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

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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.

## Introduction

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

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

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

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

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

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

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

# Methods

### Field measurements

In January 2016, temperature loggers (HOBO U22 Pro-v2) were deployed with 15-minute logging intervals at sites within the lagoons and on the reef slopes of the atolls (Figure 3). We focus on data from 12 representative sites in a water depth of 6-9 m, and one shallower 3 m site (site 3a). The temperature loggers were calibrated in a room temperature water bath before and after the deployment (Lentz et al. 2013), ensuring they read to within 0.1°C of each other. In addition, four RBR Solo pressure sensors (tide gauges) continuously recorded pressure at 1 Hz and were deployed inside and on the outer slope of North Reef and Seringapatam Reef at ~6 m depth. The tide gauges were recovered in April 2016, after recording 185 tidal cycles.

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

### Satellite temperature and atmospheric data

Sea surface temperature (SST) was obtained from NOAA Coral Reef Watch daily nighttime global 5 km satellite coral bleaching heat stress monitoring product v3.1 between 1985 and 2017 (NOAA Coral Reef Watch 2018). Daily sea surface temperature anomalies (SSTA), degree heating weeks (DHW) and bleaching alert areas (BAA) were also obtained from this dataset between 2015-2016. Hourly atmospheric data (including air temperature and pressure, wind vectors, cloud cover, humidity, longwave radiation, shortwave radiation) were extracted at ~25 km resolution from the National Centers for Environmental Prediction's (NCEP's) Climate Forecast System Version 2 (CFSv2, http://cfs.ncep.noaa.gov/, Saha et al. (2011)).

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

$$Q_{net} = Q_{SWR} + Q_{LWR} + Q_{lt} + Q_{sb}. \tag{1}$$

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

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

## Data analysis

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

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

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

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

## Results

### Thermal conditions

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

The October 2015 to October 2016 SST record for the waters surrounding Scott Reef revealed several periods above the threshold to be classified as a MHW, initially starting in October 2015 (Figure 4b). The longest continuous MHW (237 d) occurred from 19 March to 10 November 2016 with a mean temperature anomaly of 1.4°C, and a maximum temperature anomaly of 2.5°C on 2 March 2016. There were two notable decreases over the period shown, in which the SSTs fell outside of MHW conditions: in mid-December 2015 (where the SST dropped by 2.5°C over 16 d) and late January 2016 (where the SST dropped by 1.3°C over 8 d). The 2.5°C temperature decrease in SST mid-December 2015 corresponds to the onset of the Australian summer monsoon, which creates negative air-sea heat fluxes (i.e., ocean cooling) due to increased cloud cover, wind and rainfall (see Benthuysen et al. 2018 for more detail). For the second event, moderate wind speeds of up to 10.5 m $s^{-1}$ and low pressure of 1006 hPa at the end of January (Figure 5b,c) coincided with the passage of Tropical Cyclone (TC) Stan, a category 3 cyclone that traversed southwards ~300 km to the west of Scott Reef on 27 January 2016 (Figure 1a). Cyclone Stan caused a 1.3°C temperature decrease at Scott Reef that alleviated the MHW conditions across the region for the following 25 days. The summer MHW corresponded with coral bleaching heat stress that peaked at 16.6°C-weeks in early May, experienced 4°C-weeks (i.e., significant coral bleaching) for 173 d, and reached NOAA's CRW alert level 2 (i.e., mortality likely) for 58 d.

### Air-sea heat exchange

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

The 'exposed' reef temperature sites (sites 1-6 and 11 in Figure 3), defined as those not bounded by a near-continuous reef rim, had similar in situ temperatures to the offshore SST, i.e., the difference in temperature relative to offshore SST ($\Delta T$) was ~0°C (shown for sites 2, 4 and 11 in Figure 6b). In contrast, at sites within the enclosed lagoons of North Scott and Seringapatam Reef (i.e., sites 9, 10, 13-15), the difference between in situ temperatures and those offshore generally followed a similar pattern to the variation of the net air-sea heat flux ($Q_{net}$), whereby lagoon temperatures were warmer than offshore ($\Delta T > 0$°C) in all months apart from May through July (shown for sites 10 and 13 in Figure 6c). The exception was one site in the southern Seringapatam lagoon (site 15), where the temperature difference did not correlate with the variation in the net heat flux. Temperatures here were cooler than those offshore ($\Delta T < 0$°C) for ~75% of the time, compared to ~30% of time for the next closest lagoon site (site 14, ~2 km away).

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

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

## Cool water influence and bleaching observations

For each site, we calculated the mean daily temperature and mean daily temperature range from in situ loggers for the deployment period between January and April (Figure 8a,b). Generally, cooler mean daily temperatures (30.7 - 31°C) were observed at sites located on the reef slope sites exposed to offshore waters and those in the South Reef lagoon. Within the shallow enclosed lagoons of North Reef and Seringapatam, there were three sites with warmer mean temperatures (31.3 – 31.5°C, sites 10, 15 and 16), but also sites where the mean temperatures were similar to the exposed sites (30.8 – 30.9°C sites 9 and 14). With the exception of the cooler site (site 15) within the Seringapatam lagoon (with the largest mean daily range of 1.6°C), small mean daily temperature ranges <0.4°C were observed in the semi-enclosed lagoons, increasing to a maximum of 0.7°C on the eastern reef slopes and within South Reef. The three sites that are more exposed to deeper oceanic water on the western reef slopes and in the channel experienced larger mean ranges of >0.9°C. At site 3, temperature drops of up to 2.7°C as the tide flooded were sometimes detected. Bleaching scores revealed severe bleaching across the study area, with 92% of sites being >61% bleached (Figure 8c). The only site with less severe bleaching (between 31–60%) was in southern Seringapatam (site 15). Generally, lower incidences of bleaching were found at sites where the daily mean temperature range was larger. We show the relative change in coral cover of the two most widely distributed species with contrasting susceptibilities to bleaching (Figure 8d,e). Overall, mortality that occurred following bleaching was lower for the massive *Porites* than for *Acropora.* The maximum reduction in cover of massive *Porites* was 55%, whereas *Acropora* cover decreased by >85% at all sites not subject to cooling, and there were five sites where the decrease was 100%. For both coral groups, mortality was far lower at sites 3, 4 and 15, reflecting the role of local mechanisms of cooling in reducing mortality rates of corals with contrasting susceptibilities.

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

## **Discussion**

During the austral summer of 2015-2016, an extreme and prolonged MHW was observed across tropical northwestern Australia, which caused severe coral bleaching and mortality at the three atolls of the Scott Reef system. The extended MHW through the winter months likely compounded the effects of the summer MHW by decreasing the potential for corals to recover. Persistent thermal anomalies can cause disease outbreak (Miller et al. 2009) and also inhibit reproduction; typically coral spawning would be expected in both autumn and spring on these reefs, but neither spawning nor visible eggs were observed around the predicted spawning dates in 2016 (Foster et al. 2018). In this region, MHWs are typically related to El Niño conditions, whereas for the subtropical reefs further south along the Western Australia (WA) coast (i.e. south of 22°S), MHWs are associated with La Niña conditions (Zhang et al. 2017; Xu et al. 2018). During El Niño, the Australian Monsoon tends to weaken, resulting in reduced cloud cover and winds, which increases the net air-sea heat flux input at regional scales (Zhang et al. 2017; Benthuysen et al. 2018). During La Niña years, the intensification of the Leeuwin Current, a poleward flowing eastward boundary current, transports anomalously warm tropical water southwards along the subtropical coast of WA that can result in large temperature anomalies (Feng et al. 2013), which in turn can severely impact coastal ecosystems throughout southwestern Australia (Wernberg et al. 2013). Latitudinal differences in temperature anomalies during the peak period of the MHW in 2016 revealed minimal heat stress along the southern Pilbara and Midwest-Gascoyne coasts, while positive anomalies were sustained at Christmas Island, the oceanic atolls and inshore Kimberly, consistent with regional warming patterns expected during El Niño conditions (Figure 4a).

The study focused on the tide-dominated reefs of the Scott Reef atoll system, which have previously demonstrated remarkable recovery (over decadal timescales) from severe disturbances, including bleaching events and tropical cyclone damage (Gilmour et al. 2013). The Scott Reef system is geographically isolated from other reef systems, and consequently is thought to receive a negligible supply of larvae from external sources, relying primarily on local brood stock to replenish the reef over ecological time scales (Gilmour et al. 2009; Underwood et al. 2009; Underwood et al. 2018). It is therefore important to determine how the local oceanography can help to alleviate heat stress and subsequent coral bleaching within specific areas within the reefs, given that any remnant populations surviving a mass beaching event could help to facilitate future reef recovery. Based on the patterns of the temperature variability and the bleaching response across the three atolls, we can identify three different cooling mechanisms observed at Scott Reef that acted to reduce heat stress during the 2015-2016 MHW.

### Cooling mechanism 1: Tropical Cyclone Stan

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

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

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

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

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

The largest temperature range was, however, observed inside the southern lagoon of Seringapatam, where water was cooled over the shallow reef rim at night-time (consistent with a negative hourly $Q_{net}$, not shown). As the tide began to flood, this cooled water was transported into the lagoon and caused large decreases in night-time temperatures at the adjacent lagoon site during neap tide (Figure 7). At North Reef, flushing through channels is generally spatially-limited to those areas adjacent to the channels (Green et al. 2018a), and it is therefore unlikely that this site is influenced by any exchange through the northeastern channel. This mechanism was only observed at neap tide as during spring tide when the flows are strong, the tides would contribute to mixing of lagoon and oceanic waters, and also decrease the lagoon residence time. During neap tide, higher residence times combined with low tidal energetics and enhanced nocturnal cooling due to the shallower depths over the reef rim allowed cooler, denser water from the reef rim to sink to the lagoon floor. This resulted in concurrent temperature differences of up to 2.9°C with a central lagoon site. The temperature remained cooler until the tidal range increased, which likely promoted mixing with warmer lagoon surface and offshore waters, causing temperatures to return to similar values as the other sites during spring tide. As a result of the extended period of cooler temperatures which halved the MHW duration compared to other sites (Table 1), considerably less bleaching (31-60%) and mortality was observed (the relative decrease in cover of *Acropora* was 11% despite being the dominant species, compared to 100% at other lagoon sites of Seringapatam). Therefore survivors from this site will be important in the recovery of the broader reef that experienced severe bleaching.

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

### Cooling Mechanism 3: internal tides

The final cooling mechanism is related to the presence of internal tides, which occur due to the combination of steeply sloping bathymetry, large tidal range and stratified water column surrounding Scott Reef. In the channel separating North and South Reef, internal tides cause isotherm displacements of up to 100 m during spring tide, allowing cooler water to mix with surface waters (Rayson et al. 2018). In the western entrance to South Reef, cool water intrusions of up to 4.5°C have been detected at 40 m depth as cooler, deeper offshore water is advected upslope as the tide floods into the lagoon (Green et al. 2018b). In the shallower environments these intrusions are intermittently observed, but temperature drops of up to 2.7°C concurrent with flooding tide were sometimes detected at site 3. As the reef lies on the edge of the continental shelf, depths plummet more rapidly on the west side (~1000 m) than on the east (~500 m). The internal tide processes that originate in the deeper ocean on the west are reflected in the higher daily temperature range and the comparatively moderate bleaching observed in the west and channel sites during 2016, consistent with studies showing that large diurnal temperature variability can mitigate the risk of bleaching at the reef-scale (Safaie et al. 2018). Such thermocline shoaling delivers cooler, deeper water into shallow reef environments, and has previously been demonstrated to reduce thermal warming sufficiently enough to reduce bleaching (Wall et al. 2015; Schmidt et al. 2016). At the sites exposed to cooler water at Scott Reef (3, 3a and 4) 61–90% of communities were bleached, compared to >91% in the eastern sites (1 and 5), and a similar pattern of variation was evident following the 1998 bleaching event at Scott Reef (Smith et al. 2008; Gilmour et al. 2013), creating an additional area in the atoll system where temperature anomalies can be reduced by the oceanic processes.

In summary, in this study we have identified three physical mechanisms that acted to locally alleviate heat stress and/or bleaching severity within different parts of the Scott Reef system of atolls during the MHW. Both the cool water intrusions and air-sea heat flux mechanisms described created local areas where bleaching severity was reduced. These processes are dependent on the relatively large tides present around these reefs, and thus similar processes may occur in other tide-dominated reefs worldwide. Although sites exposed to the cooling mechanisms experienced lower incidences of bleaching, percentages of affected corals were still substantial (>31%), highlighting that exposure to these processes will not guarantee the necessary relief from stressful or lethal temperatures on coral reefs, and may not be sufficient to prevent bleaching in the future. Marine heatwaves are occurring globally with increased frequency and severity, and the world's oceans will further warm into this century (Oliver et al. 2018). Therefore, understanding the physical processes that promote reef resilience is critical to identifying local areas of refugia, to help determine potential future patterns of survival and recovery, and focus management strategies on locations that merit strong conservation action.

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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 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 ($Q_{lt}$) 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.