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Climate change impacts on mesophotic regions of the Great Barrier Reef

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Climate change projections for coral reefs are founded exclusively on sea surface temperatures (SST). While SST projections are relevant for the shallowest reefs, neglecting ocean stratification overlooks the striking differences in temperature experienced by deeper reefs for all or part of the year. Density stratification creates a buoyancy barrier partitioning the upper and lower parts of the water column. Here, we mechanistically downscale climate models and quantify patterns of thermal stratification above mesophotic corals (depth 30 to 50 m) of the Great Barrier Reef (GBR). Stratification insulates many offshore regions of the GBR from heatwaves at the surface. However, this protection is lost once global average temperatures exceed ~3 °C above preindustrial, after which mesophotic temperatures surpass a recognized threshold of 30 °C for coral mortality. Bottom temperatures on the GBR (30 to 50 m) from 2050 to 2060 are estimated to increase by ~0.5 to 1 °C under lower climate emissions (SSP1-1.9) and ~1.2 to 1.7 °C under higher climate emissions (SSP5-8.5). In short, mesophotic coral reefs are also threatened by climate change and research might prioritize the sensitivity of such corals to stress.

Great Barrier Reef | climate refugia | mesophotic reefs | downscaling | bottom temperatures

Significance

Climate model projections of coral reefs have solely been made using surface temperatures and failed to consider vast areas of deeper, mesophotic reefs at 30 to 50 m. We identify areas of the Great Barrier Reef where thermal stratification insulates deeper reefs from surface warming. These areas may act as genuine deep-water refuges under some warming scenarios. These refugia arise where thermal stratification insulates deeper reefs from surface heatwaves. Even though many shallow species are not found in deeper areas, refugia should help protect mesophotic species. However, this protection fails to maintain today's temperatures beyond mid-century. Worse, if society follows higher-end emissions, we find that coral mortality is likely to be high even at mesophotic depths.

Mesophotic coral ecosystems are defined as reef communities in the mid to lower photic zone (30 to 150 m) that contain phototrophic taxa (1). Glynn (2) and Riegl and Piller (3) first identified deep reef areas as less affected by thermal stress events and this concept was extended to mesophotic reefs by Bongaerts et al. (4). Bongaerts and Smith (5) then identified numerous complexities associated with biophysical interactions on these reef environments making thermal protection largely circumstantial (6–8). Since mesophotic reefs are generally found on forereef environments which, through advection and mixing, are in closer contact with cooler off-shelf and subsurface waters than inshore reefs (9–13), such environments have the potential to provide mesophotic communities with a degree of refuge from the impacts of climate change.

Bleaching of mesophotic reef communities has received limited attention (4) because most coral reef research occurs at <15 m depth owing to the practicalities of conducting fieldwork using SCUBA (14). However, the potential of mesophotic coral reefs to serve as refugia from climate change has stimulated an expansion of thermal stress research in deeper reef environments (4, 5, 15) with increasing capabilities of technical diving and unmanned vehicles (16). Mass coral bleaching events are stimulated by anomalously higher temperatures relative to long-term thermal conditions (17–19). Evidence exists of mesophotic coral bleaching between 30 and 90 m in the eastern Caribbean Sea (15, 20), the western and central Pacific (21), the central Indian Ocean (22), and on the Great Barrier Reef (GBR) during the 2016 El Niño event (6). The 2016 GBR bleaching saw anomalously warm temperatures reported at 40 m, resulting in the bleaching of 40% of deeper (40 m) coral colonies in comparison to 60% bleaching in the shallower (10 m) coral colonies (6). Yet, the responses of mesophotic corals to thermal stress are variable and likely context-specific with some studies finding elevated sensitivity (15), some finding little variation in thermal sensitivity with depth (8), and others finding that thermal fluctuations from internal waves can enhance the thermal resilience of mesophotic corals (7).

Despite evidence for mesophotic bleaching, severity of bleaching is expected to decline with depth (6, 23–26) generally attributed to lower levels of photosynthetically active radiation (27) and cooler temperatures (28, 29). Stratification caused by thermal density gradients in the water column could allow for a cooler layer of water near the seabed while the surface is warm. The latest Intergovernmental Panel on Climate Change report reflects the high confidence in the literature that the ocean will continue to become more stratified owing to climate change (30–36). Increases in stratification are due to the combined effects of warming across latitudes and freshening at high latitudes increasing the buoyancy of

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surface waters (34). Initial research on increases in stratification by Sarmiento et al. (37) used a global climate model with a coupled carbon cycle model to project oceanic uptake of CO_2 in the 21st century, finding strong decreases in high latitudes as a result of stratification. This study also revealed a decrease in global mean oceanic oxygen (37). Further studies demonstrated long-term declines of oxygen and shoaling of hypoxia (38–42) associated with physical oceanographic changes of stratification, ventilation, and circulation rather than biological changes (43, 44). Climate model studies then continued to examine the role of increasing sea surface temperature and salinity enhancing upper ocean stratification (30, 32, 45, 46).

Stable stratification hampers vertical mixing and can therefore reduce the exchange of heat and other oceanographic properties with the seabed (47, 48). Patterns of warming at depth are likely to be quite different to those near the surface ocean. Further, the coarse horizontal and vertical resolution of global ocean and climate models, and the fact that these models do not include shelf sea processes such as tidal mixing, means that existing climate projections will not adequately simulate shallow water stratification. Downscaling climate models can improve the accuracy of climate projections over coastal environments (49). Here, we use a mechanistic downscaling method (50) to generate bottom temperature projections under a range of Coupled Model Intercomparison Project Phase 6 (CMIP6) (51) climate change scenarios to account for the stratification feedback.

1. Methods

The S2P3-R v2.0 downscaling approach (50) enables the study of bottom temperature climate projections. This study simulates waters between 0 and 50 m depth (*SI Appendix*, Fig. S1) and considers areas between 30 and 50 m as the upper mesophotic reef. Surface temperature refers to the uppermost layer of the water column and the bottom temperature refers to the layer just above the seabed (Fig. 1). The model is run with 2 m vertical resolution and a 0.1 m horizontal resolution (50). Stratified locations are hypothesized to provide thermal relief at the seabed when warming conditions are occurring at the surface. Glynn (2) first articulated the refuge hypothesis for coral bleaching, defining areas whose environmental conditions provide a natural resistance (avoidance) of bleaching (see also ref. 52). Here, we use a conservative approach to define potential mesophotic refuges as regions protected from any surface warming. Our metric locates areas where stratification allows thermal isolation of bottom waters during austral summer based on a location having a positive surface temperature anomaly above bottom water not experiencing a positive temperature anomaly. For example, if a grid point has a bottom temperature anomaly of −0.1 °C and a surface temperature anomaly of 1.0 °C, this would constitute an area of thermal protection related to stratification. This method is described in the Eq. **1** where SST represents sea surface temperature, SBT represents sea bottom temperature, and t represents the annual austral summer mean, calculated over December, January, February, and March.

$$\text{thermal\_protection}_t = ((SST_t - SST_{\text{climatology}}) < 0)\ AND\ ((SBT_t - SBT_{\text{climatology}}) < 0). \qquad [1]$$

Throughout the remainder of this manuscript the term thermal protection is used to refer to this state. By considering only periods without positive bottom temperature anomalies we avoid ambiguity about whether any thermal stress was experienced in response to surface warming. While thermal protection may be experienced in situations not identified by this metric, a reduction of the number of events counted by this metric is considered an indication that protection by stratification is reduced. Acknowledging that this metric is conservative, but not having an empirical basis to define a less conservative metric because it is not known how large a positive mesophotic thermal anomaly can rise without lethal effects, we compliment the analysis with a sensitivity experiment. In the sensitivity experiment, the austral summer mean bottom temperature anomaly for a specific grid point is counted as remaining 'protected' from surface warming until it exceeds one standard deviation (SD) above its austral summer climatological mean (1980 to 1999). It should be noted that in this sensitivity experiment, bottom temperatures could rise more than surface temperatures and still be counted by the metric. It should therefore not be interpreted as indicative of areas where the oceanography is offering protection as in the primary metric, but rather as where thermal stress is limited. Model anomalies in all experiments are calculated using an austral summer climatology (1980 to 1999). Areas of thermal protection are identified under four future climate emission scenarios using five climate models.

1.1. Downscaling.

This study uniquely involves the analysis of bottom temperature output, i.e., the temperature at the seabed, derived from the semidynamic S2P3-R v2.0 downscaling. CMIP6 models (51); MRI-ESM2-0 (53), EC-Earth3-Veg (54), UKESM1-0-LL (55), CNRM-ESM2-1 (56), and IPSL-CM6A-LR (57), were downscaled under climate-change scenarios; SSP1-1.9, SSP1-2.6, SSP3-7.0, and SSP5-8.5 (58). To do this, the S2P3-R v2.0 model was forced with atmospheric conditions from each model and scenario as described in McWhorter et al. (59). The spatial variability between climate models was further described in McWhorter et al. (60). Downscaled surface and bottom temperature outputs from a S2P3-R v2.0 simulation forced with the ERA5 atmospheric reanalysis product (61) were previously compared to Australia's Integrated Marine Observing System mooring system observational bottom temperature data for validation in Halloran et al. (50). Simulated bottom water temperatures tend to follow a 1:1 relationship with observed temperatures but south of the Cape York Peninsula temperatures

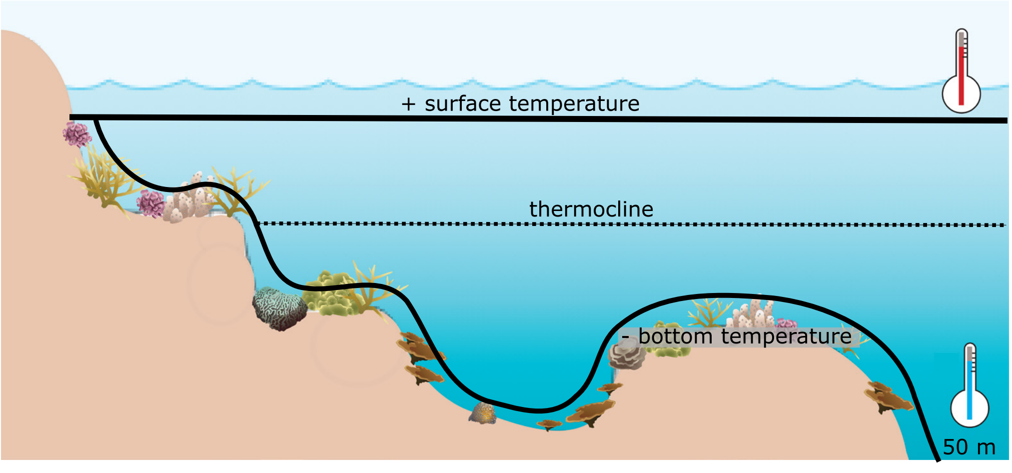

Fig. 1. The conceptual diagram shows how anomalies for the surface and bottom layer of the downscaled model output were calculated, referred to as thermal protection. A positive surface temperature anomaly above a negative bottom temperature anomaly was used to find areas of thermal refuge during projected warming events.

tend to display a cold bias of approximately one degree (50). Downscaled SSTs compared to satellite SSTs on the GBR contained a positive bias in the north and a negative bias in the south potentially due to a lack of simulated lateral advection (50). The S2P3-R v2.0 downscaling captures much of the interannual variability in SSTs with a temperature bias of <0.5 K (50).

While recent progress in the decarbonization of global energy systems means that SSP5-8.5 is a highly unlikely scenario, it is the only scenario that has persisted, largely unchanged, across CMIP versions and is therefore valuable as a comparator. The strong signal it provides is valuable in determining impacts at given global mean temperature thresholds and understanding mechanisms.

1.2. Summer Metrics Applied to Surface and Bottom Temperature Outputs. Typically used bleaching metrics such as Degree Heating Weeks (62) and the number of severe bleaching events/decade (59) could not be applied in this study because the thermal stress anomalies at which corals undergo bleaching at deeper depths (>15 m) is largely unknown (63).

The bottom and surface temperature anomaly data were used to locate areas that contain a positive surface temperature anomaly above bottom waters not experiencing a positive temperature anomaly, i.e., locations where surface warming, and therefore increased buoyancy was potentially insulating bottom waters from summer heat. Since bleaching on the GBR typically occurs during austral summer months (64), surface and bottom temperature anomalies were calculated across December, January, February, and March (64) as annual austral summer means from 2000 to 2100. The anomalies were calculated in relation to the average annual summer mean conditions from 1980 to 1999. The areas of thermal protection are spread across the austral summer months and models (*SI Appendix*, Figs. S2 and S3) indicating that a single month or model does not dominate the analysis. The GBR Marine Park Authority (GBRMPA) (65) boundary was used to mask the values within the GBRMPA boundary for consistency.

1.3. Validation. The ERA5 atmospheric reanalysis product (61) was downscaled using S2P3-R v2.0 to relate the observational data to the climate model data. Downscaled ERA5 outputs are used to explore the controls on thermal protection and to ground-truth the results (60). Analysis of the ERA5-driven simulation was identical to that of the CMIP6-driven simulations. The climatology period was set as 1980 to 1999 (inclusive) and the years chosen for the comparison between the climate models and observations were 2000 to 2019 (inclusive) (Fig. 2 *A*–*C*). The areas of thermal protection were calculated as a percentage of years for each, ERA5 and CMIP6 outputs (Fig. 2 *A* and *B*). ERA5 and CMIP6 outputs were then added together to show the areas of highest agreement (Fig. 2*C*).

1.4. Downscaled ERA5-Based Wind and Tidal Energy Flux Calculations. Wind and tidal energy impact mixing (66) and therefore the seawater temperatures experienced by GBR corals (60). This study compares wind and tidal energy over areas of thermal protection and non-thermal protection (areas that do not meet the metric criteria) to elucidate the primary controls on stratification.

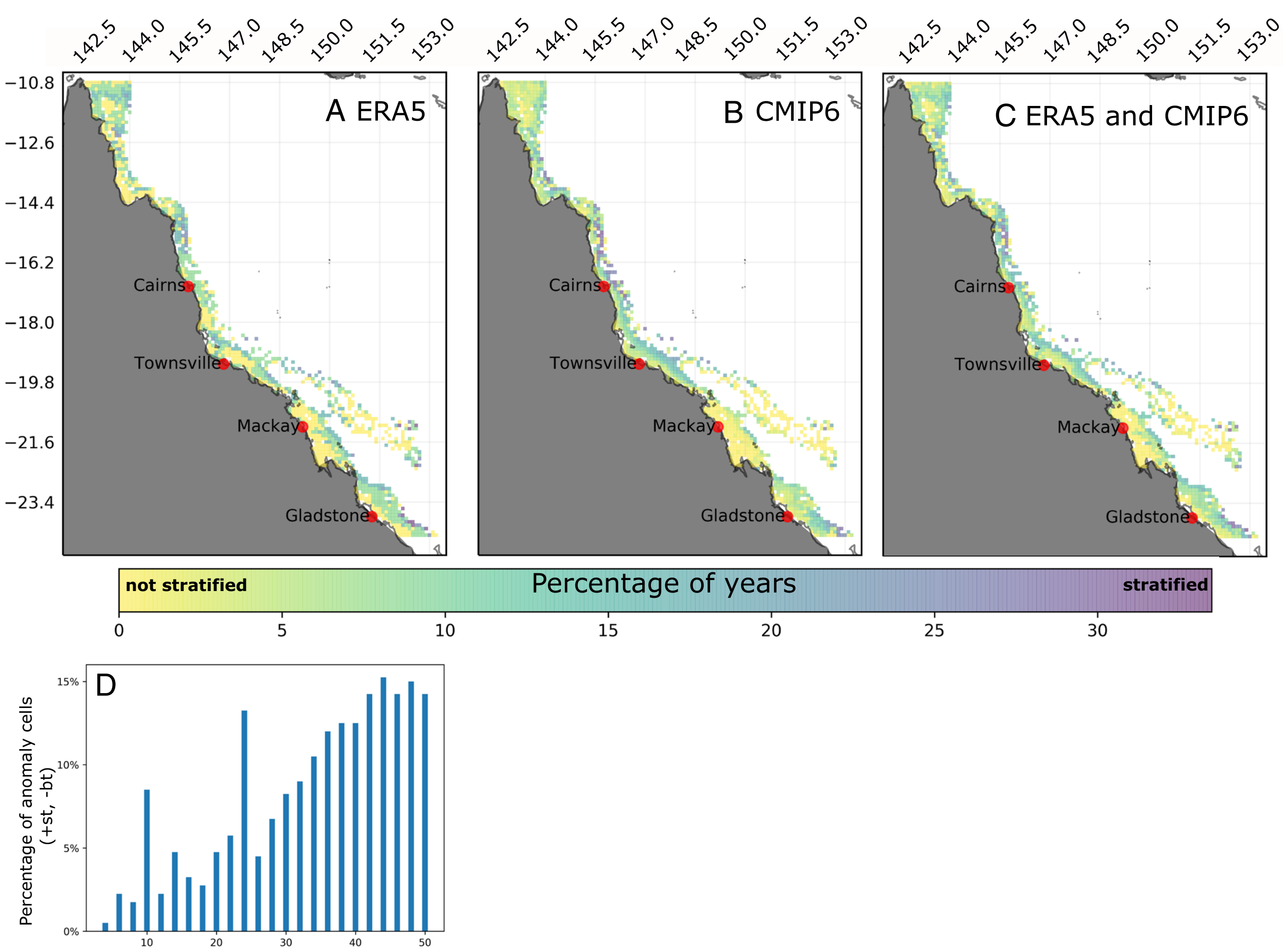

Fig. 2. Mesophotic reef refugia (0 to 50 m) are shown as density maps from (*A*) observations, (*B*) climate model simulations, and (*C*) both observations and climate models combined. Downscaled observations from ERA5 surface and bottom temperatures were calculated to identify the thermal protection pattern (positive surface temperature anomaly above a negative bottom temperature anomaly) during summer months based on a climatology from 1980 to 1999, anomalies are calculated from 2000 to 2019 during summer months (December, January, February, and March). Areas with identified thermal protection are shown using four climate scenarios (SSP1-1.9, SSP1-2.6, SSP3-7.0, and SSP5-8.5) and five downscaled climate models from 2000 to 2019 summer months relative to summer conditions from 1980 to 1999. (*D*) The bathymetry grid over the GBR used in this study is shown (0 to 50 m) as the distribution of the range of depths for the thermal protection locations based on climate models as a percentage of cells per depth bin.

Wind and tidal energy outputs were extracted from the S2P3-R v2.0 downscaled ERA5 simulation. The energy flux calculations, including the statistical methods used for comparison, are described in McWhorter et al. (60). Additive mixed effect models were used to explore differences in wind and tidal energy between the thermal protection locations and the nonthermal stratification protection locations using the "bam" function (67) in R version 4.1.1 (68) where longitude and latitude were included as a smooth function to account for the spatial correlation of the data. Pairwise comparisons were determined using the 'pairs' function (69) in R version 4.1.1 (68).

2. Results

Mesophotic reef refugia are primarily found in offshore areas (Fig. 2 *A*–*C*) defined by the agreement of thermal protection locations between downscaled simulations driven by CMIP6 models and an observation-based reanalysis. For nearshore areas, agreement was high around the east of Cape York, north of Cairns, and northwest of Townsville (Fig. 2*C*). Climate model and ERA5 simulations diverged most strongly in the waters east of Mackay (Fig. 2 *A*–*C*). Most of the thermal protection locations from the climate model outputs are in waters of 30 to 50 m depth, but the stratification pattern is distributed across all depths (0 to 50 m) (Fig. 2*D*). Depth is therefore not the only variable determining these conditions.

Spatial patterns between the downscaled observationally derived product (ERA5) and the downscaled climate models also show agreement for the areas without thermal protection (Fig. 2 *A*–*C*). Areas lacking thermal protection include the shallow nearshore area that branches off in the central and southern GBR and parts of the far north and southern GBR. These locations show general agreement with the shallow water refugia locations seen in McWhorter et al. (60) where vertical mixing was found to suppress surface warming.

The locations of thermal refuges can be attributed to depth and a lack of mixing from tides (Figs. 2 *A*–*D* and 3*A*). The spatial distribution of tidal energy in the model is determined by the interaction of tides with bathymetry, and assuming minimal sea-level rise, this will not change into the future. Wind was also tested as a contributor to vertical mixing properties. No significant difference in wind-driven mixing was seen between areas where thermal protection was and was not seen (Fig. 3*B*).

While stratification may still provide relative protection to some mesophotic reefs throughout the coming century, we find that the refuge afforded by this metric of thermal protection is lost under high emissions climate scenarios (SSP3-7.0, SSP5-8.5) from mid-century onward (Fig. 4). There is a relationship between the reduction in the number of locations experiencing thermal protection and the evolution of global average air temperatures throughout the century in each scenario. Declines in the number of thermal refuges correlate inversely with the general rising pattern of warming expected in each climate scenario (Fig. 4).

The percentage of model grid cells experiencing protection by thermal stratification will reduce with any concomitant surface and bottom temperature warming above climatology. Our projections show median bottom temperature values increase by ~2 °C under high climate emissions scenarios (SSP3-7.0, SSP5-8.5), ~1 °C in SSP1-2.6 and less than 1 °C in SSP1-1.9 after mid-century in areas identified under our metric as thermal refuges (Fig. 5 *A* and *B*).

We found that median bottom temperatures remain near 28 °C over the coming decades, consistent with nonbleaching conditions in a previous study on the GBR (6). However, warming increases in higher scenarios after mid-century (Fig. 5 *A* and *B*) such that median bottom temperatures exceed 30 °C for "refuges" under higher emission climate-change scenarios SSP3-7.0 and SSP5-8.5 (Fig. 5*B*). Given the magnitude of projected increases in global average ocean surface temperatures under high emissions scenarios it is likely that bleaching and mortality will be experienced at least down to the upper mesophotic zone (30 to 50 m) in these scenarios.

From 2050 to 2060, the magnitude of the warm bottom temperature anomaly in SSP1-1.9 shows an increase of 1 °C in 35% of cells but is much greater—at 1.7 °C—in 40% of cells under SSP5-8.5 (Fig. 6 *A*–*D*). The time period just after mid-century was selected as this is the time of committed warming from SSP1-1.9 and when the other analyzed climate scenarios are expected to increase rapidly (34). The bottom temperature anomalies within SSP5-8.5 are regionally distinct (Fig. 6*B*) as the far north and northern GBR are expected to experience less bottom warming than the central and southern GBR. Under SSP1-1.9, the higher bottom temperature anomalies, while less severe, are most obvious in the far north and in some nearshore regions of the central GBR (Fig. 6*A*).

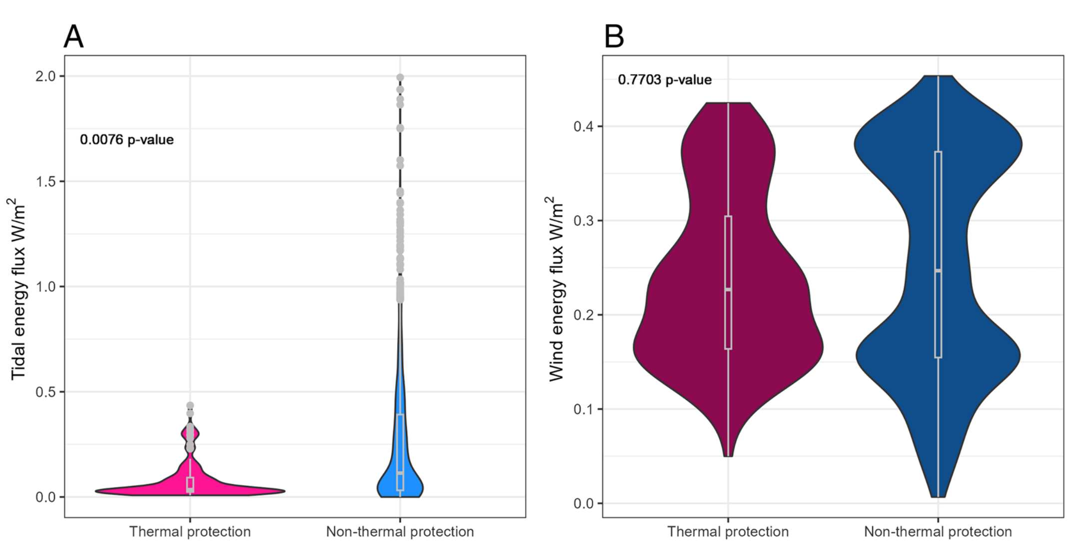

Fig. 3. The downscaled ERA5 simulation shows (*A*) tidal energy flux and (*B*) wind energy flux from 1999 to 2019 in thermal protection and non-thermal protection locations. To use a pairwise comparison, additive mixed effect models explored differences between thermal protection and non- thermal protection locations using the bam function in R version 4.1.1 where longitude and latitude were included as a smoothed function to account for the spatial correlation of the data. Pairwise comparisons were determined using the pairs function in R version 4.

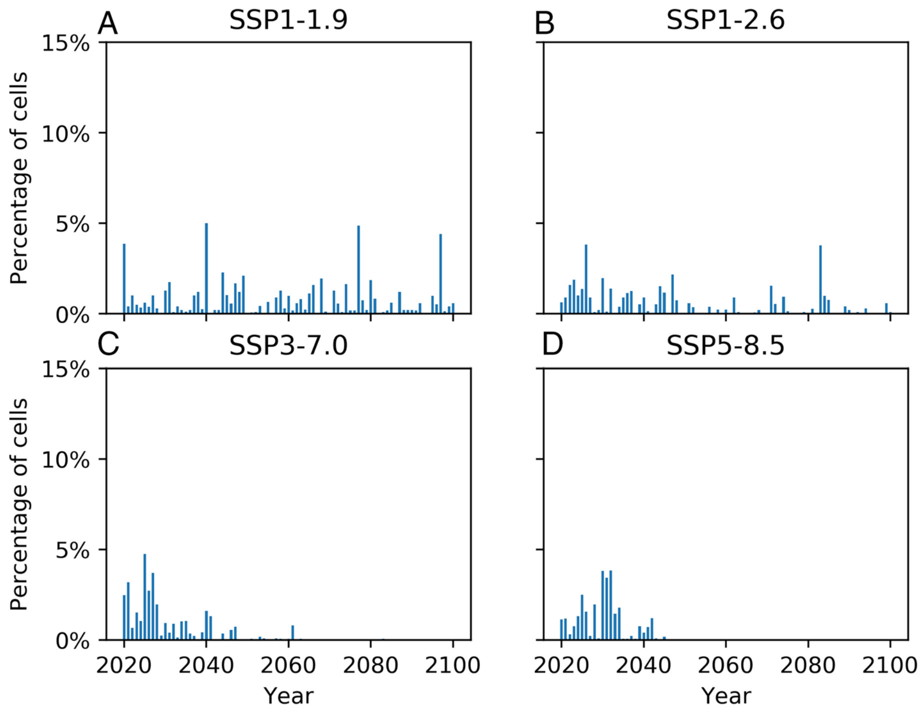

Fig. 4. The thermal protection locations are shown as a percentage of annual cell counts for (*A*) SSP1-1.9, (*B*) SSP1-2.6, (*C*) SSP3-7.0, and (*D*) SSP5-8.5.

The sensitivity experiment, in which the bottom temperature is allowed to increase up to one SD above the climatological value, identifies similar regions of 'protection' to the main analysis between ERA5 and CMIP6 for areas east of Cape York and offshore Townsville (*SI Appendix*, Fig. S4 and Fig. 2 *A*–*C*). However, disagreement is seen between the sensitivity analysis and the original metric for the shallow areas that branch off in the central and southern GBR and some nearshore shallow locations off Mackay and Gladstone. (*SI Appendix*, Fig. S4). Discrepancy arises because the relaxed criteria of the sensitivity experiment means that it is identifying areas of minimal warming rather than where the oceanographic conditions are providing protection by stratification.

While there is divergence between the locations identified by the main metric and the locations calculated in the sensitivity experiment, there is agreement in that the number of thermal protection locations will rapidly decline under the higher climate change scenarios during the second half of the century (*SI Appendix*, Fig. S5), although from a higher baseline. Agreement is also seen between the experiments demonstrating in the second half of the century, under the higher end climate scenarios, temperatures exceed 30 °C even in protected cells (Fig. 5 and *SI Appendix*, Fig. S6).

3. Discussion

Rises in SST are expected to increase stratification under a warming planet (34). If this results in new areas being stratified throughout the summer months, or stratification strengthening, it could help protect mesophotic reefs from heatwaves. Our results suggest considerable, yet conservative scope for such refuges for the immediate future but the efficacy of such protection is highly sensitive to future emission profiles.

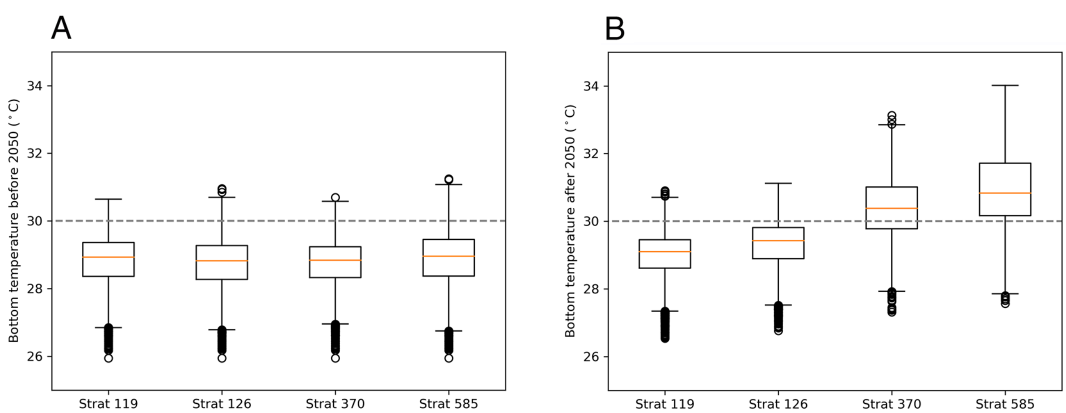

Fig. 5. Ensemble bottom temperature values per scenario in areas with austral summer thermal protection (Strat) from (*A*) 2000 to 2050 and (*B*) 2051 to 2100 are shown. Bottom temperatures were calculated as ensemble means from austral summer months within each scenario, SSP1-1.9, SSP1-2.6, SSP3-7.0, and SSP5-8.5. The areas of thermal protection (Strat), are consistent between (*A* and *B*), based on the thermal protection metric by stratification from 2020 to 2100. The orange line represents the median value. The box boundaries are the first quartile and the third quartile. The whiskers show the range of data. The dashed grey line shows the thermal threshold of 30 °C when bleaching typically occurs at depth based on Frade et al. (6).

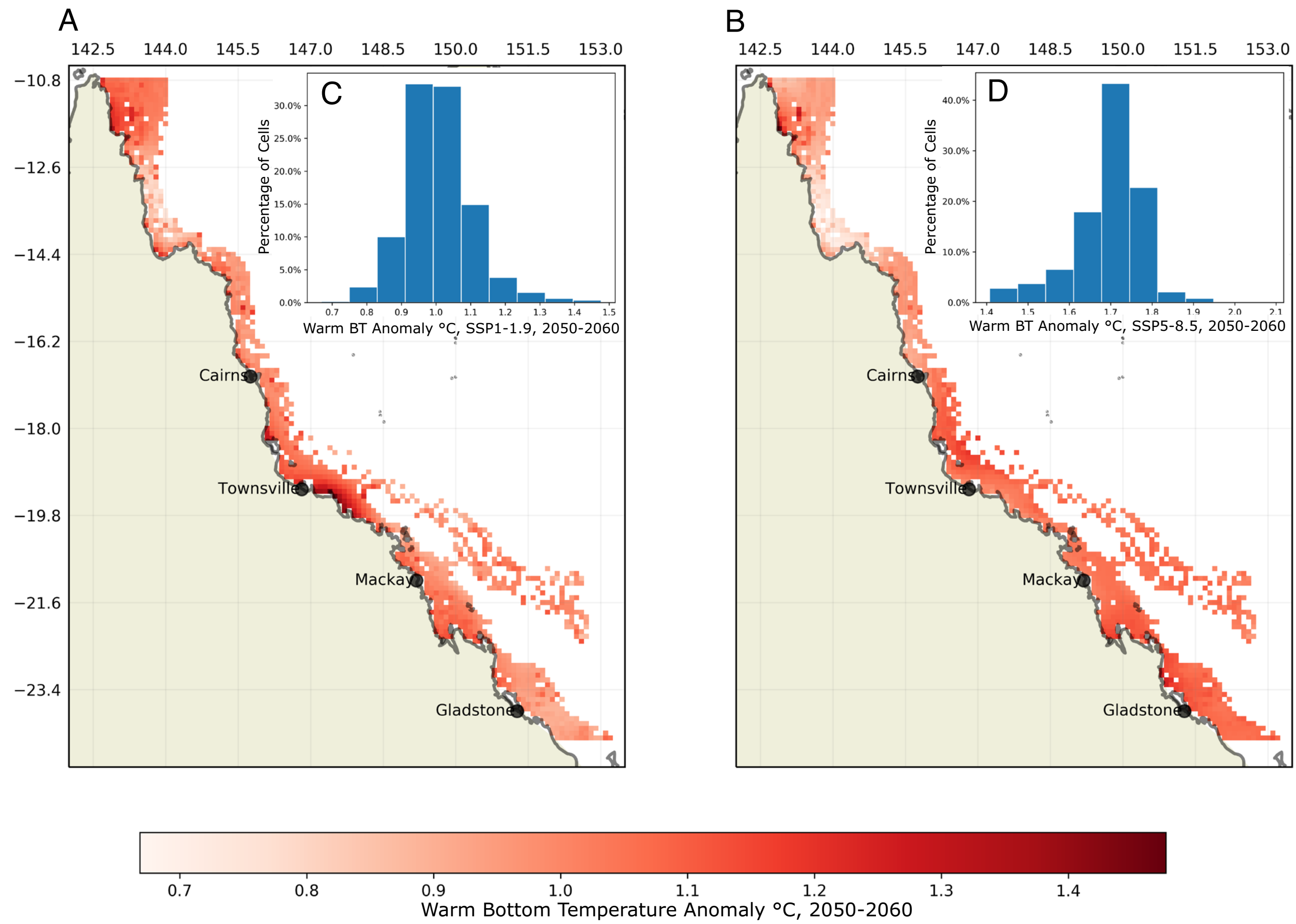

Fig. 6. Warm bottom temperature anomaly maps are shown for (*A*) SSP1-1.9 and (*B*) SSP5-8.5 and as histograms (*C*) SSP1-1.9 and (*D*) SSP5-8.5. Bottom temperature output from the S2P3-R v2.0 downscaling was used from five climate models under each of the high and low climate scenarios (SSP1-1.9 and SSP5-8.5). Daily ensemble means for bottom temperature were calculated from all five models and then an annual anomaly was calculated over 2050 to 2060 (exclusive) (depths, 0 to 50 m) based on a climatology from 1980 to 1999.

The thermal protection metric in this study identifies locations of thermal relief during the early 21st century across all SSP scenarios and falls under a logical approach of stratification. Previous approaches to guide management of mesophotic reefs have focused heavily on their role in larval dispersal (70). Here, we add the question of thermal protection from heatwaves for local persistence of biodiversity (5), which could be combined with recent estimates of larval dispersal to extend the concept of key source reefs in shallow reefs (71).

Areas with low-tidal mixing tend to match those where thermal stratification is proposed to provide refugia from thermal events and potentially areas of long-term resilience (5). Tidal mixing is determined by lunar and solar gravitational forces and bathymetry, so assuming relatively small changes in water depth, it can be considered a constant under climate change. Thus, mesophotic reef habitats protected from surface warming by stratification resulting from low-tidal mixing are likely to continue experiencing preferential conditions into the future. Future studies might consider the additional contribution of sea-level rise, though the impacts are likely to be minimal on this process. Low-tidal mixing is, however, only one factor in maintaining cool bottom water temperatures. A loss of thermal refuges could result from future changes in wind strength or overwhelming increases in sea temperatures, as seen under high end climate scenarios after mid-century.

We did not find wind mixing to be a major control on the distribution of those areas experiencing bottom water thermal protection (Fig. 3). Stronger winds will, however, mix warmer waters downwards (66) and weaker winds allow for enhanced or additional stratification (72). Simulation of the regional response of wind patterns to climate change, while in agreement in some areas important to the GBR (73, 74) are typically considered to be highly uncertain (75–77). Therefore, we do not discount the potential for improved climate projections to identify a larger contribution of wind-driven mixing to loss or gain of stratification derived protection for mesophotic GBR reefs.

Around mid-century thermal protection rapidly declines across all scenarios analysed and is completely lost under higher emission climate scenarios. The rate of loss of thermal protection approximately mirrors the rate of global warming. The warming in SSP1-1.9 and SSP1-2.6 is expected to peak just after mid-century, remaining at that higher level for SSP1-2.6 and returning to near present conditions under SSP1-1.9 (34). Temperatures within higher radiative forcing scenarios, SSP3-7.0 and SSP5-8.5, continue to increase after mid-century driving warming that may eliminate deep refugia on the GBR.

Despite a reduced number of thermal refuges under lower emissions climate scenarios after mid-century, median bottom temperatures do not exceed the 30 °C threshold where mesophotic reef bleaching has been witnessed (6). Mesophotic reefs under lower climate emission scenarios may therefore offer reprieve to certain coral species. Under increased warming in higher scenarios, the 30 °C threshold is exceeded, and the thermal refuges have been completely lost based on the metric in this study. The thermal protection spatial pattern demonstrated in this study does not incorporate contributions to water temperature from horizontal mixing processes simulated in the S2P3-R v2.0 downscaling. Therefore, it will be important to account for open ocean influences, especially boundary currents in future studies. In lieu of appropriate observational data, use of 3D hydrodynamic modelling could provide initial verification of the locations of thermal refuges while accounting for the influence of boundary currents on the thermal regime as well as entrapment of subsurface marine heatwaves (78).

Summer time conditions tend to insulate many offshore reef locations between 30 and 50 m on the GBR. Winter thermal protection, or the increased vertical transport of heat during winter, has not been examined because bleaching would not typically be expected in this season. Yet, under additional warming, winter mixing could transport the warm surface waters down to reefs that may have been protected by the thermocline, preconditioning waters to experience extreme warming during the following summer. Whilst we did not explore winter months in this study, they were simulated by the S2P3-R v2.0 model and may contribute to the progressive loss of thermal refugia under continued warming. During the 2017 mass bleaching event on the GBR, Frade et al. (6) speculated that the warming event could have occurred due to the lack of seasonal thermal relief from the previous mass bleaching event in 2016. The seasonal variability between temperatures at depth could be a critical component to their resilience, as has been demonstrated in high-latitude reef ecosystems such as in Bermuda (79–81).

In principle, mesophotic coral populations might provide larvae to shallower reefs that have been damaged by bleaching, storms, sedimentation, land-based floods, and other impacts (4, 14, 34, 82). Such corals would have to be depth-generalists yet Bongaerts et al. (83) found only ~30% of coral taxa fulfilled this criterion. Moreover, available evidence suggests weak exchange of corals across depth gradients, especially in the lower mesophotic zone (84). An increase in studies has demonstrated that mesophotic reef communities are distinct from shallow communities in assemblage composition and species turnover (84–86). In contrast, previous studies demonstrated high overlap of species across depths showing an overlap of approximately 77% for corals of shallow and upper mesophotic zones, 30 to 50 m, in the Caribbean (87, 88). In order to determine which species can use depth as a refuge, abundance, physiological performance, and genetic connectivity across depth needs to be quantified (89).

Mesophotic coral reefs may not be a genetic refuge for shallow-water corals but thermal stratification does provide meaningful refuge from stress for large areas of mesophotic reef on the GBR. Such refuge is moderately robust but is likely to be overwhelmed by rates of warming if society fails to meet the Paris agreement. Thus, like their shallow-water counterparts, mesophotic reefs are also heavily threatened by climate change and studies are needed to parameterize their thermal sensitivity more comprehensively.

Data, Materials, and Software Availability. Anonymized csv data and scripts have been deposited in Zenodo (10.5281/zenodo.10810331) (90).

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