¹ 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⁻²
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 (ΔT) 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 (ΔT
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, ~ 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 (η) 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°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°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

Acknowledgements

443 We would like to thank the Captain, crew and scientists of the R/V Solander cruises 6392, 6430
444 and 6551. This research was supported by the Australian Federal Government through the
445 Australian Institute of Marine Science and the Browse LNG Development Joint Venture
446 Participants, through the operator Woodside Energy Limited. Funding to R.H.G. was provided
447 by the ARC Centre of Excellence for Coral Reef Studies, and a UWA University Postgraduate
448 Award for International Students. On behalf of all authors, the corresponding author states that
449 there is no conflict of interest. We certify that this article was prepared as part of official duties
450 at the US Geological Survey. The article is thus in the public domain and cannot be
451 copyrighted.

References

- 452 Andréfouët S, Dutheil C, Menkes CE, Bador M, Lengaigne M (2015) Mass mortality events in atoll lagoons:
453 environmental control and increased future vulnerability. *Global Change Biology* 21:195-205
- 454 Benthuyssen JA, Oliver ECJ, Feng M, Marshall AG (2018) Extreme Marine Warming Across Tropical Australia
455 During Austral Summer 2015–2016. *Journal of Geophysical Research: Oceans*:n/a-n/a
- 456 Carrigan AD, Puotinen M (2014) Tropical cyclone cooling combats region-wide coral bleaching. *Global Change*
457 *Biology* 20:1604-1613
- 458 Davis KA, Lentz SJ, Pineda J, Farrar JT, Starczak VR, Churchill JH (2011) Observations of the thermal
459 environment on Red Sea platform reefs: a heat budget analysis. *Coral Reefs* 30:25-36
- 460 DeCarlo TM, Cohen AL, Wong GTF, Davis KA, Lohmann P, Soong K (2017) Mass coral mortality under local
461 amplification of 2 °C ocean warming. *Scientific Reports* 7:44586
- 462 Depczynski M, Gilmour JP, Ridgway T, Barnes H, Heyward AJ, Holmes TH, Moore JAY, Radford BT, Thomson
463 DP, Tinkler P, Wilson SK (2013) Bleaching, coral mortality and subsequent survivorship on a West
464 Australian fringing reef. *Coral Reefs* 32:233-238
- 465 Eakin CM, Liu G, Gomez AM, De La Cour JL, Heron SF, Skirving WJ, Geiger EF, Marsh BL, Tirak KV, Strong
466 AE (2017) Ding, Dong, The Witch is Dead (?) - Three Years of Global Coral Bleaching 2014-2017. *Reef*
467 *Encounter* 45:33-38
- 468 Falter JL, Zhang ZL, Lowe RJ, McGregor F, Keesing J, McCulloch MT (2014) Assessing the drivers of spatial
469 variation in thermal forcing across a nearshore reef system and implications for coral bleaching.
470 *Limnology and Oceanography* 59:1241-1255
- 471 Feng M, McPhaden MJ, Xie S-P, Hafner J (2013) La Niña forces unprecedented Leeuwin Current warming in
472 2011. *Scientific Reports* 3:1277
- 473 Foster T, Heyward AJ, Gilmour JP (2018) Split spawning realigns coral reproduction with optimal environmental
474 windows. *Nat Commun* 9:718
- 475 Gilmour JP, Smith LD (2006) Category 5 cyclone at Scott Reef, northwestern Australia. *Coral Reefs* 25:200-200
- 476 Gilmour JP, Smith LD, Brinkman RM (2009) Biannual spawning, rapid larval development and evidence of self-
477 seeding for scleractinian corals at an isolated system of reefs. *Marine Biology* 156:1297-1309
- 478 Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an Isolated Coral Reef System
479 Following Severe Disturbance. *Science* 340:69-71
- 480 Green RH, Lowe RJ, Buckley ML (2018a) Hydrodynamics of a Tidally Forced Coral Reef Atoll. *J Geophys Res*
481 *Oceans* 123
- 482 Green RH, Jones NL, Rayson MD, Lowe RJ, Bluteau CE, Ivey GN (2018b) Nutrient fluxes into an isolated coral
483 reef atoll by tidally driven internal bores
- 484 Gruber RK, Lowe RJ, Falter JL (2017) Metabolism of a tide-dominated reef platform subject to extreme diel
485 temperature and oxygen variations. *Limnology and Oceanography* 62:1701–1717
- 486 Gruber RK, Lowe RJ, Falter JL (2018) Benthic uptake of phytoplankton and ocean-reef exchange of particulate
487 nutrients on a tide-dominated reef. *Limnology and Oceanography* 0
- 488 Heron SF, Maynard JA, van Hooidek R, Eakin CM (2016) Warming Trends and Bleaching Stress of the World's
489 Coral Reefs 1985–2012. *Scientific Reports* 6:38402
- 490 Hobday AJ, Alexander LV, Perkins SE, Smale DA, Straub SC, Oliver ECJ, Benthuyssen JA, Burrows MT, Donat
491 MG, Feng M, Holbrook NJ, Moore PJ, Scannell HA, Sen Gupta A, Wernberg T (2016) A hierarchical
492 approach to defining marine heatwaves. *Progress in Oceanography* 141:227-238
- 493 Hoegh-Guldberg OCCS (2005) Low coral cover in a high-CO2 world. *Journal of Geophysical Research: Oceans*
494 110:n/a-n/a
- 495 Hoey A, Howells E, Johansen J, Hobbs J-P, Messmer V, McCowan D, Wilson S, Pratchett M (2016) Recent
496 Advances in Understanding the Effects of Climate Change on Coral Reefs. *Diversity* 8:12
- 497 Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger
498 M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE, Comeau S, Connolly SR,
499 Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF,
500 Hoey AS, Hobbs J-PA, Hoogenboom MO, Kennedy EV, Kuo C-y, Lough JM, Lowe RJ, Liu G,
501 McCulloch MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V,
502 Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017) Global
503 warming and recurrent mass bleaching of corals. *Nature* 543:373-377
- 504 Jokiel PL, Brown EK (2004) Global warming, regional trends and inshore environmental conditions influence
505 coral bleaching in Hawaii. *Global Change Biology* 10:1627-1641
- 506 Jonker M, Johns K, Osborne K (2008) Surveys of benthic reef communities using underwater digital photography
507 and counts of juveniles Long-term monitoring of the Great Barrier Reef Standard Operation Procedure
508 Number 10. Australian Institute of Marine Science, Townsville

509 Leichter JJ, Stokes MD, Hench JL, Witting J, Washburn L (2012) The island-scale internal wave climate of
510 Moorea, French Polynesia. *Journal of Geophysical Research-Oceans* 117

511 Lentz SJ, Churchill JH, Marquette C, Smith J (2013) Evaluation and Recommendations for Improving the
512 Accuracy of an Inexpensive Water Temperature Logger. *J Atmos Oceanic Technol* 30:1576-1582

513 Lowe RJ, Falter JL (2015) Oceanic forcing of coral reefs. *Annual Review of Marine Science* 7:43-66

514 Lowe RJ, Falter JL, Monismith SG, Atkinson MJ (2009) Wave-Driven Circulation of a Coastal Reef-Lagoon
515 System. *Journal of Physical Oceanography* 39:873-893

516 Lowe RJ, Leon AS, Symonds G, Falter JL, Gruber R (2015) The intertidal hydraulics of tide-dominated reef
517 platforms. *Journal of Geophysical Research: Oceans* 120:4845-4868

518 Lowe RJ, Pivan X, Falter J, Symonds G, Gruber R (2016) Rising sea levels will reduce extreme temperature
519 variations in tide-dominated reef habitats. *Science Advances* 2

520 MacKellar MC, McGowan HA, Phinn SR (2013) An observational heat budget analysis of a coral reef, Heron
521 Reef, Great Barrier Reef, Australia. *Journal of Geophysical Research: Atmospheres* 118:2547-2559

522 McCabe RM, Estrade P, Middleton JH, Melville WK, Roughan M, Lenain L (2010) Temperature variability in a
523 shallow, tidally isolated coral reef lagoon. *Journal of Geophysical Research-Oceans* 115

524 McGowan HA, Sturman AP, MacKellar MC, Wiebe AH, Neil DT (2010) Measurements of the local energy
525 balance over a coral reef flat, Heron Island, southern Great Barrier Reef, Australia. *J Geophys Res Atm*
526 115:D19124

527 Miller J, Muller E, Rogers C, Waara R, Atkinson A, Whelan KRT, Patterson M, Witcher B (2009) Coral disease
528 following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands.
529 *Coral Reefs* 28:925

530 NOAA Coral Reef Watch (2018) NOAA Coral Reef Watch Daily Global 5-km Satellite Coral Bleaching Sea
531 Surface Temperature Product v3.1. NOAA Coral Reef Watch, College Park, Maryland, USA

532 Oliver ECJ, Donat MG, Burrows MT, Moore PJ, Smale DA, Alexander LV, Benthuisen JA, Feng M, Sen Gupta
533 A, Hobday AJ, Holbrook NJ, Perkins-Kirkpatrick SE, Scannell HA, Straub SC, Wernberg T (2018)
534 Longer and more frequent marine heatwaves over the past century. *Nature Communications* 9:1324

535 Pedersen O, Colmer TD, Borum J, Zavala-Perez A, Kendrick GA (2016) Heat stress of two tropical seagrass
536 species during low tides – impact on underwater net photosynthesis, dark respiration and diel in situ
537 internal aeration 210:1207-1218

538 Pineda J, Starczak V, Tarrant A, Blythe J, Davis K, Farrar T, Berumen M, da Silva JCB (2013) Two spatial scales
539 in a bleaching event: Corals from the mildest and the most extreme thermal environments escape
540 mortality. *Limnology and Oceanography* 58:1531-1545

541 Price JF (1981) Upper Ocean Response to a Hurricane. *J Phys Oceanogr* 11:153-175

542 Rayson MD, Ivey GN, Jones NL, Fringer OB (2018) Resolving high-frequency internal waves generated at an
543 isolated coral atoll using an unstructured grid ocean model. *Ocean Modelling* 122:67-84

544 Rayson MD, Ivey GN, Jones NL, Meuleners MJ, Wake GW (2011) Internal tide dynamics in a topographically
545 complex region: Browse Basin, Australian North West Shelf. *Journal of Geophysical Research-Oceans*
546 116:C01016

547 Rayson MD, Ivey GN, Jones NL, Lowe RJ, Wake GW, McConochie JD (2015) Near-inertial ocean response to
548 tropical cyclone forcing on the Australian North-West Shelf. *Journal of Geophysical Research: Oceans*
549 120:7722-7751

550 Rogers JS, Monismith SG, Kowec DA, Torres WI, Dunbar RB (2016) Thermodynamics and hydrodynamics in
551 an atoll reef system and their influence on coral cover. *Limnology and Oceanography*:n/a-n/a

552 Safaie A, Silbiger NJ, McClanahan TR, Pawlak G, Barshis DJ, Hench JL, Rogers JS, Williams GJ, Davis KA
553 (2018) High frequency temperature variability reduces the risk of coral bleaching. *Nature*
554 *Communications* 9:1671

555 Saha S, Moorthi S, Wu X, Wang J, Nadiga S, Tripp P, Behringer D, Hou Y-T, Chuang H-y, Iredell M, Ek M,
556 Meng J, Yang R, Mendez MP, van den Dool H, Zhang Q, Wang W, Chen M, Becker E (2011) NCEP
557 Climate Forecast System Version 2 (CFSv2) Selected Hourly Time-Series Products. Research Data
558 Archive at the National Center for Atmospheric Research, Computational and Information Systems
559 Laboratory, Boulder, CO

560 Schmidt GM, Wall M, Taylor M, Jantzen C, Richter C (2016) Large-amplitude internal waves sustain coral health
561 during thermal stress. *Coral Reefs* 35:869-881

562 Smith LD, Gilmour JP, Heyward AJ (2008) Resilience of coral communities on an isolated system of reefs
563 following catastrophic mass-bleaching. *Coral Reefs* 27:197-205

564 Tolman HL (2008) A mosaic approach to wind wave modeling. *Ocean Modelling* 25:35-47

565 Underwood JN, Smith LD, Oppen MJHv, Gilmour JP (2009) Ecologically relevant dispersal of corals on isolated
566 reefs: implications for managing resilience. *Ecological Applications* 19:18-29

567 Underwood JN, Richards ZT, Miller KJ, Puotinen ML, Gilmour JP (2018) Genetic signatures through space, time
568 and multiple disturbances in a ubiquitous brooding coral. *Mol Ecol* 27:1586-1602

569 Wall M, Putschim L, Schmidt GM, Jantzen C, Khokiattiwong S, Richter C (2015) Large-amplitude internal waves
570 benefit corals during thermal stress. *Proc R Soc B* 282:20140650
571 Wang YH, Dai CF, Chen YY (2007) Physical and ecological processes of internal waves on an isolated reef
572 ecosystem in the South China Sea. *Geophysical Research Letters* 34:L18609
573 Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T, Bennett S, Rousseaux CS (2013)
574 An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature*
575 *Climate Change* 3:78
576 Xu J, Lowe RJ, Ivey GN, Jones NL, Zhang Z (2018) Contrasting Heat Budget Dynamics During Two La Niña
577 Marine Heat Wave Events Along Northwestern Australia. *Journal of Geophysical Research: Oceans*
578 Zhang N, Feng M, Hendon HH, Hobday AJ, Zinke J (2017) Opposite polarities of ENSO drive distinct patterns
579 of coral bleaching potentials in the southeast Indian Ocean. *Scientific Reports* 7:2443
580 Zhang ZL, Falter J, Lowe R, Ivey G, McCulloch M (2013) Atmospheric forcing intensifies the effects of regional
581 ocean warming on reef-scale temperature anomalies during a coral bleaching event. *Journal of*
582 *Geophysical Research: Oceans* 118:4600-4616
583 Zinke J, Gilmour JP, Fisher R, Puotinen M, Maina J, Darling E, Stat M, Richards ZT, McClanahan TR, Bejer M,
584 Moore C, Graham NAJ, Feng M, Hobbs JPA, Evans SN, Field S, Shedrawi G, Babcock RC, Wilson SK
585 (2018) Gradients of disturbance and environmental conditions shape coral community structure for
586 south-eastern Indian Ocean reefs. *Divers Distrib* 24:605-620

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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 η 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 90th 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 (ΔT) 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 (η) 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.