

Rising sea levels will reduce extreme temperature variations in tide-dominated reef habitats

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Temperatures within shallow reefs often differ substantially from those in the surrounding ocean; therefore, predicting future patterns of thermal stresses and bleaching at the scale of reefs depends on accurately predicting reef heat budgets. We present a new framework for quantifying how tidal and solar heating cycles interact with reef morphology to control diurnal temperature extremes within shallow, tidally forced reefs. Using data from northwestern Australia, we construct a heat budget model to investigate how frequency differences between the dominant lunar semidiurnal tide and diurnal solar cycle drive ~15-day modulations in diurnal temperature extremes. The model is extended to show how reefs with tidal amplitudes comparable to their depth, relative to mean sea level, tend to experience the largest temperature extremes globally. As a consequence, we reveal how even a modest sea level rise can substantially reduce temperature extremes within tide-dominated reefs, thereby partially offsetting the local effects of future ocean warming.

INTRODUCTION

Climate-driven warming of the ocean arguably poses the greatest threat to the world's coral reefs, by increasing the frequency and severity of thermal stresses that can lead to mass coral bleaching (1–5). This threat has motivated considerable research devoted to improving predictions of regional ocean warming patterns that are being driven by both long-term climate change (time scale of decades) and the intensification of shorter-term climate patterns, such as the El Niño–Southern Oscillation (ENSO) cycle (6, 7). Although regional ocean warming events occur over large spatial scales (hundreds of kilometers), it is increasingly apparent that temperature anomalies, thermal stresses, and associated bleaching responses can often be much more pronounced within shallow reef systems than in the surrounding ocean and can vary over much smaller spatial scales (tens to hundreds of meters) (8–11). This is because local air-sea heat fluxes to the water column of shallow reefs can cause local temperatures to rise (or even fall) by several degrees Celsius relative to the surrounding ocean (12–14) and local thermal stresses to be several times higher than that caused by regional warming of offshore waters alone (15). At the same time, however, the greater temperature variability found in shallow, back reef habitats appears to instill a much higher degree of resilience to thermal stress among reef-building coral than in more open and well-flushed habitats (8, 16, 17).

To better understand the small-scale or “local” (<1 km) thermodynamics of reef systems, a number of previous studies have focused on developing detailed heat budgets of specific reef systems or, even further, developed coupled hydrodynamic-thermodynamic numerical models capable of accurately simulating reef temperature variability at both high spatial (tens of meters) and temporal (hours) resolution (9, 18, 19). The concept behind these models is simple: net air-sea surface heat fluxes either warm or cool the reef water column, with the resulting temperature response dependent on both a reef's average depth and water residence times. Whereas the average depth is dependent only on the morphology of a reef system, water residence times depend on

both the reef morphology and the strength of hydrodynamic forces driving circulation (15). To date, most of these detailed reef thermodynamic studies have focused primarily on so-called wave-dominated reef systems (20), where circulation is predominantly driven by wave breaking in the surf zone (9, 12, 21). In turn, the results of these studies have supported a practical framework for predicting local warming patterns for this broad class of wave-dominated reefs on the basis of properties of incident wave conditions and reef morphology (15). At the same time, however, many tropical reef systems worldwide experience only minimal or moderate wave energy, and their circulation is instead predominantly driven by tidal forcing. These “tide-dominated” reefs may comprise roughly a third of reefs worldwide (20) and experience very different hydrodynamics from wave-dominated systems. For many of these strongly tidally forced reefs, the offshore tidal amplitude (scale of meters) is often greater than the depth of the reef platform relative to mean sea level (scale of decimeters), resulting in the offshore sea level falling below the reef at low tide. These dynamics can result in large asymmetries in tidally driven flows over the reefs, where the duration of the falling (ebb) tide is greatly elongated relative to the duration of the rising (flood) tide, as a result of water draining off the reef being slowed by a topographic barrier (for example, a shallow reef crest or “rim”) and/or by bottom friction associated with large reef roughness (22).

The fact that the depths of many reef systems at mean sea level (or at least their crests) are so shallow relative to local tidal amplitudes largely reflects the ability of these systems to actively accrete to a minimum depth that environmental conditions will allow (for example, due to light, aerial exposure, and temperature) (23–25). However, there is a reason to believe that future rates of reef accretion will no longer be able to keep up with rising sea levels as a result of (i) the effects of ocean warming and acidification depressing rates of reef carbonate production and accelerating rates of reef bioerosion (26–28) and (ii) the rapid acceleration of sea level rise (29, 30); both of which are largely the result of anthropogenic changes to the Earth's climate. Given that sea level will likely rise by at least 0.5 to 0.8 m over the 21st century under a business-as-usual scenario (31), with a number of studies indicating that values exceeding 1.5 m are possible [see review by Nicholls *et al.* (32)], the mean depth of many tidally driven reefs will likely become comparable to or exceed their local tidal amplitude (scale of a meter for both). This will no doubt

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have profound effects on how water and heat are exchanged in tidally driven reef systems and, more importantly, on the extreme environmental variability to which many reef communities are exposed.

Several studies have already documented how interactions between tidal cycles and solar heating cycles can regulate temperature variability within reefs, often through correlative observations of enhanced diurnal temperature fluctuations when low tides occur around midday (14, 33, 34). Still, other researchers have explicitly modeled reef temperature variability on the basis of detailed heat budgets for particular tidally forced reefs (13, 19). Nevertheless, because existing studies have tended to focus on the circulation and thermodynamics of particular reef sites, we currently lack a broad universal model of how tidal and solar heating cycles interact with reef morphology to regulate temperature variability within tide-dominated reefs, similar to what has already been developed for wave-dominated reefs. The development of such a model is necessary for us to move beyond site-specific observations to predicting the broader impact that long-term trends in both ocean warming and sea level rise will have on coral reef communities living in tidally driven habitats throughout the world.

The objective of this study is to provide a practical framework for predicting how tides, solar heating cycles, and reef morphological properties interact to control reef heat balances and temperature extremes within tide-dominated reef systems. We then use this framework to explore how local temperature extremes will likely change in the future as a result of rising sea level. Although the magnitude of future temperature extremes in shallow reef habitats will be influenced by long-term trends in ocean warming and net atmospheric heat fluxes (both of which will vary regionally), this study specifically focuses on the effects of rising sea level on the thermal conditions of tide-dominated reef habitats, which have remained unexamined to date. Thus, we currently lack the ability to predict the physical impacts of rising sea level on reef thermal regimes across a wide geographic range of reef systems, regardless of their particular regional climate. To accomplish this objective, we first examine the heat budget of a macrotidal reef platform in northwestern Australia as a case study of tidally driven reef thermodynamics. Using detailed field measurements of hydrodynamics, water tempera-

ture, and air-sea heat exchange, we develop a simple but accurate one-dimensional (1D; cross-reef) heat budget model to investigate how local surface heating and tidally driven advection control reef temperature variability. Second, we generalize our model to suit a wide range of tidal regimes and reef morphologies and, in the process, develop a set of simple dimensionless parameters that more broadly describe temperature variability within tide-dominated reefs globally. We find that reefs with tidal amplitudes comparable to or greater than their depth relative to mean sea level generally experience the largest temperature extremes because of the elongation of shallow, low tide conditions (that is, when surface heat exchange can drive the greatest temperature fluctuations). By assessing a number of reef systems from across the globe, we finally show how rapid sea level rise could substantially reduce diurnal temperature extremes within these reefs over the next century, thereby partially countering the effects of global ocean warming.

RESULTS

Heat balances on an intertidal reef platform

Tallon Island is located off the northeast tip of the Dampier Peninsula in the Kimberley region of northwestern Australia (Fig. 1). The reef platform on the eastern side of Tallon is very flat (thus lacking a shallower crest, a characteristic of some reefs) and located near mean sea level, such that its relative depth is $h_{\text{MSL}} \approx 0$ m [Fig. 2A; see Lowe *et al.* (22) for details]. Because the spring tidal range at this site can exceed 8 m, the offshore sea level can fall several meters below the reef platform at low tide. Nonetheless, the reef platform remains fully submerged over each tidal cycle because of the hydraulic trapping of water on the reef by resistance from bottom stresses over the rough and relatively wide (~1400 m) reef before draining down the reef slope [refer to Lowe *et al.* (22) for a detailed description of Tallon reef and a more general assessment of the hydrodynamics of tide-dominated reef systems]. As a consequence, the minimum water depth on the reef at low tide (h_{min}) is ~0.5 m (Fig. 2A) (22). Here, we use high-resolution temperature data and meteorological measurements of air-sea heat exchange that were

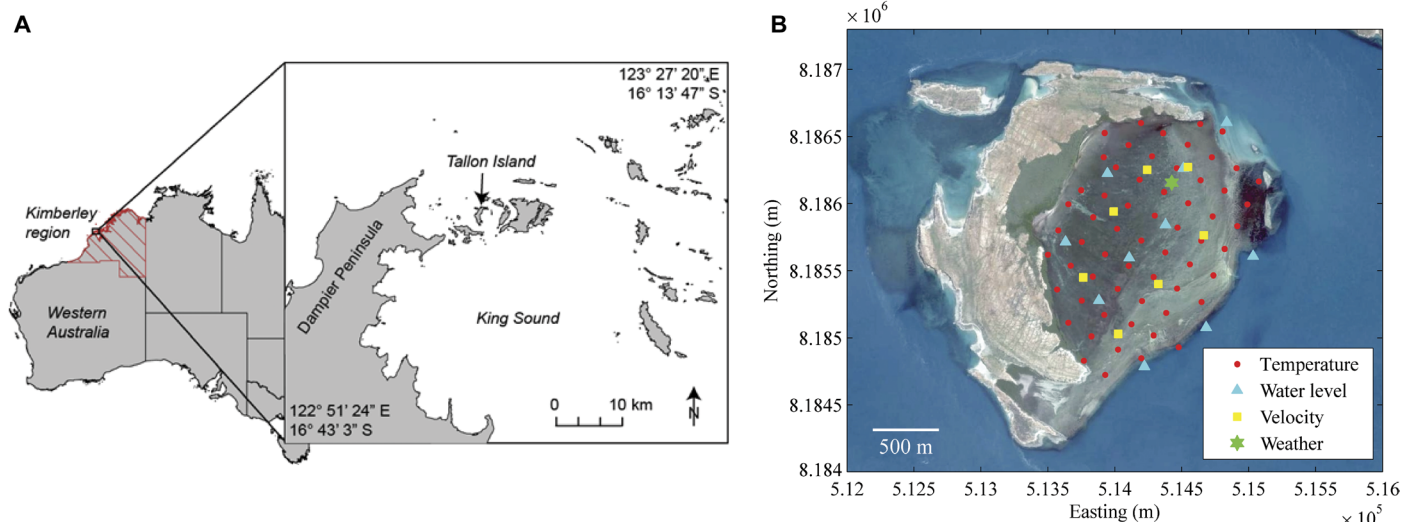


Fig. 1. Study site and field instrument configuration. (A) Location of Tallon Island in the Kimberley region of northwestern Australia [refer to Lowe *et al.* (22) for details]. (B) Configuration of the field instrument array.

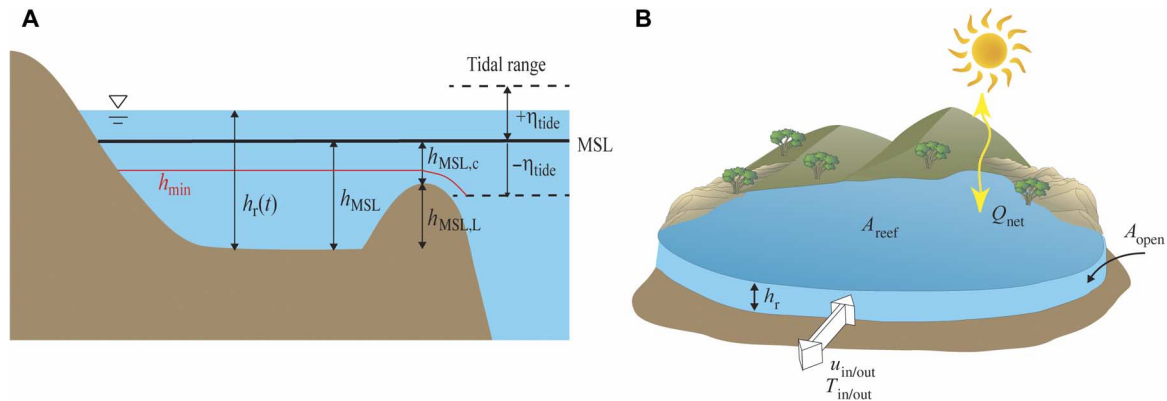


Fig. 2. Schematic of the reef heat budget model. (A) Reef cross section identifying the reef depth $h_r(t)$ that varies between the maximum amplitude (η_{tide}) above the depth h_{MSL} at mean sea level and the minimum depth h_{min} of the lagoon or platform (refer to the text for details). The total depth h_r at the back of the reef (or lagoon) is composed of the depth over the crest ($h_{MSL,c}$), if present, and the depth of the back of the reef relative to the crest ($h_{MSL,L}$). **(B)** Oblique view of a reef with surface area A_{reef} where water instantaneously exchanges over an area A_{open} between the reef and the ocean, with flow velocity $u_{in/out}$ and temperature $T_{in/out}$. Air-sea heat exchange on the reef occurs through Q_{net} .

simultaneously collected with measurements of currents and water level during a 2-week hydrodynamic field study in March to April 2014 (Fig. 1B and Materials and Methods) [see Lowe *et al.* (22) for details]; however, this present study focuses solely on the resulting thermodynamics of the reef. More specifically, we examine how interactions between the tidal and solar heating cycles drive diurnal variations in reef water temperature and heat transport through the application of a simple 1D (cross-reef) thermodynamic model (see Materials and Methods). The model is based on conservation of thermal energy within the reef (Eq. 7, Materials and Methods), which considers how diurnal temperature variations within a reef are generated by net surface heat fluxes (Q_{net}) at the air-water interface as well as heat exchange through advection of water between the reef and surrounding ocean. This model is then used below as the foundation to more broadly investigate the mechanisms that generally regulate temperature variations within tide-dominated reefs.

During the field study, the offshore tidal range reached a maximum of ~ 7.5 m near the middle of the study during spring tide (~ 1 April) and a minimum of ~ 4 m during neap toward the beginning and end (Fig. 3A). Despite the sinusoidal variations in water levels offshore, water levels over the reef platform were highly asymmetric, with water draining very slowly off the reef during ebb tide, as a result of the large “truncation” of tidal variability over the reef (that is, the duration of the ebb was ~ 10 hours, whereas the flood was only ~ 2 hours) [Fig. 3A; also see Lowe *et al.* (22)]. Because of the 12.4-hour period of the dominant M2 (semidiurnal) tide, the time of the offshore low tide minima gradually shifted forward over the study period. Initially, the first low tide of the day occurred before sunrise and gradually shifted to just before noon by the end of the experiment (Fig. 3D).

Diurnal variations in net surface heat fluxes (Q_{net}) did not vary substantially over the course of the experiment, typically ranging from -200 W m^{-2} at night to $+600 \text{ W m}^{-2}$ during the day (Fig. 3B). This consistency was due to the cloud-free skies that persisted over most of the experiment, a condition that is typical during the “dry season” in the Kimberley (April through October) due to its tropical monsoon climate. Variations in Q_{net} were dominated by net heating from the combined short- and long-wave radiation (Q_{sw+lw}) during the day and net cooling from latent heat fluxes (Q_{lt}) during the night (Eq. 6, Materials and Methods).

Daily temperature variability in reef water temperature (T_r ; spatially averaged over the reef platform) ranged from as small as $\sim 2^\circ\text{C}$ during the initial period of the study to as large as $\sim 8^\circ\text{C}$ during the latter period and exhibited fairly complex but periodic behavior (Fig. 3C, black line). Nonetheless, our simple reef heat budget model (Eq. 9, Materials and Methods) could accurately reproduce both the shape and magnitude of the complex diurnal temperature reversals over the course of the study (Fig. 3C, red line). The maximum diurnal temperature fluctuations were greatest toward the end of the study when low tide occurred slightly before solar noon, despite the tidal range being lower at this time (Fig. 3D). Therefore, the maximum observed temperature fluctuations were not in phase with the maximum daily tidal amplitude (Fig. 3, A and C); that is, diurnal temperature fluctuations were not greatest during the largest spring tides. This is because once the offshore sea level drops below the reef crest, the depth of the remaining ebb tide and the duration of its period on the reef are determined solely by the morphology of the reef, regardless of how low offshore sea levels reach (that is, ~ 2 m during neap versus ~ 4 m during spring). We find that the phase difference between the semidiurnal (M2) tide and solar heating cycles generally has the most substantial influence on the reef heat balance, such that the magnitude of daily temperature variation ($\Delta T_r = T_{max} - T_{min}$, where T_{max} and T_{min} are the daily temperature maxima and minima, respectively) is mostly independent of the spring-neap phasing at Tallon Island (see the Supplementary Materials for further details).

Reef temperature modulation through interacting tidal and solar heating cycles

To more generally investigate how properties of tidal and solar heating cycles and reef morphology interact to regulate temperature variability within a wide range of reef systems, we recast the governing heat budget equations (Eqs. 9 and 10, Materials and Methods) into their dimensionless forms. To further simplify our analysis and identify a set of fundamental dimensionless parameters that control temperature variability, we consider idealized tidal and solar heating cycles that nonetheless retain the periodicity and magnitude exhibited by our in situ data. Variation in reef tidal depth (h_r) is thus assumed to occur at a tidal period τ_{tide} , with tidal amplitude η_{tide} (equivalent to one-half the range) and phase difference ϕ_0 relative to solar noon. The offshore mean sea level

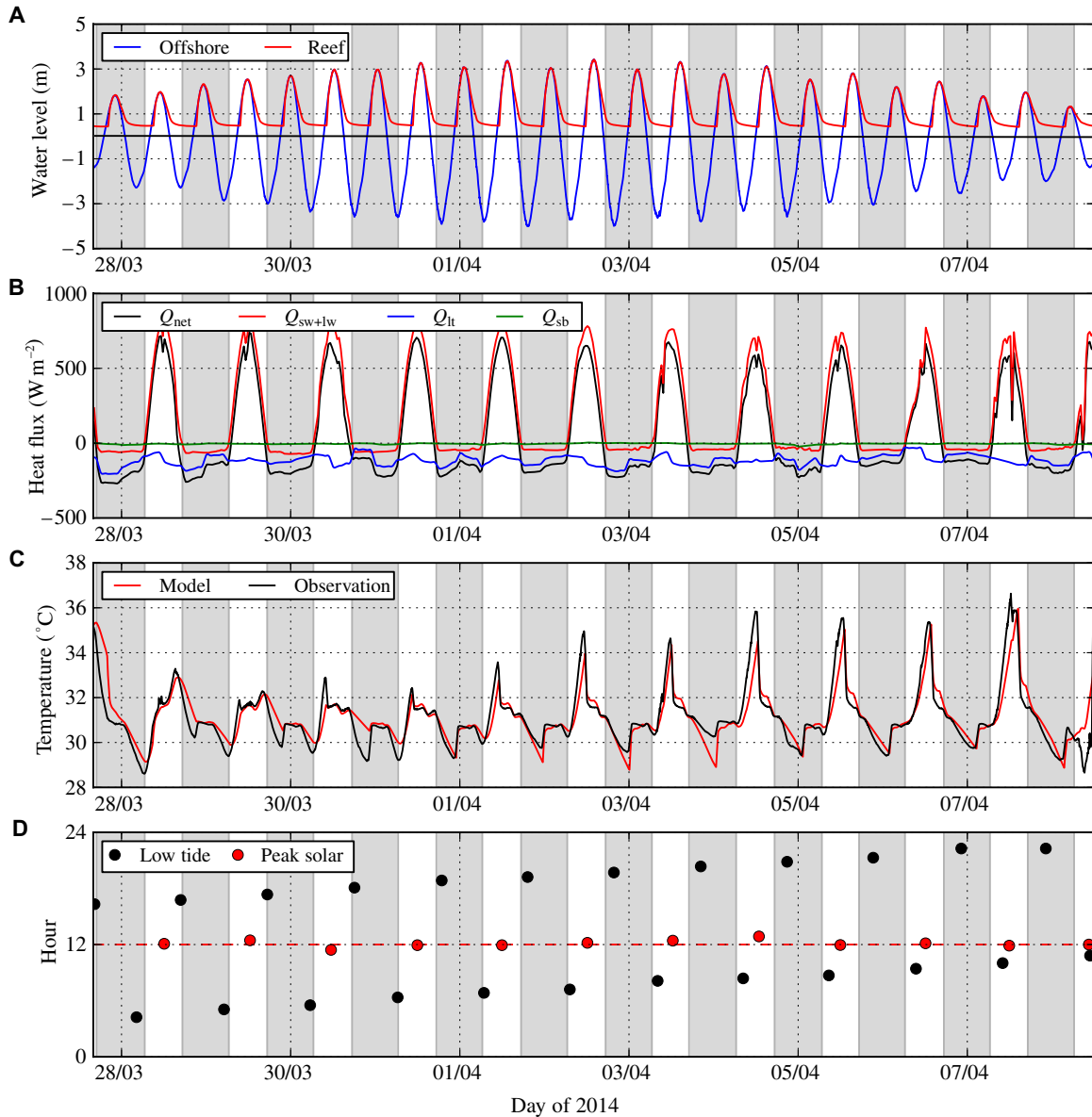


Fig. 3. Observations and model predictions of the reef heat budget for Tallon reef during the study period. (A) Time series of the water level variability (relative to mean sea level) measured at a site on the reef platform (red) and at a site offshore on the forereef slope (blue). The solid horizontal black line denotes offshore mean sea level ($z = 0$ m). (B) Terms that comprise the total net air-sea heat fluxes Q_{net} (Eq. 6, Materials and Methods), including the combined net short- and long-wave radiation ($Q_{\text{SW}+\text{lw}}$), the latent (Q_{lt}) and sensible (Q_{sb}) heat flux contributions. Refer to Materials and Methods for a description of each heat flux term. (C) Observed spatially averaged reef temperature T_r compared with the model predictions. (D) Hour of day when minimum low tide measured offshore occurred and when peak solar irradiance occurred each day. The horizontal red dashed line corresponds to the mean hour of peak solar irradiance during the study at approximately noon.

coincides with a reef depth h_{MSL} , and we assume that there is a minimum water depth h_{min} , where water is effectively trapped on the reef (Fig. 2A); that is, this reef water depth variability is governed by

$$h_r(t) = h_{\text{MSL}} + \eta_{\text{tide}} \cos\left(\frac{2\pi t}{\tau_{\text{tide}}} + \phi_0\right) \quad (1)$$

with the minimum depth h_{min} (such that $h_r \geq h_{\text{min}}$ always), leading to tidal truncation for reefs with $h_{\text{MSL}} \leq h_{\text{min}} + \eta_{\text{tide}}$. In this general model,

we consider cases in which the minimum depth h_{min} may be due to water ponding behind a shallower reef crest (in which case, h_{min} is roughly equal to the mean lagoon depth $h_{\text{MSL,L}}$, as shown in Fig. 2A) and/or bottom friction restricting the flow of water off the reef [as in the case of Tallon reef; see Lowe *et al.* (22)]. Although water may continue to drain off the reef once the offshore sea level drops below the top of the reef platform or reef crest, these residual flows are generally very shallow (decimeters) and very slow (centimeters per second) (19, 22). As a consequence, the contribution of advective heat fluxes to reef temperature changes becomes

negligible relative to surface heat fluxes, and hence, advection is effectively ignored during this stage of low tide in our simplified model.

Likewise, we assume a sinusoidal variation in the net surface heat flux term Q_{net} occurring with period τ_{solar}

$$\begin{aligned} Q_{\text{net}}(t) &= +Q_{\text{net,max}} \cos\left(\frac{2\pi t}{\tau_{\text{solar}}}\right) & t_{\text{sunrise}} \leq t \leq t_{\text{sunset}} \\ Q_{\text{net}}(t) &= -Q_{\text{net,night}} & \text{at night} \end{aligned} \quad (2)$$

where $Q_{\text{net,max}}$ and $Q_{\text{net,night}}$ are the magnitudes of the maximum net daytime heating (mostly short- and long-wave radiation) and constant nighttime net cooling rates (mostly latent), respectively (see Materials and Methods). Although this is an idealized representation of the diurnal heating cycle (Fig. 3C), it nonetheless captures the dominant diurnal behavior of the physics driving net heat fluxes within reefs (including Tallon) and has also been successfully used to model heat budgets and temperature variability within other reefs, such as in the Great Barrier Reef (19).

With these definitions, we can further simplify our heat budget model by constructing dimensionless variables (denoted with an asterisk) for time (t^*), reef water depth (h_r^*), and temperature (T^*) to reduce the number of free parameters needed to constrain the prevailing physics

$$\begin{aligned} t^* &= \frac{t}{\tau_{\text{solar}}}, & h_r^* &= \frac{h_r}{\eta_{\text{tide}}}, & Q_{\text{net}}^* &= \frac{Q_{\text{net}}}{Q_{\text{net,max}}} \\ T_r^* &= \frac{T_r - T_0}{Q_{\text{net,max}} \tau_{\text{solar}} / (\rho_0 c_p \eta_{\text{tide}})} \end{aligned} \quad (3)$$

where c_p and ρ_0 are the specific heat capacity and density of seawater, respectively, and by definition, t^* is equivalent to the time in (solar) days. It can be shown that the general solution to the time-varying dimensionless reef temperature $T_r^*(t^*)$ based on the governing equations (Eqs. 11 to 13, Materials and Methods) depends on only the following three dimensionless parameters

$$\tau^* = \frac{\tau_{\text{tide}}}{\tau_{\text{solar}}}, \quad h_{\text{MSL}}^* = \frac{h_{\text{MSL}}}{\eta_{\text{tide}}}, \quad h_{\text{min}}^* = \frac{h_{\text{min}}}{\eta_{\text{tide}}} \quad (4)$$

which describe the ratio of tidal and solar periods (τ^*), and two dimensionless depths, which describe the ratios of the depth at mean sea level relative to the tidal amplitude (h_{MSL}^*) and at low tide (h_{min}^*).

To demonstrate the general responses of the model, we first consider its application to an idealized version of Tallon reef, where $h_{\text{min}} = 0.5$ m and $h_{\text{MSL}} = 0$ m, the tide consists solely of an M2 mode (the dominant mode at Tallon) such that $\tau_{\text{tide}} = 12.42$ hours, and the tidal amplitude is $\eta_{\text{tide}} = 3$ m, which is halfway between the spring maximum (4 m) and neap minimum (2 m); the results of which yield $\tau_{\text{solar}}/\tau_{\text{tide}} = 0.52$, $h_{\text{MSL}}^* = 0$, and $h_{\text{min}}^* = 0.17$ (table S1). To assess the variability in T_r^* over multiple tidal cycles (days), we initialize each simulation with $\phi_0 = 0^\circ$ and advance forward in time, such that there is an additional 0.84-hour (~50-min) lag in the solar cycle relative to the tidal cycle each day. The results reveal the presence of a low-frequency modulation of the diurnal fluctuations in T_r^* , with a beat period of $\tau_{\text{low}} = |\tau_{\text{solar}}\tau_{\text{tide}}/(2\tau_{\text{tide}} - \tau_{\text{solar}})| \approx 14.8$ days, which are generated by the daily phase drift between the M2 tide and the

diurnal solar cycle (Fig. 4A, black line). Although this low-frequency modulation of temperature occurs at a similar frequency to spring-neap tidal cycles [which are governed by tidal interactions between the M2 tide and other semidiurnal constituents, particularly S2 (35)], it is instead generated solely by interactions between diurnal solar heat fluxes and the dominant semidiurnal (M2) tidal constituent (because the daily tidal amplitude here is constant). We note that the daily averaged temperature variability is negligible (Fig. 4A, red line), indicating that the diurnal temperature variability oscillates about an effectively constant mean value. This is because the time scale of the tidal variability is much shorter than the diurnal solar cycle (that is, $\tau_{\text{tide}} \ll \tau_{\text{solar}}$), which prevents the net accumulation of heat on the reef over a full day.

We can use the Tallon reef example ($h_{\text{MSL}}^* = 0$ and $h_{\text{min}}^* = 0.17$) to further investigate how the magnitude of the maximum diurnal temperature fluctuations ΔT_r^* (defined as the difference in the daily maximum and minimum of T_r^*) varies for different instantaneous phase differences $\Delta\phi_i$ between the solar and tidal cycles (Fig. 4B). Here, $\Delta\phi_i$ is defined as the instantaneous phase mismatch between the maximum tide and solar noon on a given day. The maximum dimensionless temperature fluctuation ($\Delta T_r^* \approx 1.8$) occurs when $\Delta\phi_i$ is slightly less than 180° (roughly equivalent to when low tide occurs just before solar noon), which defines a general condition of optimal warming (or cooling) when tidal truncation leads to extended periods of low water depth ($h_r = h_{\text{min}}$). Alternatively, we can consider the hypothetical case in which offshore mean sea level is sufficiently high enough that tidal truncation does not occur (that is, the reef platform becomes too deep at low tide); for this example, h_{MSL}^* is increased to $h_{\text{min}}^* + 1 = 1.17$ so that the low tide depth is exactly equal to the minimum depth of $h_{\text{min}} = 0.5$ m (or $h_{\text{min}}^* = 0.17$) for Tallon (Fig. 4B). For this alternate case, the maximum dimensionless temperature fluctuations are substantially reduced ($\Delta T_r^* \approx 0.5$), with the maximum warming/cooling for this case instead occurring earlier in the tidal cycle, or when $\Delta\phi_i \approx 120^\circ$. That is, the combination of a symmetric tidal variation (with reduced low tide duration) and deeper water column leads to much lower temperature variations for a given maximum net heat flux $Q_{\text{net,max}}$ and tidal amplitude η_{tide} .

General influence of sea level rise on reef temperature extremes

We further apply the model using a realistic range of reef depths and tidal amplitudes to more generally assess how tides, surface heat fluxes, and reef morphology interact to drive reef temperature variability across a broader range of reef morphologies and tidal amplitudes. Using this more global model, we will then assess the sensitivity of the diurnal temperature extremes to sea level rise for a number of other reef systems from across the Indo-Pacific region. We consider six sample reefs that have both detailed tidal records and accurately surveyed reef profile bathymetry relative to mean sea level, thus providing us with robust estimates of both h_{MSL}^* and h_{min}^* (Table 1 and table S1). Like most tropical reef systems worldwide, all of these reefs experience dominantly semidiurnal tides (see below). In addition, four of these six reefs have detailed temperature data that show diurnal temperature extremes ranging from 1.5° to 6.5°C , depending on the reef morphology, local tidal amplitude, time of the year, and weather conditions (Table 1). Here, we investigate how maximum diurnal temperature fluctuations (in dimensionless form ΔT_r^*) over the 14.8-day cycle respond to variations in the dimensionless reef depth parameters h_{MSL}^* and h_{min}^* (Eq. 4). Previous analyses have shown that tidal truncation occurs only when the depth of the reef

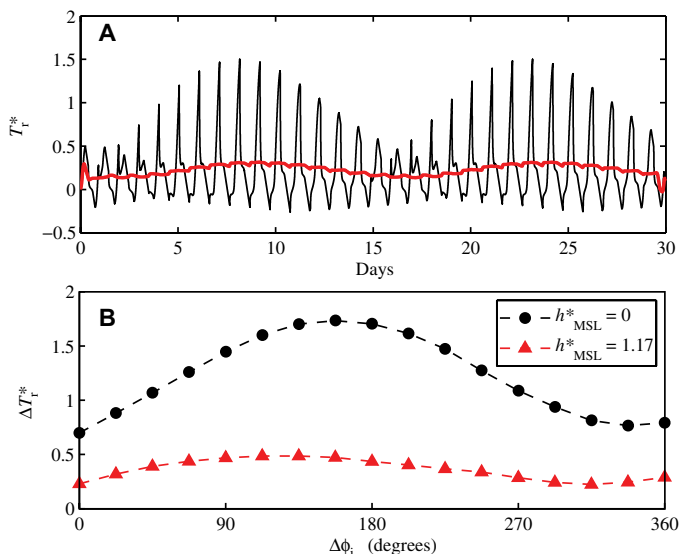


Fig. 4. Response of reef temperature to interacting solar heating and a dominant semidiurnal tidal cycle. (A) Reef temperature variability (black line; in dimensionless form T_r^* per Eq. 3) over 30 days for an idealized Tallon reef ($h_{MSL}^* = 0$ and $h_{min}^* = 0.17$) driven by a dominant M2 tide, illustrating the ~ 14.8 -day modulation of the temperature fluctuations caused by the phase drift between the maximum tidal elevation and solar irradiance. The red line denotes a 1-day moving average. **(B)** Maximum diurnal temperature variation ΔT_r^* (defined as the difference between the daily maximum and minimum value of T_r^*), as a function of the instantaneous phase difference between the tidal and solar cycle ($\Delta \phi_i$). Results shown are for an idealized Tallon reef under present-day sea level ($h_{MSL}^* = 0$), as well as a hypothetical scenario where mean sea level is increased so that the depth at low tide is equal to h_{min} (equivalent to $h_{MSL}^* = 1.17$) and tidal truncation no longer occurs.

falls below a common physical boundary of $h_{MSL}^* \leq h_{min}^* + 1$ (22) or, in dimensional terms, when $h_{MSL} \leq h_{min} + \eta_{tide}$. The model reveals that ΔT_r^* increases when h_{MSL}^* and/or h_{min}^* is decreased. This is mainly due to the net incident heat flux being distributed over a shallower water column (Fig. 4). However, we further note that there is a very abrupt increase in ΔT_r^* when $h_{MSL}^* < h_{min}^* + 1$ (that is, when tidal truncation occurs). This is due to tidal truncation extending the duration of low water depths on the reef, thus elongating periods of enhanced heating/cooling of the shallow water column and, as a consequence, making the response of diurnal temperature variability to a changing sea level highly nonlinear.

To assess how sea level rise will specifically affect temperature extremes within each of these reef environments, we assume that both future tidal conditions and $Q_{net,max}$ remain unchanged. The former is determined solely by celestial mechanics, whereas the latter is reasonable given that, with the exception of potential regional changes in cloud cover and decadal changes in solar radiation, $Q_{net,max}$ should remain relatively constant. Two sea level rise scenarios are considered on the basis of predicted end-of-the-century scenarios (see Materials and Methods): a 0.7-m rise based on the Intergovernmental Panel on Climate Change (IPCC) projections from Coupled Model Intercomparison Project Phase 5 (CMIP5) (31) and a 1.5-m rise that captures the upper end of semiempirical projections [see summary by Nicholls *et al.* (32)]. In both cases, rates of sea level rise far exceed typical reef accretion rates (36). One very important aspect of our simple tidally driven heat ex-

change model is that if $Q_{net,max}$ is kept constant (even approximately so), then the ratio of a given temperature extreme (ΔT_r) following sea level rise relative to present-day values is independent of the particular local value of $Q_{net,max}$, due to the linear form of governing differential equation (Eqs. 3 and 11, Materials and Methods). Thus, although detailed in situ measurements of $Q_{net,max}$ may not be available for most reef sites, these data are not actually necessary for predicting how much temperature extremes at a given reef site will change as a consequence of sea level rise on a percentage basis.

Our results indicate that 0.7 m of sea level rise would reduce present maximum diurnal temperature ranges (ΔT_r) by 7 to 65% across the six reef sites, whereas 1.5 m of sea level rise would reduce ΔT_r by 18 to 86% (Table 1). Reefs that already presently experience moderate tidal truncation (that is, where the offshore low tidal elevation falls just below the minimum depth) will experience the most substantial reductions in temperatures under future sea level rise. These examples of reef systems near the “tipping point” include Lady Elliot in the Great Barrier Reef and the Cocos Islands in the eastern Indian Ocean (Fig. 5). Thus, for reefs such as Lady Elliot, where ΔT_r typically ranges from 2.5° to 5.5°C at present, these extremes are predicted to be reduced to 1.5° to 3.3°C under 0.7 m of sea level rise and to just 0.5° to 1.2°C under 1.5 m of sea level rise.

A more general consequence of these results is how diurnal temperature extremes within different types of reefs worldwide will be affected by a rise in mean sea level depending on their mean depth and regionally specific tidal amplitudes. As shown in Fig. 5A, it is clear that those reefs presently located in a regime near the cusp of tidal truncation (that is, those reefs with $h_{MSL}^* \approx h_{min}^* + 1$) will experience the most substantial reductions in temperature extremes under future sea level rise due to the abrupt transition in ΔT_r^* that occurs when h_{MSL} becomes deeper than $h_{min} + \eta_{tide}$ and tidal truncation ceases, as illustrated in Fig. 5B. Given that many coral reef crests are presently located near mean sea level (37), it is very common for the offshore sea level to fall below the elevation of many reefs at low tide and hence experience some form of tidal truncation regardless of the regional tidal amplitude.

Implications for other tidal regimes

The analysis thus far has focused on how diurnal temperature extremes respond to the interaction between a dominant semidiurnal tide and the diurnal solar heating cycle; however, there are some regions where diurnal tidal modes ($\tau_{tide} \sim 24$ hours) are dominant (Fig. 6). The relative importance of diurnal versus semidiurnal tides is conventionally determined by the tidal form factor $F_{tide} = (a_{K1} + a_{O1})/(a_{M2} + a_{S2})$ (38), where a_{K1} and a_{O1} are the amplitudes of the two primary diurnal constituents (K1 and O1, respectively) and a_{M2} and a_{S2} are the amplitudes of the two primary semidiurnal constituents (M2 and S2, respectively). Tidal regimes with $F_{tide} < 1.5$ are classified as mainly semidiurnal, whereas those with $F_{tide} > 1.5$ are mainly diurnal (38). A vast majority of the world’s coral reef systems ($\sim 82\%$) experience mainly semidiurnal tides (Fig. 6A), including all of the six sample Indo-Pacific reefs considered in Table 1 (with $F_{tide} < 0.5$). As a result, the simplified model described earlier based on a single semidiurnal (M2) tide can provide a reasonable approximation for the tidal regime of most reefs worldwide.

Nevertheless, for the smaller portion of coral reefs dominated by diurnal tides, such as in parts of the Caribbean and in the South China Sea (Fig. 6A), the two primary diurnal tidal constituents are the K1 (luni-solar diurnal), with a period of 23.93 hours, and the O1 (principal lunar diurnal), with a period of 25.82 hours. Because these “diurnal” tidal

Table 1. Projected temperature changes due to sea level rise for sample tidally forced reefs globally. Labels refer to sites plotted in Fig. 5. Tidal amplitudes (η_{tide}) represent average values (that is, intermediate between spring and neap). F_{tide} denotes the tidal form factor (see text for details). Diurnal temperature range changes (% ΔT_r change) are relative to present conditions with a mean sea level (MSL) of 0 m. Present temperature ranges (ΔT_r) are drawn from literature values and projected for different mean sea level rise scenarios (+0.7 m and +1.5 m) using the model. NA, not available.

Label	Site	η_{tide}	F_{tide}	ΔT_r (% change)		ΔT_r (range)			References
				MSL +0.7 m	MSL +1.5 m	Present	MSL +0.7 m	MSL +1.5 m	
Ⓐ	Tallon Island, Kimberley, northwestern Australia	3.0 m	0.13	−7%	−18%	2.5–6.5°C	2.3–6.0°C	2.0–5.3°C	This study
Ⓑ	Warraber Island, Torres Strait	1.2 m	0.46	−23%	−72%	2.0–5.0°C	1.5–3.8°C	0.6–1.4°C	
Ⓒ	Cocos (Keeling) Islands, eastern Indian Ocean	0.6 m	0.48	−65%	−86%	NA	NA	NA	(51)
Ⓓ	Lady Elliot, Great Barrier Reef	0.8 m	0.42	−39%	−78%	2.5–5.5°C	1.5–3.3°C	0.5–1.2°C	(52)
—	Ofu, American Samoa	0.5 m	0.15	−36%	−62%	1.5–6.0°C	1.0–3.8°C	0.6–2.3°C	(19, 53)
—	Rarotonga, Cook Islands	0.4 m	0.16	−38%	−63%	NA	NA	NA	(14, 54)
									(55)

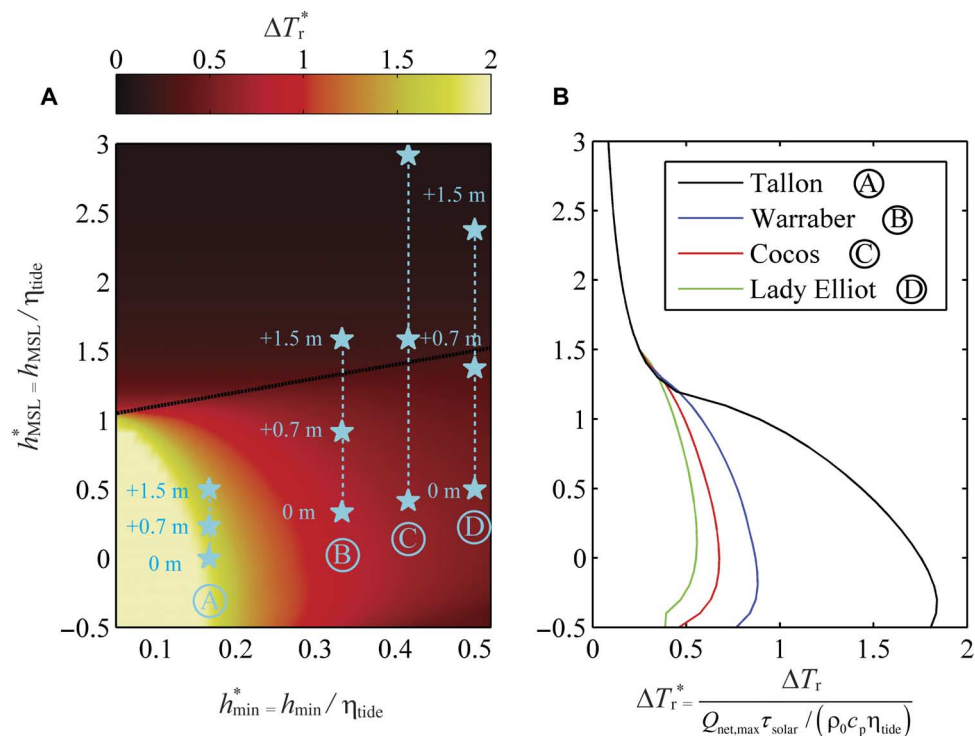


Fig. 5. Diurnal temperature extremes for various reefs worldwide and their response to sea level rise. (A) Magnitude of the maximum diurnal temperature fluctuation (in dimensionless form) as a function of the normalized minimum reef water depth (h_{min}^*) and normalized reef depth relative to mean sea level (h_{MSL}^*). Tidal truncation occurs below the black line ($h_{\text{MSL}}^* \approx h_{\text{min}}^* + 1$). The location of four reefs within this parameter space (Ⓐ to Ⓓ; see Table 1) are shown for three mean sea level scenarios (0 m relative to present, a future +0.7-m rise, and a future +1.5-m rise). Ⓐ, Tallon island; Ⓑ, Warraber island; Ⓒ, Cocos Islands; Ⓓ, Lady Elliot island. (B) Response of ΔT_r^* for the four reefs with fixed h_{min}^* but varying h_{MSL}^* .

modes are close (but not equal) to 24 hours, their interaction with the daily solar cycle can lead to longer-term variations in diurnal temperature cycles at period τ_{low} , much similar to the case for semidiurnal tides. This frequency interaction can be expressed in terms of period as

$$\tau_{\text{low}} = \left| \frac{\tau_{\text{solar}} \tau_{\text{tide}}^{\text{diurnal}}}{\tau_{\text{tide}}^{\text{diurnal}} - \tau_{\text{solar}}} \right| \quad (5)$$

where $\tau_{\text{tide}}^{\text{diurnal}}$ represents the particular diurnal tidal period. Thus, the solar heating interaction with the K1 tide leads to a very long period ($\tau_{\text{low}} \approx 365$ days) modulation of diurnal temperature fluctuations, whereas the O1 tide drives a shorter ($\tau_{\text{low}} \approx 14.2$ days) modulation (see the Supplementary Materials for further details). As shown in figs. S1 and S2 for the K1 and O1 tides, respectively, the interaction between a diurnal tide and solar heating cycle can similarly lead to enhanced diurnal temperature fluctuations when phases of low tide occur near solar noon. However, because of the reduced role of advective heat exchange for the longer diurnal tidal period as a consequence of the changes in water level occurring more slowly, the reef heat budget (and hence temperature fluctuations) is less sensitive to increases in mean sea level (figs. S1 and S2). In addition, in contrast to the semidiurnal tidal case (Fig. 4A), the match in time scales of $\tau_{\text{tide}}^{\text{diurnal}}$ and τ_{solar} leads to a more substantial daily averaged temperature variability over the same long period (τ_{low}) because some heat can accumulate on a reef over a given day.

DISCUSSION

Our results demonstrate how the phase differences between tidal and solar heating cycles can drive variability in diurnal temperature extremes within reefs. The present study focused specifically on the interaction associated with the principal lunar semidiurnal (M2) tidal

constituent that tends to be the dominant constituent in most coral reef regions globally and particularly in the tropics. Although other tidal constituents with different frequencies can similarly induce different frequency interactions with the solar heating cycle, the general framework and model described here can also be applied to investigate the influence of any specific tidal time series, including that under mixed conditions (semidiurnal + diurnal). For the generally dominant M2 constituent considered here, the interaction between the different tidal and solar forcing periods leads to an approximately 14.8-day modulation of the diurnal temperature fluctuations. We note that our results are similar to the ~14.8-day thermal cycle theorized and observed by Vugts and Zimmerman (39) within periodically drying tidal flats in estuaries; however, the physical mechanisms driving temperature variations in these estuarine systems are not the same as in the reef systems considered here. In Vugts and Zimmerman (39), the tidal modulation in the heat balances occurs through large tidal changes in the wetted surface area of shallow tidal flat systems (which alters air-sea heat exchange), with the response to heat advection being neglected over the large scales considered in these studies (that is, at scales larger than a tidal excursion length). However, most reef systems have well-defined shorelines bounded by sloping beaches or, in the case of Tallon Island, rocky coastal topography, which results in only minimal changes in reef surface area over a tidal cycle. In turn, tidally driven advection drives substantial heat exchange between a reef and the ocean, which plays a dominant role in the tidal modulation of reef heat balances by modifying reef water residence times.

The particular morphology of a reef also plays a very important role in regulating temperature variability. As a consequence, water level variability in tide-dominated reefs is frequently asymmetric, with longer fall durations than rise durations (19, 22, 40–42). This effect of tidal truncation arises from the restriction of water draining off a reef, either by bottom friction or by topographic constraints, such as a shallower crest (22), which can have a very important influence on the magnitude of

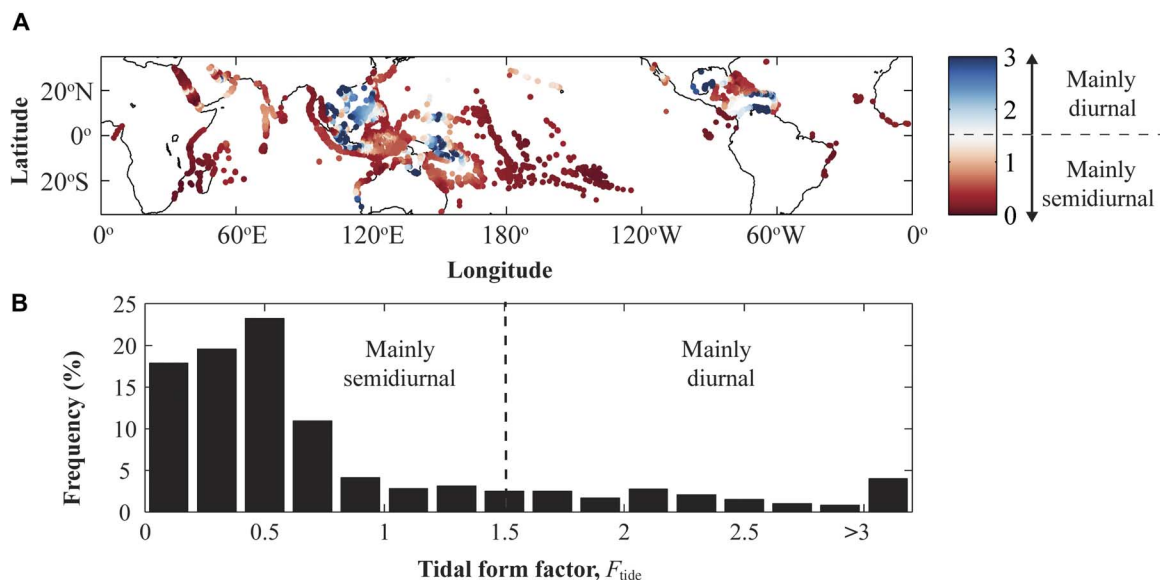


Fig. 6. Global spatial distributions and frequency distributions of the tidal regimes of warm-water coral reefs. (A) Map of the tidal form factor (F_{tide}) for coral reefs. Tidal regimes with $F_{\text{tide}} > 1.5$ are classified as mainly diurnal, and those with $F_{\text{tide}} < 1.5$ are classified as mainly semidiurnal. Note that values are capped at a maximum of 3. **(B)** Frequency histogram of global coral reef systems based on the tidal form factor. Values >3 are expressed as a summation in the final bar.

diurnal reef temperature variations. This tidal asymmetry acts to extend the low tide period when shallow water persists on a reef, thereby enhancing daytime warming (or nighttime cooling). This substantially increases not only the magnitude of diurnal temperature extremes but also the phase difference between solar heating and tidal cycles when these maximum temperatures occur.

An important implication of these results is how sea level rise could alter reef heat balances in the future and, hence, may partially contribute to limiting local reef temperature extremes in the presence of a globally warming ocean. At first, it may seem intuitive that reefs with large tidal exposure would be less sensitive to sea level changes, given that the degree of mean sea level change will be comparatively smaller than natural sea level variations these reefs already experience on a daily basis. However, in terms of diurnal temperature variability, our results indicate that reefs subject to large tidal amplitudes can be affected just as much by a sea level rise as those subject to small tidal amplitudes (Fig. 5A). Reefs that are already close to the critical depth at which tidal truncation ceases (that is, near $h_0^* \approx h_{\min}^* + 1$) are particularly close to a tipping point where even a relatively small increase in mean sea level can lead to a substantial reduction in the magnitude of diurnal temperature fluctuations. In some cases, reefs that presently experience $+5^\circ\text{C}$ diurnal temperature extremes could see a $>2^\circ\text{C}$ reduction in these temperatures from a 0.7-m sea level rise or a $>4^\circ\text{C}$ reduction by a 1.5-m rise (Table 1), amounts that are comparable in magnitude to projected warming of the tropical oceans by the end of the century under a business-as-usual scenario [2° to 4°C (43)]. However, it is not yet known how much future reductions in local temperature variability will ameliorate the more chronic thermal stresses imposed by long-term increases in regional ocean temperature.

Finally, although the focus of this study has been on the temperature extremes of tide-dominated reefs, the results are also relevant to understanding how tides influence the variation of other reef water quality parameters. For example, like temperature, changes in reef water column oxygen, partial pressure of CO_2 ($p\text{CO}_2$), and pH are also governed just as much by the morphology of a reef and the hydrodynamic forces driving circulation as they are by the fluxes driving their addition and removal from the water column (37). For example, the specific processes responsible for driving changes in oxygen, $p\text{CO}_2$, and pH (that is, production, respiration, and net calcification) also exhibit light-dependent diurnal periodicities similar to the net atmospheric heat fluxes driving temperature variations in the present model, albeit with much greater spatial variation in the biologically driven bottom boundary fluxes (20). Thus, we expect sea level rise to also cause reductions in daily extremes of oxygen, $p\text{CO}_2$, and pH that are in similar proportion to the reductions in daily temperature extremes that we report here. Although there is little doubt that rising levels of atmospheric $p\text{CO}_2$ will cause substantial changes to ocean temperature and chemistry over the following century, we conclude that rising sea levels will likely help moderate the extreme conditions presently found in many shallow, tide-dominated reef habitats.

MATERIALS AND METHODS

Experimental design

A field study of the thermodynamics of the reef platform on Tallon Island was conducted for ~2 weeks in March to April 2014. During this time, we measured water currents at 7 sites using current meters and current profilers, and water level at 10 sites using pressure sensors

[Fig. 1; see Lowe *et al.* (22) for additional details on the hydrodynamic measurements]. For the purpose of this study, we also measured temperature every minute at 64 locations distributed on a regular grid (Fig. 1) using the HOBO U22 Water Temp Pro (Onset). Following Lentz *et al.* (44), each temperature logger was calibrated in a water bath at controlled temperature both before and after the deployment, such that the root mean square errors were estimated to be $<0.1^\circ\text{C}$ in all cases. The instruments were deployed on top of small lead weights (sampling ~0.1 m above the bed) and were also wrapped in white tape to minimize any solar heating (44).

Meteorological data were obtained using a weather station mounted on a scaffolding that was deployed on the reef (Fig. 1B). The weather station measured wind speed and direction, air temperature, relative humidity, barometric pressure, and net solar radiation (with a radiometer) every minute. The radiometer was deployed on a horizontal pole ~1 m away from the scaffolding and measured the net incoming and outgoing short- and long-wave (infrared) radiation over the reef water surface ($Q_{\text{sw+lw}}$). Following an approach similar to that of Zhang *et al.* (9) [see also McCabe *et al.* (19)], the meteorological and water temperature data were used to compute the individual terms that comprise net surface heat fluxes (Q_{net}), that is

$$Q_{\text{net}} = Q_{\text{sw+lw}} + Q_{\text{lt}} + Q_{\text{sb}} \quad (6)$$

where Q_{lt} is the latent heat flux and Q_{sb} is the sensible heat flux. The latent and sensible heat flux terms were calculated using the COARE (Coupled Ocean-Atmosphere Experiment) bulk algorithms (45), as detailed by Zhang *et al.* (9).

Reef heat budget

The reef heat budget model was derived from the integral form of the thermal energy equation, which considers changes in the water temperature T within the reef, heat exchange by the advection of water on/off the reef, and the net surface heat fluxes through Eq. 6 (19, 46)

$$\underbrace{\frac{d}{dt} \int_V T dV}_{\text{reef warming/cooling}} + \underbrace{\int_{A_{\text{open}}} T u dA}_{\text{heat advection}} = \underbrace{\frac{1}{\rho_0 c_p} \int_{A_{\text{reef}}} Q_{\text{net}} dA}_{\text{net surface heat fluxes}} \quad (7)$$

which were evaluated over the reef control volume shown in Fig. 2B. Here, ρ_0 is the seawater density, c_p is the specific heat capacity of seawater, A_{open} is the vertical perimeter area along the reef edge, A_{reef} is the plan area of the reef platform area, and V is the volume of water on the reef. Following McCabe *et al.* (19), we simplified the model by assuming (i) that the temperature is approximately uniform throughout the reef, that is, $T(x, y, z) \approx T_r$, where T_r is a representative (spatially averaged) reef temperature, and (ii) that Q_{net} is likewise approximately spatially uniform and incoming water of temperature T_{in} rapidly mixes with water on the reef. McCabe *et al.* (19) also described a more complex model that considers the propagation of a thermal front during the initial flood phase of the tide; however, here, we considered the reef to be horizontally well mixed, which still accurately reproduces the main reef temperature variability (Fig. 3C) and results in a much simpler model that can be readily applied to a wider range of reefs and forcing conditions.

For a quasi-1D reef where water flows in/out of the reef approximately uniformly along the edge, the incoming/outgoing flow speed

($u_{\text{in/out}}$) can be estimated from the rate of change of the water level on the reef h_r according to mass conservation

$$u_{\text{in/out}} = -\frac{A_{\text{reef}}}{W_r(h_r - h_{\text{MSL,L}})} \frac{dh_r}{dt} \quad (8)$$

where W_r is the reef perimeter width and $h_{0,L}$ is the depth of the back reef (or lagoon) relative to the reef crest (see Fig. 2). With Eq. 8 and these uniform-property assumptions, the evaluation of the integrals in Eq. 7 leads to the following governing reef heat balance equation

$$\frac{d}{dt}(T_r h_r) - T_{\text{in/out}} \frac{dh_r}{dt} = \frac{Q_{\text{net}}}{\rho_0 c_p} \quad (9)$$

subject to the inflow/outflow temperature conditions

$$\begin{aligned} T_{\text{in/out}} &= T_0 & \text{if} & \quad \frac{dh_r}{dt} \geq 0 \\ T_{\text{in/out}} &= T_r & \text{if} & \quad \frac{dh_r}{dt} < 0 \end{aligned} \quad (10)$$

where T_0 is the surrounding (offshore) temperature and T_r is the reef water temperature.

Equation 9 was used to assess the reef temperature variability on Tallon reef and also to investigate the broader role of tides on reef heat balances (see Results). For Tallon reef, T_r and h_r were based on the spatially averaged temperature and water depth, respectively, measured by instruments on the reef; T_0 was from the temperature measured offshore by instruments on the reef slope; and Q_{net} was from the measured net heat fluxes. The numerical solution for T_r was obtained using Euler forward differencing. For Tallon reef, Lowe *et al.* (22) showed that inflows/outflows are generally uniform along the reef, except during the initial ~2 hours of ebb tide where flow accelerating around the island generates a northward flow on the reef, resulting from the inflow of ocean water in the southern area of the reef and an outflow in the north. We thus considered this effect on the heat advection term in Eq. 7, where the heat fluxes at four segments of the reef were estimated from the measured currents along the reef edge at sites V1 to V4, which slightly improved predictions (typically by <15%) during this brief phase of the tide.

To generalize the heat budget model to investigate how tidal, solar, and reef morphology parameters more broadly control temperature variability within reefs, we considered dimensionless forms of the governing Eqs. 9 and 10 through substitution of dimensionless forms of the variables defined in Eq. 3

$$\frac{d(T_r^* h_r^*)}{dt^*} - T_{\text{in/out}}^* \frac{dh_r^*}{dt^*} = Q_{\text{net}}^* \quad (11)$$

$$\begin{aligned} T_{\text{in/out}}^* &= 0 & \text{if} & \quad \frac{dh_r^*}{dt^*} \geq 0 \\ T_{\text{in/out}}^* &= T_r^* & \text{if} & \quad \frac{dh_r^*}{dt^*} < 0 \end{aligned} \quad (12)$$

where T_r^* and $T_{\text{in/out}}^*$ are the dimensionless forms of the reef water temperature and inflow/outflow temperature, respectively. For the idealized (sinusoidally varying) tidal forcing considered in Eq. 1, the reef water depth in dimensionless form becomes

$$h_r^*(t^*) = h_{\text{MSL}}^* + \cos\left(\frac{2\pi\tau_{\text{solar}}}{\tau_{\text{tide}}} t^* + \phi_0\right) \quad (13)$$

such that tidal truncation occurs when $h_{\text{MSL}}^* \leq h_{\text{min}}^* + 1$. From Eq. 2, the net surface heat flux term varies sinusoidally during the day (reaching a maximum $+Q_{\text{net,max}}$) and is constant at night ($-Q_{\text{net,night}}$); the constant night cooling rate was chosen to be equal to 25% of the daytime maximum warming rate ($Q_{\text{net,max}}$), which is typical of many tropical reef systems worldwide (9, 12, 47), including Tallon reef in the present study (Fig. 3B). Therefore, the dimensionless net surface heat flux term becomes

$$\begin{aligned} Q_{\text{net}}^*(t^*) &= \cos(2\pi t^*) & t_{\text{sunrise}}^* \leq t^* \leq t_{\text{sunset}}^* \\ Q_{\text{net}}^*(t^*) &= -0.25 & \text{at night} \end{aligned} \quad (14)$$

Equations 11 to 13 can be readily solved using numerical integration to predict temperature variability on the reef as a function of the three dimensionless input parameters ($\tau_{\text{tide}}/\tau_{\text{solar}}$, h_{MSL}^* , h_{min}^*) defined in Eq. 3.

Assessing changes in temperature extremes for select reefs worldwide

Representative reef morphology properties and tidal conditions were obtained from existing literature on six tidally forced reefs in the Indo-Pacific (Table 1 and references therein), which were used with the heat budget model as case studies to investigate how the thermal regimes of these reefs would change under future sea level rise scenarios. Both the reef depth relative to mean sea level (h_{MSL}) and minimum depth at low tide (h_{min}) were estimated from either direct observed tidal water depths (when available) or accurately surveyed bathymetry obtained on the reef platform relative to mean sea level. Tidal amplitudes (η_{tide}) were estimated from reported tidal records, on the basis of the average of the spring and neap tidal amplitudes. Estimates of diurnal temperature ranges (ΔT_r) were obtained from in situ temperature records available in the literature for two of the sites (Lady Elliot and Ofu), from data in the present study (Tallon Island), and from the Australian Institute of Marine Science (<http://data.aims.gov.au>) for Warraber Island. Diurnal temperature ranges (ΔT_r^* , in dimensionless form) were predicted for each reef and for three sea level scenarios (0 m present day, +0.7-m rise, and +1.5-m rise) using values of h_{MSL}^* and h_{min}^* computed for each reef and sea level. The +0.7-m rise was based on the end-of-century predictions from the IPCC Fifth Assessment Report (31) based on CMIP5 model projections under a business-as-usual scenario (RCP8.5), whereas the +1.5 scenario was based on semi-empirical projections of the sea level response to a 4°C global temperature rise (29, 30, 32, 48). Percentage changes in future diurnal temperature ranges ΔT_r were obtained by normalizing the modeled sea level rise scenario values with the present-day values. Future diurnal temperature ranges (in degrees Celsius) were computed using the modeled percentage changes in ΔT_r and the present-day temperature observations.

To assess how the relative importance of semidiurnal versus diurnal tides varies globally for warm-water coral reefs within the $\pm 30^\circ$ latitude bands, we joined global coral reef distributions from the 1-km-resolution United Nations Environment Programme World Conservation Monitoring Centre data set (49) with the spatial distribution of tidal form factors F_{tide} computed from the M2, S2, K1, and O1 tidal constituent amplitudes that were derived from the Oregon State University Tidal Inversion Software (OTIS) (50).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/2/8/e1600825/DC1>

Supplementary Methods

Supplementary Results

table S1. Tidal amplitudes and reef morphology parameters for sample tidally forced reefs globally.

table S2. Sensitivity of the projected temperature changes to spring and neap amplitude variations.

fig. S1. Response of reef temperature to an interacting solar heating cycle and a diurnal (K1) tidal cycle.

fig. S2. Response of reef temperature to an interacting solar heating cycle and a diurnal (O1) tidal cycle.

Reference (56)

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