



Reef Restoration and Adaptation Program

T13: ULTRA-THIN SURFACE FILMS

A report provided to the Australian Government by the Reef Restoration and Adaptation Program

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1. PREAMBLE

The Great Barrier Reef

Visible from outer space, the Great Barrier Reef is the world's largest living structure and one of the seven natural wonders of the world, with more than 600 coral species and 1600 types of fish. The Reef is of deep cultural value and an important part of Australia's national identity. It underpins industries such as tourism and fishing, contributing more than \$6B a year to the economy and supporting an estimated 64,000 jobs.

Why does the Reef need help?

Despite being one of the best-managed coral reef ecosystems in the world, there is broad scientific consensus that the long-term survival of the Great Barrier Reef is under threat from climate change. This includes increasing sea temperatures leading to coral bleaching, ocean acidification and increasingly frequent and severe weather events. In addition to strong global action to reduce carbon emissions and continued management of local pressures, bold action is needed. Important decisions need to be made about priorities and acceptable risk. Resulting actions must be understood and co-designed by Traditional Owners, Reef stakeholders and the broader community.

What is the Reef Restoration and Adaptation Program?

The Reef Restoration and Adaptation Program (RRAP) is a collaboration of Australia's leading experts aiming to create a suite of innovative and targeted measures to help preserve and restore the Great Barrier Reef. These interventions must have strong potential for positive impact, be socially and culturally acceptable, ecologically sound, ethical and financially responsible. They would be implemented if, when and where it is decided action is needed and only after rigorous assessment and testing.

RRAP is the largest, most comprehensive program of its type in the world; a collaboration of leading experts in reef ecology, water and land management, engineering, innovation and social sciences, drawing on the full breadth of Australian expertise and that from around the world. It aims to strike a balance between minimising risk and maximising opportunity to save Reef species and values.

RRAP is working with Traditional Owners and groups with a stake in the Reef as well as the general public to discuss why these actions are needed and to better understand how these groups see the risks and benefits of proposed interventions. This will help inform planning and prioritisation to ensure the proposed actions meet community expectations.

Coral bleaching is a global issue. The resulting reef restoration technology could be shared for use in other coral reefs worldwide, helping to build Australia's international reputation for innovation.

The \$6M RRAP Concept Feasibility Study identified and prioritised research and development to begin from 2019. The Australian Government allocated a further \$100M for reef restoration and adaptation science as part of the \$443.3M Reef Trust Partnership, through the Great Barrier Reef Foundation, announced in the 2018 Budget. This funding, over five years, will build on the work of the concept feasibility study. RRAP is being progressed by a partnership that includes the Australian Institute of Marine Science, CSIRO, the Great Barrier Reef Foundation, James Cook University, The University of Queensland, Queensland University of Technology, the Great Barrier Reef Marine Park Authority as well as researchers and experts from other organisations.

2. EXECUTIVE SUMMARY

Reflective surface films deployed above a coral community potentially reduce bleaching through a combination of lowering the temperature of the water and reducing the light absorbed by the coral symbionts, thus reducing the build-up of reactive oxygen stress. In this study we assume the only mechanism for bleaching is the temperature-mediated light-driven build-up of reactive oxygen and restrict our calculations to investigating the effect of surface films on subsurface photosynthetically available radiation (PAR). Thus, we do not consider the cooling effect of the film on reactive oxygen. We set up 20 x ~200m resolution individual reef scale configurations of the eReefs-coupled hydrodynamic-biogeochemical model to reproduce realistic conditions from the 2016/17 summer. Numerical experiments were used to investigate the residence time of the water above the reef, and the change in the build-up of reactive oxygen concentration per cell with reduced PAR. The outputs were spatially resolved, allowing us to consider the optimal locations for surface film deployment. The simulations showed that in many locations, the 30 percent reduction in PAR could reduce reactive oxygen species concentration to below a toxic level. However, the residence time on many of the reefs was only a few hours, so the cost of deploying a surface film that moved with the currents was likely to be high. Some of the 20 reefs had residence times of days and, of these, the reef on the western flank of Lizard Island was the best candidate for surface films.

The finding of a large reduction in bleaching with a 30 percent reduction in PAR is broadly consistent with field manipulations and has been used in the ecological modelling described in the RRAP report [T6—Modelling Methods and Findings](#). Further work on optimising field deployments of surface films, considering relative effects of surface films on coral diversity and other more detailed questions, will require further refinement of some of the simple assumptions used in the eReefs bleaching model.

3. INTRODUCTION, BACKGROUND AND OBJECTIVES

The scientific consensus is that the most important coral process leading to climate-change-induced mass bleaching is the build-up of reactive oxygen species in coral symbionts, resulting in zooxanthellae expulsion (Suggett et al., 2008). Other processes, such as fresh-water exposure, also cause bleaching but are considered less important in the context of climate change.

The eReefs-coupled hydrodynamic-biogeochemical model represents the physical environment (temperature, nutrients, spectrally resolved light) driving coral dynamics (Figure 1). Further, through a process of nesting, the eReefs modelling system is capable of propagating regional scale processes such as pollutant runoff and climate-driven hydrodynamic phenomena to the scale of individual reefs.

To capture the process of reactive oxygen species build-up, the eReefs-coupled hydrodynamic-biogeochemical model explicitly represents coral host biomass, as well as zooxanthellae biomass, intracellular pigment concentration, nutrient status, and the state of reaction centres and the xanthophyll cycle (Baird et al., 2018). Photophysiological processes represented include photoadaptation, xanthophyll cycle dynamics, and reaction centre state transitions.

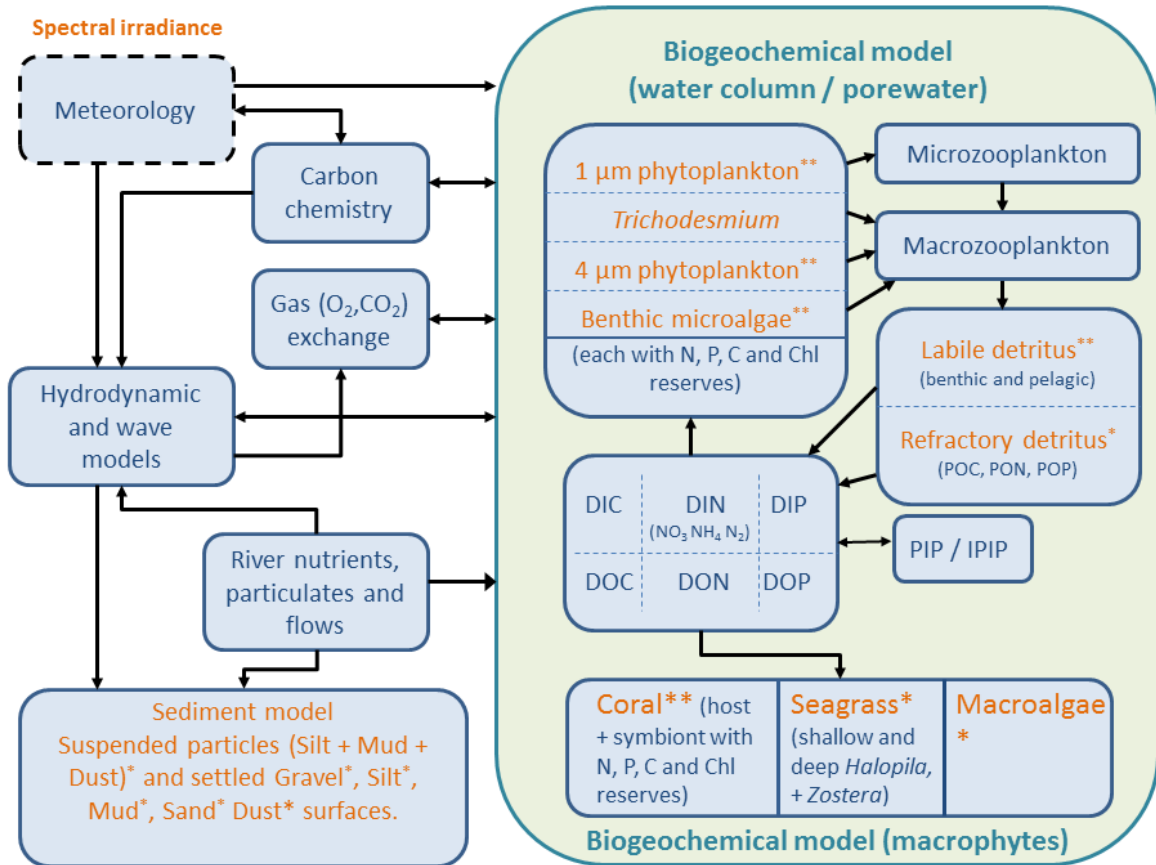


Figure 1: Schematic showing the eReefs-coupled hydrodynamic, sediment, optical, biogeochemical model. Orange labels represent components that either scatter or absorb light, thus influencing seabed light levels.

In the eReefs bleaching model, reactive oxygen species build-up depends on light because reactive oxygen species are generated by unutilised photons and temperature, as warmer temperatures inhibit the enzyme RuBisCO (Ribulose-1,5-bisphosphate carboxylase/oxygenase) whose activity is required for the productive use of solar radiation for photosynthesis, leaving more unutilised, or excess, photons. A full description of the bleaching parameterisation was documented and assessed at a Great Barrier Reef-wide scale (Baird et al., 2018). A more focused description of the bleaching model for the purpose of assessing the impact of PAR reduction is given in the next section.

4. METHODS

Summary of the model representation of reactive oxygen build-up with reduced photosynthetically available radiation.

In the eReefs bleaching model, when light intensity is reduced, initially less photons are absorbed by the pigments within the zooxanthellae. With a smaller flux, less excess photons will be present after those demanded for RuBisCO-mediated carbon fixation have been utilised. The smaller fraction of excess photons results in less state transitions of the reaction centres (from Q_{ox} to Q_{red} to Q_{in}) and less production of reactive oxygen species (Figure 2).

Photon / energy pathways through the model photosystem

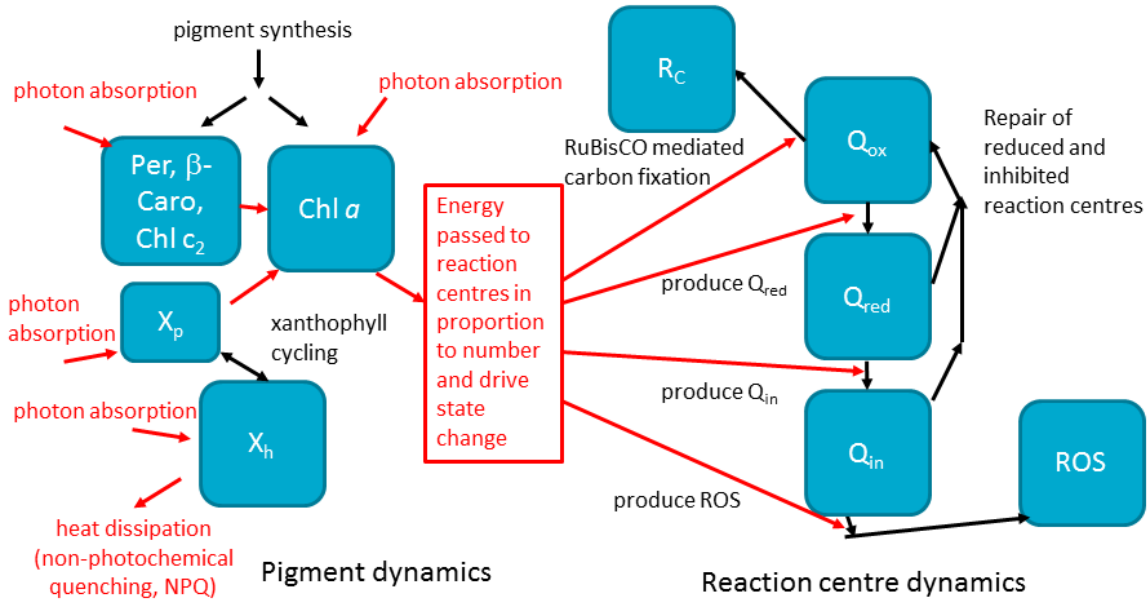


Figure 2: Schematic of the eReefs bleaching model. Note the temperature dependence of bleaching occurs because the process of RuBisCO-mediated carbon fixation is inhibited at temperatures above the summer maximum.

If seabed temperatures are above the summer climatology maximum, then the RuBisCO-mediated carbon fixation is inhibited, leading to more excess photons. However, if the seabed temperature is reduced, more photons are used in carbon fixation, resulting in, like reduced photosynthetically available radiation, a smaller number of excess photons and less state transitions of the reaction centres (from Q_{ox} to Q_{red} to Q_{in}) and less production of reactive oxygen. Thus, the emergent feature of the bleaching model is that symbionts do not build up lethal reactive oxygen concentrations in low light at high temperature (because there are no excess photons) or in bright sun at moderate temperatures (because the combination of photoadaptation, carbon fixation and reactive oxygen detoxification prevents toxic concentrations). But at high temperatures, carbon fixation is inhibited and, with high light, the photoadaptation and detoxification processes cannot prevent reactive oxygen build-up. After a period of time this leads to bleaching.

The mathematical relationship between temperature and RuBisCO-mediated carbon fixation is difficult to know. In order for the bleaching model to have a similar response to thermal stress as observations on the Great Barrier Reef in 2016, we assumed:

$$a_{Q_{ox}^*} = (1 - \exp(-(2 - \Delta T)))/(1 - \exp(-2))$$

where ΔT is the temperature anomaly and is calculated as the difference between the model seabed temperature and the spatially and temporally varying climatological temperature at that depth (Ridgway and Dunn, 2003). The form of the above equation was based on a general line of reasoning that bleaching stress begins at a temperature anomaly of 1°C (the NOAA bleaching index uses 1°C above climatology; the above equation reduces $a_{Q_{ox}^*}$ to 0.73 at +1°C), and that for a sustained period (2 summer months), 2°C (equivalent to 16 degree heating weeks) causes maximal stress (in the above equation, $a_{Q_{ox}^*} = 0$ at +2°C). If the climatological temperature is below 26°C, then ΔT is given by the model seabed temperature minus 26°C. The constant 2°C represents the temperature anomaly above which activity of oxidised reaction centres is zero. For

$\Delta T < 0^\circ\text{C}$, $a_{\text{Qox}}^* = 1$, and all oxidised reaction centres are available for carbon fixation, and $\Delta T > 2^\circ\text{C}$, $a_{\text{Qox}}^* = 0$, and all oxidised reaction centres are unavailable for fixation. Both the constant 2°C , and the use of a seasonally varying seabed climatological temperature which is based on all available, but nonetheless limited number, *in situ* observations and interpolated onto a coarse 0.5° grid, are key uncertainties worth consideration in future work.

One of the important implications of using this formulation is the effect of temperature on bleaching saturates at 2°C above the climatology.

Reactive oxygen species per symbiont as a measure of stress

Coral symbionts naturally contain low concentrations of reactive oxygen species (reactive oxygen species) such as hydrogen peroxide as a result of metabolic processes (Suggett et al., 2008), but reactive oxygen species becomes toxic at high concentrations. Due to the difficulty in measuring reactive oxygen species concentration (it is often measured as a fluorescent signal rather than a mass per unit volume), there is no precise value for toxicity in the literature. There may also be different levels of toxicity for the different symbiont species (*Durusinium* vs. *Symbiodinium*) as well as for different coral hosts.

In the model, we have a parameter for the lowest toxic level of reactive oxygen species, $\text{ROS}_{\text{threshold}} = 0.0005\text{mg O cell}^{-1}$ (Baird et al., 2018; this number is relative since the reactive oxygen species measurements they are based on are relative and should not be used to infer a precise number). This was a value that was exceeded in the 1km eReefs model at sites that began bleaching in 2017. Interestingly, even under extreme bleaching conditions, the model reactive oxygen species per cell rarely exceeded $0.001\text{mg O cell}^{-1}$. While $0.0005\text{mg O cell}^{-1}$ is arbitrary, it is noteworthy that laboratory experiments show reactive oxygen concentrations only appear toxic when they exceed half their maximum values (Suggett et al., 2008). Thus, our value of $\text{ROS}_{\text{threshold}} = 0.0005\text{mg O cell}^{-1}$ is at least loosely consistent with both field and laboratory studies.

In the eReefs bleaching model we consider zooxanthellae expulsion as a function of how much greater the reactive oxygen concentration is above the threshold (i.e. mortality = $a[\max(0, \text{reactive oxygen species} - \text{ROS}_{\text{threshold}})]^b$, where a is a rate coefficient, b is a power exponent). However, due to the uncertainty of the values of a and b (b is 1 in this study), we consider a more robust measure of the model-predicted threat of bleaching to be the reactive oxygen concentration, rather than the rate of expulsion predicted by the model.

Solar radiation calculations

The experiments involve perturbations in the solar radiation field, so a detailed explanation of the forcing is required. The model is forced by three-hourly total cloud cover obtained from the Bureau of Meteorology (BoM) regional reanalysis product (ACCESS-R). At each hydrodynamic time step (i.e. 18s), the shortwave solar radiation reaching the surface is calculated including the effect of solar elevation (a function of latitude, longitude, time of day, date) and the imposed cloud cover.

The optical model within the biogeochemical model decomposes the above sea surface short wave radiation into 23 wavebands and uses a spectrally resolved vertical attenuation rate to determine the light at each model level (Baird et al., 2016). The vertical attenuation rate is

calculated from 20+ optically active constituents (such as different types of suspended sediments, phytoplankton) that either absorb or scatter light (Figure 1).

The breakdown of photosynthetically available radiation into individual wavelengths is important for both the attenuation through the water column, and the absorption by the pigments contained within the symbiont (Figure 3). Thus, light reaching the bottom at 440nm will, for the same number of photons, result in approximately 10 times the potential build-up of reactive oxygen species than at 550nm, because the absorption coefficient at this wavelength is 10 times greater. In the eReefs-coupled model, which resolves the greater absorption by phytoplankton at the chlorophyll absorption peaks, poor water clarity due to phytoplankton will have a greater protective effect against excess light than sediment for the same energy-weighted vertical attenuation. Because the relevant measure of light for the purposes of reactive oxygen species build-up is the flux of photons, photosynthetically available radiation is calculated as a quantum-weighted measure.

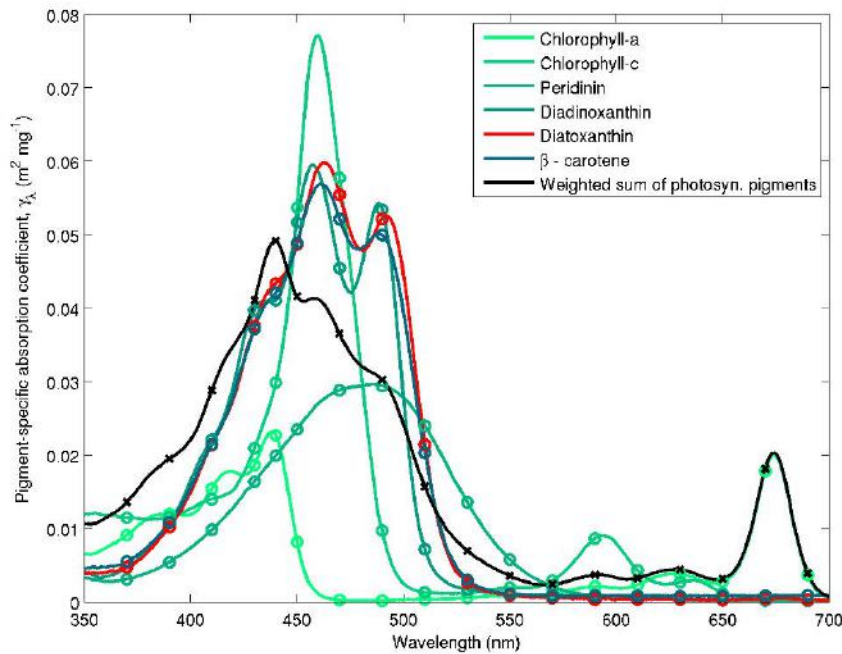


Figure 3: Pigment-specific absorption coefficient of the pigments the 5mm radius symbiont cells used to capture photons in the bleaching model (Baird et al., 2018).

In the surface film experiments, the solar radiation perturbation involves reducing the shortwave solar radiation by 30 percent across all wavelengths [Note: 30 percent was an early estimate, later replaced by 20 percent in T3 – the implication of using 20 percent, or 10 percent, are considered below]. Because vertical attenuation is well represented by an exponential decay, a 30 percent reduction in subsurface solar radiation reduces the radiation at every depth and wavelength by exactly 30 percent. However, the photons absorbed, and the reactive oxygen species build-up will not necessarily be 30 percent different due to cellular photoacclimation, photoadaptation and the physiological-dependent ability of the cells to detoxify.

Relocatable Coastal and Ocean Model (RECOM)

The eReefs Project has developed coupled hydrodynamic, sediment, optical, biogeochemical models at 1km and 4km resolution for the entire length of the Great Barrier Reef (named GBR1 and GBR4 respectively). In order to model higher resolution processes, a web-based automatic model configuration generator, RECOM, was developed (www.ereefs.info). The applications in this study have essentially been downscaling exercises. By this we mean the same model equations and parameters applied at the regional Reef-scale are applied at the finer resolution (typically 200m), with the inflow conditions of currents, dissolved and particulate tracers provided by the regional model.

An example RECOM output from Davies Reef, near Townsville, is shown in Figure 4. For both the RECOM configuration (seen in the centre of the figure with a high resolution grid, every second arrow plotted in black), and the GBR1 model (larger area, but obscured by the RECOM output in the centre, every arrow plotted in grey) that provides boundary conditions for the RECOM model. The figure shows near surface (see title for layer depths in both models) temperature and velocity. The velocity arrows were scaled so their length represents the speed of the current, as well as the distance travelled over a time period (see legend top left). The thin black lines show depth contours from the GBR100v4 Beaman bathymetry. Additionally, inserts show surface elevation, near-surface temperature and incoming solar radiation at the pink symbol with the black dot over a month, 10 days and 10 days respectively, centred on the time of the surface plot (as indicated by a pink circle with black border) from the RECOM model. The temperature insert shows both the RECOM (black line, pink circle) and GBR1 (grey line, pink square) temperature time-series. Finally, above the surface elevation panel is a representation of the moon phase, depicting the phase of the moon at the time of the plot. In this example, GBR1 model in this region is approximately 1km resolution, while the RECOM configuration is about 200m (animation is available at <https://research.csiro.au/ereefs/models/models-about/recom/>).

The exception to the downscaling approach (i.e. external model is identical to the nested model) is that we have included the bleaching coral model described above in the RECOM configuration, but it is not represented in the regional configuration, GBR1_H2p0_B2p0_Cfur_Dhnd, used in the nesting. The next version of the regional models, GBR1_H2p0_B3p0_Cbas_Dhnd, will contain the bleaching processes, as well as many other improvements, but is not available at present (runtime for the regional models are several months). For the purposes of this study, the effect of a bleaching parameterisation 10s of kilometres upstream of the RECOM-resolved reef, rather than the original eReefs non-bleach parameterisation, will be small, so this is assumption will not affect the results.

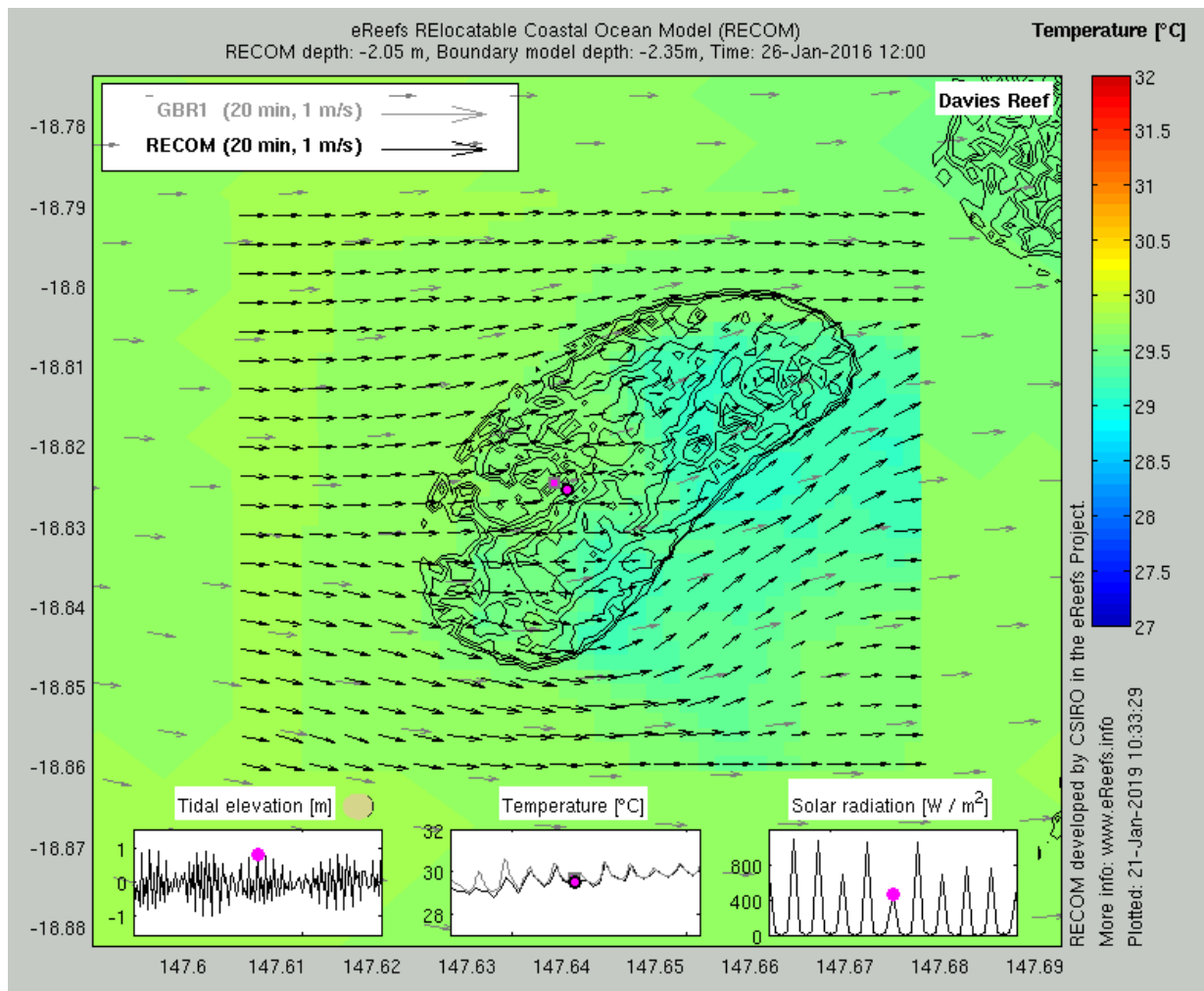


Figure 4: Downscale RECOM configuration for Davies Reef. For details see text.

Configuration of the individual reefs.

RECOM simulations were set up as follows:

Simulation period:	December 1, 2016 through to April 30, 2017 (150 days)
External forcing:	GBR1_H2p0_B2p0_Cfur_Dhnd
Initial condition:	GBR1_H2p0_B2p0_Cfur_Dhnd on December 1, 2016
Integration time-step:	Hydrodynamic (3D – 18s, 2D – 3s), Biogeochemical (30 mins)
Horizontal resolution:	150-300m, varies with reef
Vertical resolution:	Approx. 0.3m at surface, 5m at 60m, varies with reef
Sediment layers:	4
ROBUST flag:	4
Solar radiation exposure:	70 percent and 100 percent of BoM ACCESS-R driven estimates.

RECOM includes a 'ROBUST' setting that ranges from 1 to 10, whereby a lower setting corresponds to a more realistic but potentially less stable hydrodynamic configuration, and a higher setting corresponds to a more stable but potentially less accurate solution. For all the above reef applications, we used a ROBUST flag = 4. Perhaps the most significant compromise with this option is the outer eight grid cells (or four arrows shown in Fig. 4) have additionally horizontal viscosity. Nonetheless, Figure 4 shows that even a 40x40 grid resolves features such as island wakes around a reef that are not resolved in the 1km model.

For more description of the regional and RECOM configurations see Section 2.5 of Baird et al., (2018).

The reefs that were configured in RECOM were: Arlington, Otter, Bay Island, Pandora, Bowden, Peart, Britomart, Havannah Island, Pith, Bunker, High Island, Cat, Jessie-Kent, Rib, Centipede, John Brewer, Russell Island, Coates, Knuckle, Cockburn, Lady Musgrave, South Warden, Corbett, Lagoon, Stanley, Crispin, Taylor, Davies, Lizard Island, Eden, Low Wood Island, Farquharson, Tongue, Mason, UNReef18d023, Fitzroy Island, Warthon, Wilson, and Opal.

Experimental design

The individual reefs were configured using the RECOM interface. The interface user (Mark Baird, Mathieu Mongin or Élodie Bougeot) aimed to isolate an individual reef, to have a horizontal resolution around 200m, and to avoid strong bathymetry gradients near the boundaries. The individual reefs were chosen to (1) coincide with long-term Australian Institute of Marine Science observations sites; (2) sites of particular interest to users (i.e. Opal Reef for a conservation project); (3) to provide a variety of hydrodynamic environments (reef size, tidal range, lagoon structure). While this is a non-random selection procedure, the application to tens of reefs demonstrated a wide variety of reef environments.

For each reef, the hydrodynamic model was run as a downscaled version of GBR1_H2p0 (Herzfeld, 2015). From this downscaled version, the time-integrated volume transport across each grid face was stored every 30 minutes. The hydrodynamic output (temperature, salinity, velocities etc.) is independent of the surface film.

The biogeochemical model (including coral bleaching processes and the age tracer) is then run twice from the same initial conditions on 1 December 2016 using the same time-integrated volume transport. The first time it is run it is exposed to the full solar radiation (no reduction case), the second to 30 percent less solar radiation (30 percent reduction case). Under this experimental design, the temperature of the water for the two runs is identical, but the seabed light and photons absorbed is different.

5. SUMMARY OF FINDINGS

In order to understand the impact of solar radiation, first we look in detail at one reef, Otter Reef, a midshelf reef east of Hinchinbrook Island. We analyse the coral dynamics from 1 December 2016 – 30 April 2017, under the no reduction, and 30 percent reduction, of solar radiation. Following this, we consider 20 reefs, concentrating on the spatially resolved reduction in reactive oxygen species concentration. Finally, we look at the spatially resolved residence time of the individual reefs to assess the feasibility of applying films.

Analysis of Otter Reef

A snapshot of the surface state variables at Otter Reef on 9 April 2017 provides a context for analysis of the modelled zooxanthellae state. Figure 5 shows the water column variables affecting the coral host and symbiont: temperature, dissolved inorganic nitrogen concentration (DIN), dissolved inorganic phosphorus concentration (DIP), particulate organic matter concentration (POM), as well as the spatially resolved residence time (age). Other physical variables affecting the corals are climatological seabed temperature (T_{clim} , see Baird et al., 2018) for details of the data used for the climatology), which in combination with seabed temperature,

determines the activity of the RuBisCO enzyme (a_{ox}^* , which takes a value between 0 inactive and 1 fully active) and the seabed quantum-weighted photosynthetically available radiation (photosynthetically available radiation). The corals are quantified by the biomass of the host, here converted to a percent cover as seen from above using $cover = 100 (1 - \exp(-\Omega B))$, where B is the biomass, and Ω is the nitrogen-specific polyp area coefficient. The zooxanthellae are quantified by the nitrogen biomass of the cellular structural material (CS), and the physiological state by the normalised reserves (a value between zero and 1), of carbon, R_C^* , nitrogen, R_N^* and phosphorus, R_P^* .

At Otter Reef for most of the summer of 2017, the concentrations of DIN are low relative to phosphorus. As a result, at the surface, symbionts are strongly N limited, as demonstrated by $R_N^* \ll R_P^*, R_C^*$. Only the deepest corals show light limitation $R_C^* < 0.5$ at midnight. Photoacclimation is quantified by the C:Chl ratio, photoadaptation by the fraction of heat dissipating (X_h) to photoabsorbing (X_p) xanthophyll pigment, while the photosystem state is resolved to oxidised, Q_{ox}^* , reduced, Q_{red}^* , and inhibited, Q_{in}^* . Finally, the amount of reactive oxygen species, reactive oxygen species, as well as rates of mucus production, inorganic and organic nitrogen uptake, and bleaching are given to understand the model behaviour (Figure 5).

The shallowest reefs have the xanthophyll cycle switched to heat dissipating pigments ($X_h > X_p$), but otherwise the pigments are photoabsorbing. Reactive oxygen build-up is only occurring in the shallowest reef sites. At sites with a seabed depth greater than 20m, the reaction centres are almost entirely oxidised, and for those less than 5m they are inhibited. At intermediate depths reaction centres are spread across the oxidised, reduced and inhibited states.

The same variables are reproduced for the 30 percent reduction (Figure 6). The first point to make is that, by design, the hydrodynamic variables (surface temperature, age, climatological temperature) are identical. Second, the water column variables (DIN, DIP, POM), whose dynamics are dominated by flow into the model domain from the same boundary conditions are also very similar. As a result of this similarity, the vertical attenuation above the reef is almost identical. For an identical vertical attenuation, the seabed photosynthetically available radiation is exactly 30 percent less than the 100 percent case.

A useful calculation is to determine the shallowing of the depth in the 30 percent reduction case relative to the no reduction case. Assuming an exponential decay of light with depth, the shallowing of the photosynthetically available radiation isocline is given by $\log_e(100/70)/K_{d, \text{photosynthetically available radiation}}^1$, where $K_{d, \text{photosynthetically available radiation}}$ is the vertical attenuation of photosynthetically available radiation light. At this time, spatial-mean vertical attenuation coefficient of photosynthetically available radiation is $\sim 0.1 \text{ m}^{-1}$, so the isocline has shallowed by 3.57m. So, under similar seabed physical conditions, the corals in the 30 percent reduction case will behave similarly to corals 3.57m shallower than in the no reduction case.

The internal reserves in the symbiont of nitrogen and phosphorus remain very similar between the no reduction and 30 percent reduction cases – nitrogen was most limiting at all depths (Baird

¹ Assume $E_{bed,100} = E_{surf,100} e^{-kz_{100}}$, where k is vertical attenuation rate, z is depth, E_{bed} is light at the seabed, and E_{surf} is light at the surface. Similarly, if light is reduced to X percent, $E_{bed,X} = E_{surf,X} e^{-kz_X}$. Now find the depth, z_X , at which $E_{bed,100} = E_{bed,X}$. That is $E_{bed,100} e^{-kz_{100}} = E_{bed,X} e^{-kz_X}$ Rearranging, $\log_e \frac{E_{surf,100}}{E_{surf,X}} = -k z_X + k z_{100}$. Finally, $z_X = z_{100} + \frac{\log_e \left(\frac{100}{X} \right)}{k}$. For X = 70 percent, $k = 0.1 \text{ m}^{-1}$, $z_X = z_{100} + 3.57 \text{ m}$. For X = 10 percent, $z_X = z_{100} + 1.05 \text{ m}$

et al., in prep). The extreme nitrogen limitation of a midshelf reef in April 2017 is characteristic of the relative low runoff years that preceded this time. While such low runoff may be extreme, bleaching years have tended to be low flow years. In contrast, reserves of fixed carbon are greater in the no reduction case. Other differences include some switching of xanthophyll pigments in the no reduction case that is not evident in the 30 percent reduction case, as well as more oxidised and less inhibited reaction centres. For each of these physiological traits, the changes can be thought of a change at one location, or alternative a changing spatial distribution representing an approximately 3.57m shallowing of equivalent environments.

The above analysis is based on midday snapshot across the whole reef. It is now instructive to investigate time-series for both the no-reduction and 30 percent reduction cases at two depths (Figure 7, Figure 8). In these figures, panels A show the light at sea surface (thin black line) and at the coral surface (photosynthetically available radiation, $\text{mol photon m}^{-2} \text{d}^{-1}$, scaled on the y-axis to the monthly running mean photosynthetically available radiation over the period given in the title, thick black line), and the normalised reserves of nitrogen, phosphorus and carbon. The normalised growth rate is also shown. Panels B show the state of the xanthophyll cycle as the fraction of heat absorbing (X_h) and heat dissipating (X_p) pigments, the RuBisCO activity (a_{ox}^* varying between inactive at 0 and fully active at 1), the carbon to chlorophyll ratio (scaled on the y-axis so the minimum C:Chl ratio of 20 g/g is 0, and 1 is 180 g/g), and the fractional reduction in photosynthetically available radiation from the surface. Panels C show the state of the reaction centres, and the concentration of reactive oxygen per cell in the symbiont above a threshold value that initiates zooxanthellae expulsion (mg O cell^{-1}), as well as the total reactive oxygen per coral host.

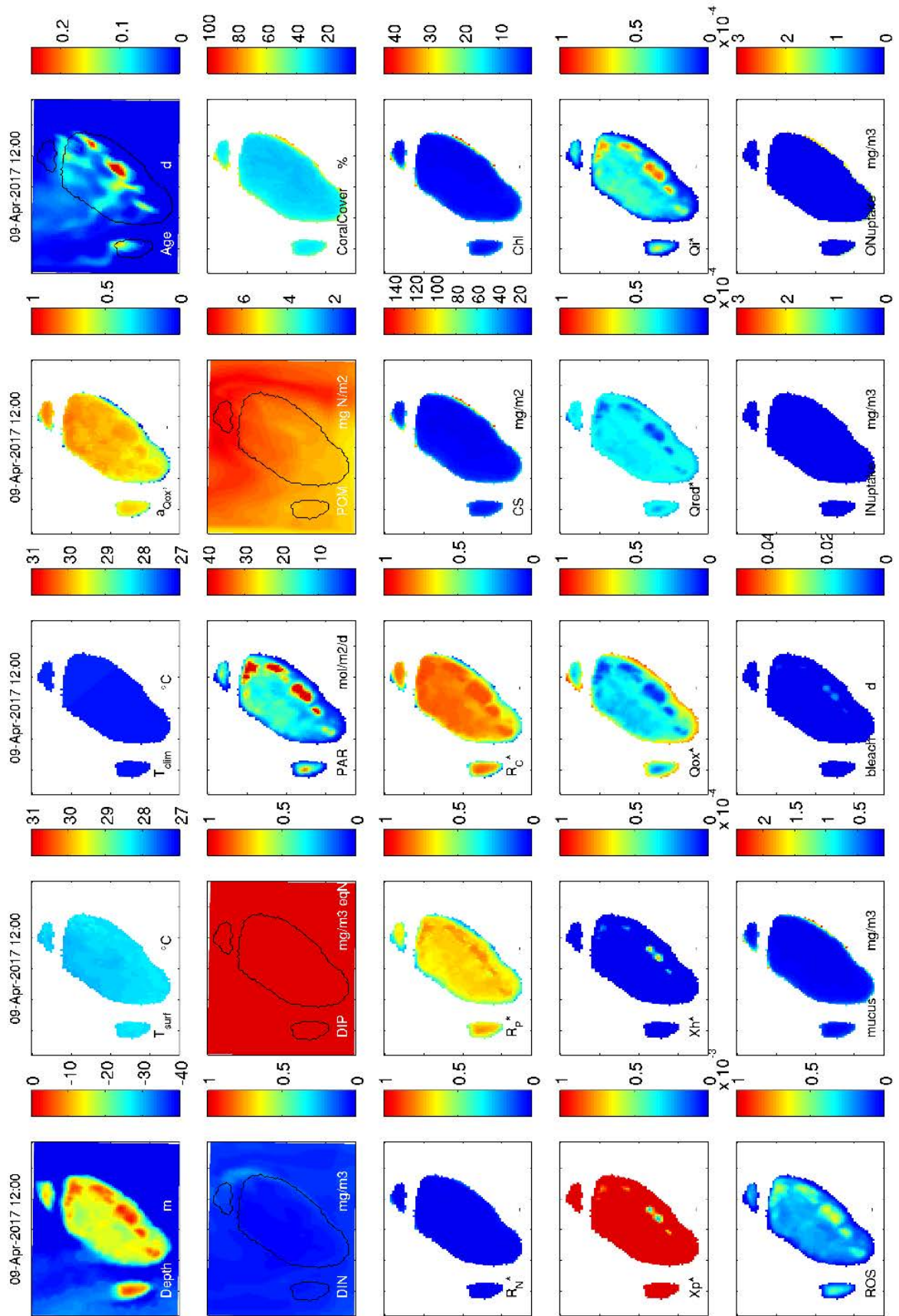


Figure 5: Coral-related state variables at midday on 9 April 2017 in the ~200m nested model at Otter Reef exposed to 100 percent solar radiation.

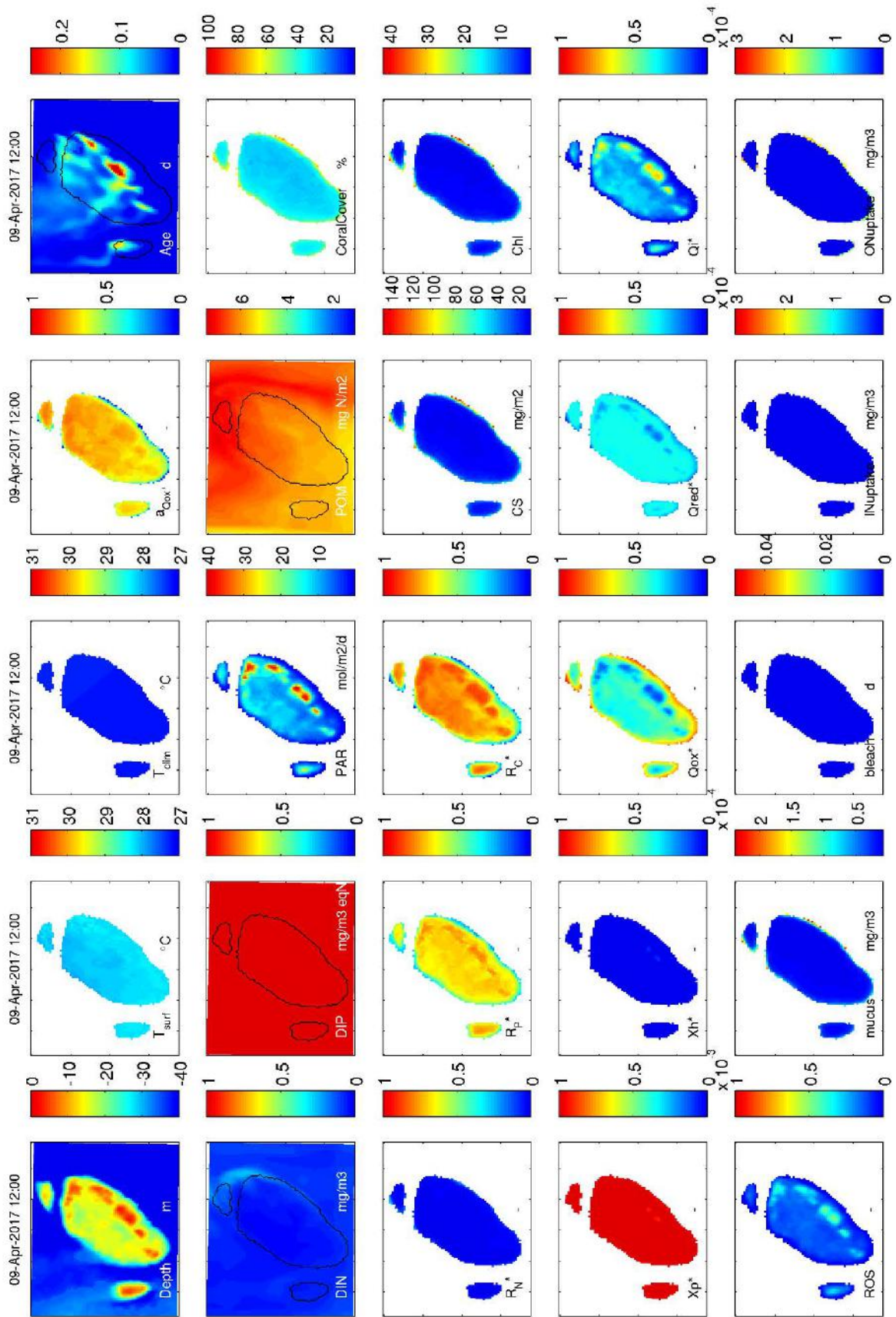


Figure 6: Otter Reef exposed to 70 percent radiation. For more details see earlier figure.

The impacts of reduced solar radiation on the symbiont pigments at 3m deep (Figure 7) are:

1. A slight decrease in the C:Chl ratio, as the reduced photosynthetically available radiation generates more light-limited symbionts that synthesise more pigment.
2. Several days where the xanthophyll cycle was in the photoabsorbing state.

Impacts 1 and 2, which are acclimations to the different light regime, act to reduce the difference in the scenarios. Nonetheless, the number of photons reaching the reaction centres in the no-reduction case is still greater, so the impacts in the reaction centres are:

1. The peak inactive reaction centre fraction $(Q_i+Q_{red})/(Q_{ox} + Q_i+Q_{red})$ is significantly higher in the no-reduction case by about 0.1.
2. The reactive oxygen per symbiont is about 40 percent higher in the no-reduction case and exceeds the toxic level (0.5) for the entire month, while it exceeds it for only for a few days, and not by much, in the 30 percent reduction.

The 18m deep site (Figure 8) has significantly greater pigment per symbiont and the xanthophyll cycle was in the photoabsorbing state almost permanently. With these adjustments, the reaction centres received more light than they would otherwise have received, but still remained primarily active in both cases. Interestingly, even at 18m depth, with the solar radiation reduced 30 percent, the symbiont cells were more limited by nitrogen than light ($R_N^* < R_I^*$) or phosphorus. As noted above, 2017 was generally low nutrient load year (Baird et al., in prep).

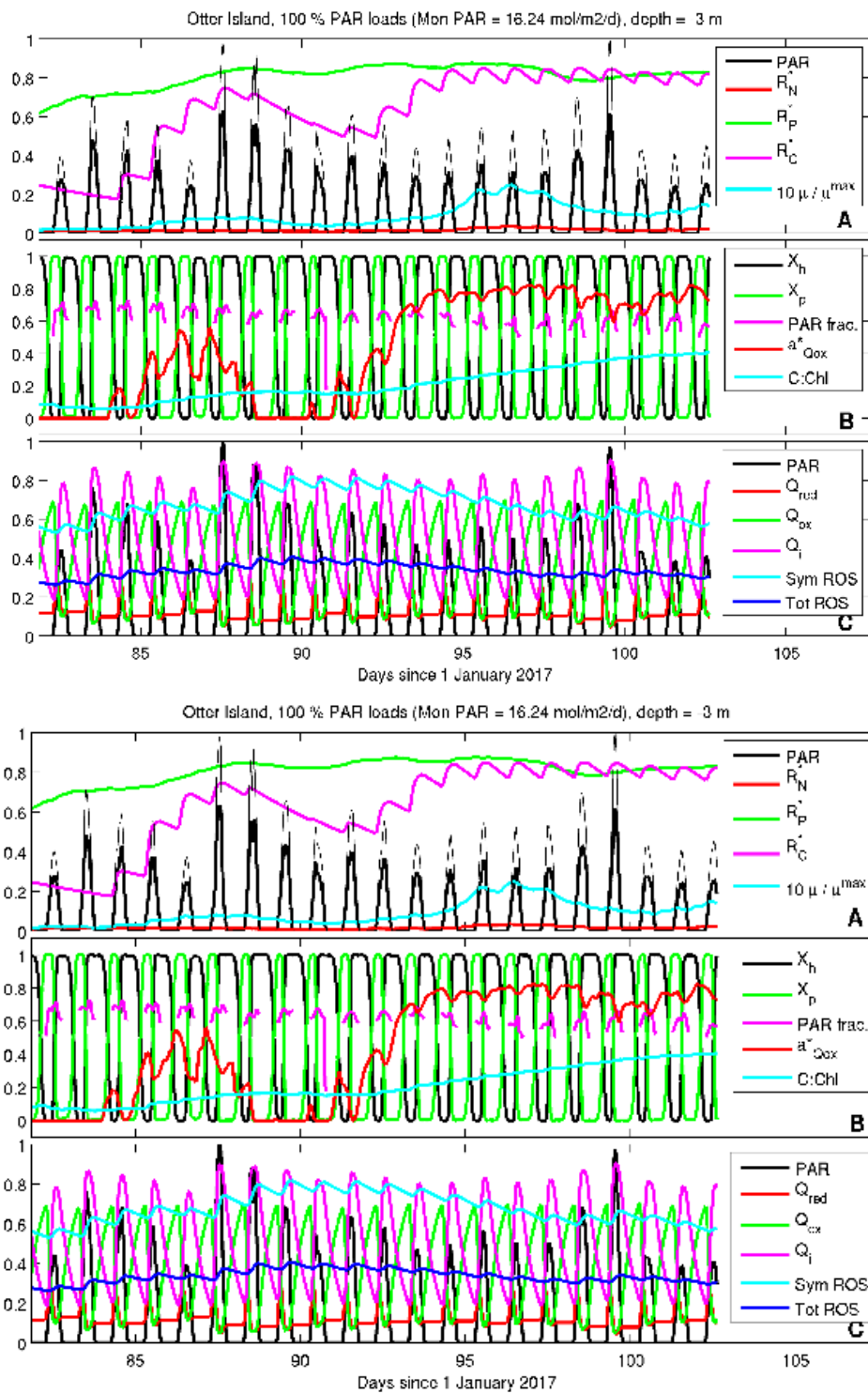


Figure 7: Model behaviour on Otter Reef at a 3m site with 100 percent solar radiation (top three rows) and with 70 percent solar radiation (bottom three rows) site.

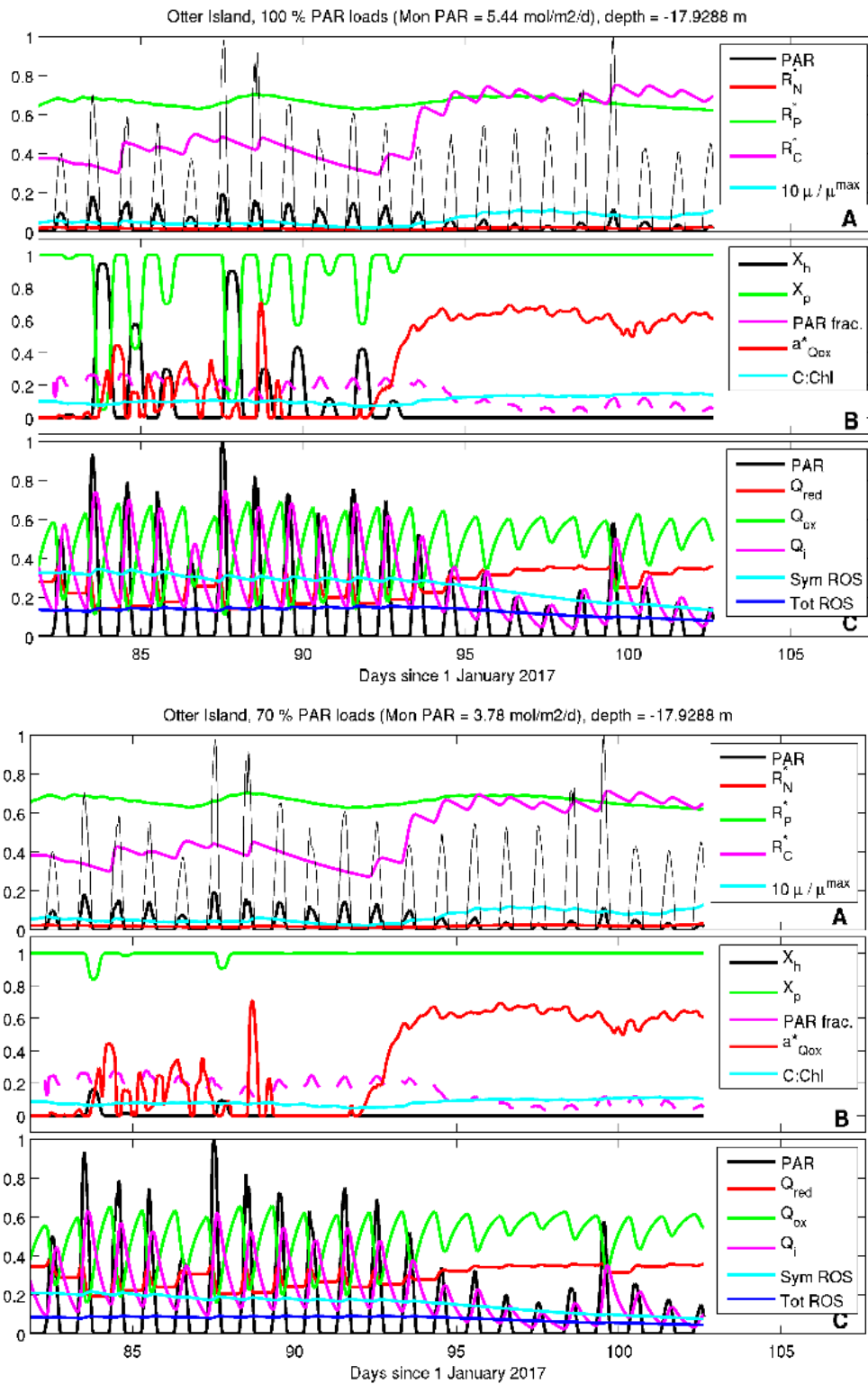


Figure 8: Model behaviour on Otter Reef at a 17m site with 100 percent solar radiation (top three rows) and with 70 percent solar radiation (bottom three rows) site.

Temporal-mean reduction in reactive oxygen species concentration across reefs

The above analysis gives an insight into the causal relationship of temperature-mediated, light-driven build-up of reactive oxygen, and how it is likely to be impacted by environmental forcing, particularly a reduction in solar radiation. This section expands our scope to the realistic conditions existing on 19 reefs across the Reef. By necessity we will no longer attempt to follow the casual chain of reasoning as to the difference across and between reefs, but rather analyse the output of the high-resolution models as a means of assessing the effectiveness of reduced solar radiation. Thus, we will not attempt to explain the effect of variability between reefs and within reefs in the thermal stress, nutrient concentrations, water clarity and cloud cover, latitudinal location, all of which potentially change bleaching stress in the model.

A 30 percent reduction in solar radiation significantly reduces the reactive oxygen stress at a single location, and, perhaps more significantly, reduces the area on each reef that builds up toxic levels of reactive oxygen. Figure 9 shows the impact of a constant 30 percent reduction in surface photosynthetically available radiation on the change in reactive oxygen species concentrations in the symbionts. White areas do not contain corals. Grey areas contain corals that had reactive oxygen below stress level even with no light reduction. Dark red areas experienced some bleaching stress, but the 30 percent reduction in solar radiation removed 100 percent of the stress. And the red through to blue gives the fraction of the stress removed. (Animation: https://research.csiro.au/ereefs/wp-content/uploads/sites/34/2018/11/RO_all_ken.gif).

The animation shows a 30 percent reduction is sufficient to reduce reactive oxygen stress to zero in most of the areas where there was bleaching stress. Only in the shallow areas, especially of Cockburn Reef, does a 30 percent reduction not completely stop bleaching.

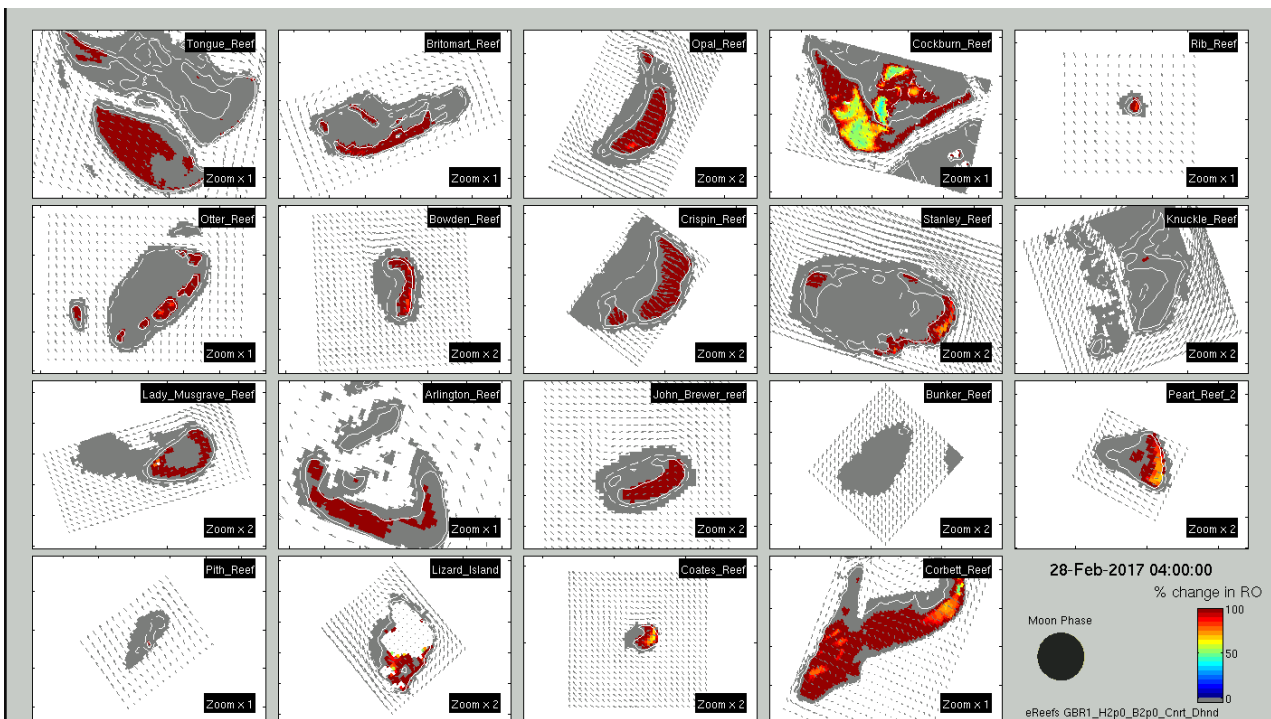


Figure 9: Change in percentage of reactive oxygen concentration per symbiont cell above the bleach stress level with a 30 percent reduction in light.

An interesting point from Figure 9 is that a 30 percent reduction in solar radiation reduced reactive oxygen stress by at least 50 percent, and up to 100 percent. The reason for this non-linear response is two-fold. First, symbiont cells naturally have a fraction reactive oxygen species that is not toxic. So even if the decrease in reactive oxygen species is proportional to solar radiation, the amount above the toxic level is not. And second, the cells have an ability to productively use a certain quantity of photons for carbon fixation. So, it is only above this flux of photons that the cells begin building up reactive oxygen species. These two reasons explain why in the model the cells appear to suddenly build up a toxic level of reactive oxygen when a light threshold is exceeded, and why this can be modified through either a reduction in light or a reduction in thermal stress.

The non-linear response is important in part because surface films are unlikely to achieve a 30 percent reduction uniformly across a specific reef. Figure 10 shows the effect of smaller reductions than 30 percent. Assuming the toxic level is $0.0005 \text{ mg O cell}^{-1}$, it is clear the solar radiation reduction is incrementally less effectively in reducing reactive oxygen stress, and that even a 10 percent reduction has significant benefits.

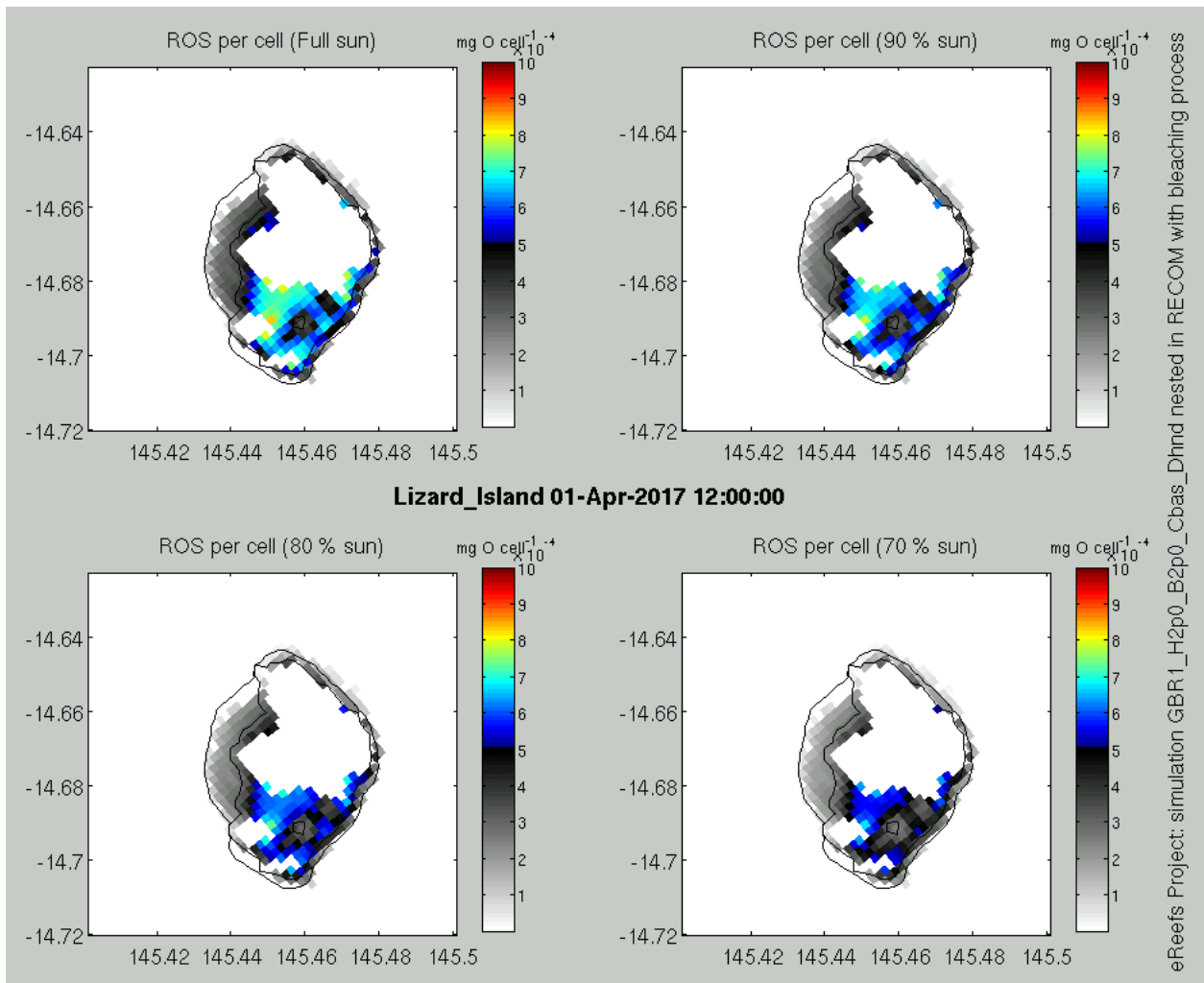


Figure 10: Reactive oxygen concentration per cell at Lizard Island at midday on 1 April 2017 with no, 10 percent, 20 percent and 30 percent reductions in solar radiation.

Spatially resolved residence time

Several of the interventions considered for improving coral health under climate change, such as cool water injections and surface films, involve a modification of the water column above the reefs that can then be advected off the reef through tidal, wind and offshore current driven circulation. To quantify the time water resides on a reef, we used ‘tracer age’, or simply ‘age’. This metric has an advantage over other residence time metrics in that it provides a spatially resolved time-scale, rather than a single number for each region (Monsen et al., 2002, Mongin et al., 2016).

Generally, ‘age’ quantifies the spatially resolved residence time of water in different regions. Age tracer (τ) is advected and diffused by the hydrodynamic model, using the same numerical schemes as other tracers such as salinity. When inside the region of interest, the age increases at the rate of 1 d d^{-1} . When the age tracer is outside the region of interest, it does not increase in age, but rather decays at 0.1 d^{-1} . The region of interest is taken to be anywhere in the model domain that the seabed is shallower than 10m relative to mean sea level.

Using this definition of age, we are calculating the relative ability per unit area to modify the water above a whole reef. Consideration of the relative ability to modify portions of a reef are considered in [T12—Cool Water Injection](#).

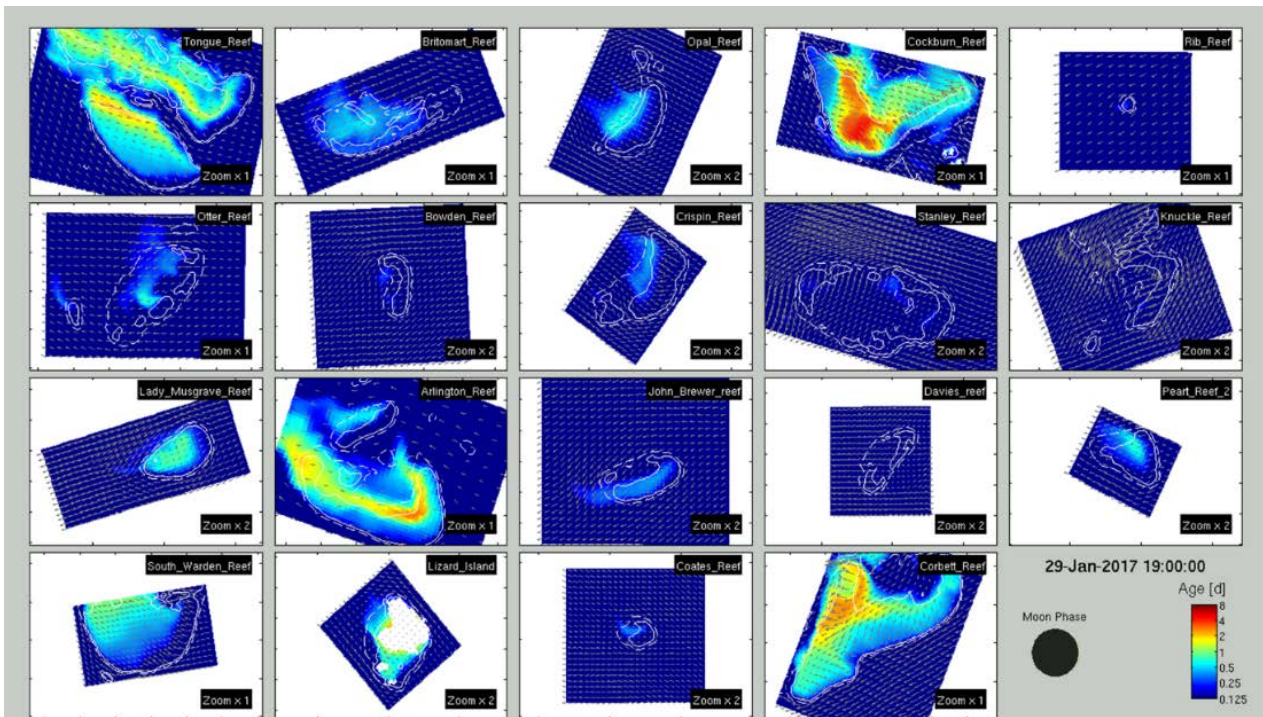


Figure 11: Spatially resolved residence time (age) of the individual reefs. Animation: https://research.csiro.au/ereefs/wp-content/uploads/sites/34/2018/11/RO_all_ken.gif

A surface snapshot of age is given in Figure 11, and a time series of the reef-wide age shown in Figure 12. In general, the reefs tend to have greater mean age when:

1. in regions of smaller tides (central Great Barrier Reef)
2. during and immediately after neap tides (after the first or third quarters of the moon)
3. the reef is large, particularly if the width of the reef is greater than a daily tidal oscillation
4. the reef is aligned in the direction of the dominant tidal oscillations
5. winds are slack

6. local ocean currents are inhibited by other geographical features.

Thus, the longest mean age is found on two large reefs just north of Princes Charlotte Sound (Corbett and Cockburn Reefs), where flow is slowed by the presence of many reefs, tides are moderate, reefs are aligned across the main axis of the tidal ellipse. In contrast, small reefs like Bowden Reef have mean residence times of less than an hour. Lizard Island reef is particularly interesting because, for a small reef, it has a relatively long residence time.

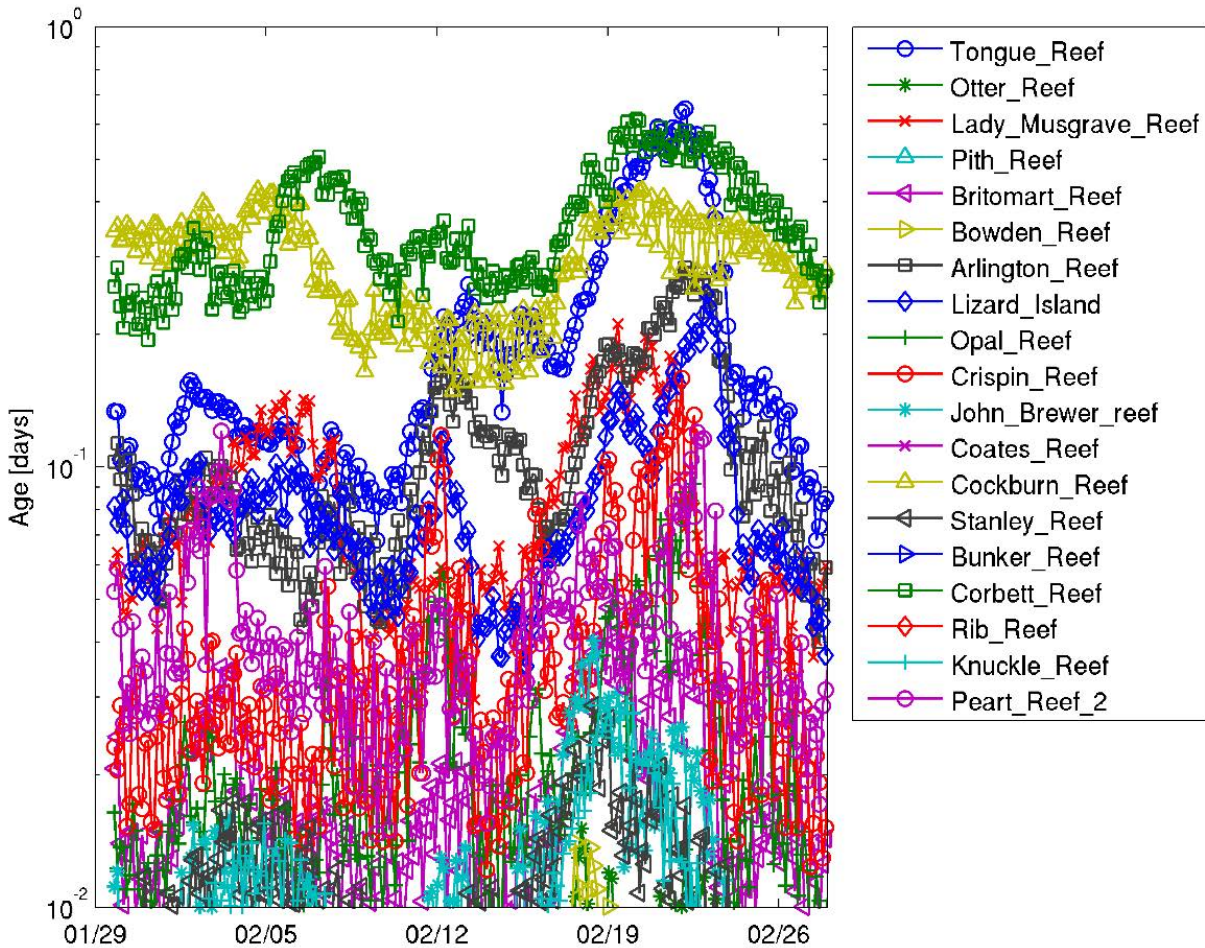


Figure 12: Time series of the mean age of water above reefs. Aging occurs when water is in less than 10m from the mean sea level.

6. DISCUSSION

Strengths and limitations to the predictive skill of the bleaching model

The greatest strength of the eReefs bleaching model is it represents the major components of the symbiont's photophysiology (nutrients, pigments and reaction centre states) so it can capture the dynamical interactions between these components. Additionally, the equations that represent the physiological processes that link incoming solar radiation to reactive oxygen generation (chlorophyll synthesis, xanthophyll cycling, reaction centre transitions) are mechanistically formulated, and stoichiometric constrained.

Perhaps the greatest limitation to any model of bleaching on reefs of the Great Barrier Reef is the spatial resolution of the model itself, the bathymetry data that is used to defined model grid cell depths (GBR100v4, Rob Beamon), and the distribution of corals on this horizontal model grid. Water depth is important because it determines the amount of solar radiation reaching the bottom – and in some cases if the corals are exposed at low tide. The spatial distribution of habitats is important because coral cover is generally highest on the fore reef and reef slope, but poor spatial resolution of either benthic habitats in the model configuration will place corals in locations they may not be, and then ascribe a benefit for bleach protection to that location.

We openly recognise we do not have the knowledge to follow all processes mechanistically. Thus, the inactivation of the RuBisCO-mediated carbon fixation, the repair rate of inhibited reaction centres, and the detoxification rate of reactive oxygen species are temperature-dependent empirical formulations, for which the underlying biochemical reactions are not resolved. Additionally, the reactive oxygen concentration that initiates bleaching, $ROS_{\text{threshold}}$, and the mathematical form of the expulsion above this threshold are based on simple reasoning.

One potential bleaching pressure not considered is the effect of the absorption of photons in the ultra-violet range beyond that of the absorption of photons at other photosynthetically available wavelengths. The fact that studies have struggled to distinguish the effects of changing temperature and photosynthetically available radiation from that of ultra-violet alone (Banaszak and Lesser, 2009) suggests direct UV damage is less important than temperature-mediated light-driven reactive oxygen build-up.

A further limitation in the bleaching model is it considers one symbiont species hosted by one coral species. Thus, the model is unable, within one simulation, to consider the competition between two corals, although it could in theory be used to see if one coral bleaches less than another. Up until this point only one parameter set for a coral has been used, based on laboratory rates.

Limitations to assessing reefs on the Great Barrier Reef

Perhaps the greatest limitation of the modelling undertaken here is the inherent assumption that all seabed regions with a depth of less than 10m from the mean sea level contain corals of equal value. The clearest reason why this is a poor approximation is that on the Great Barrier Reef, reef slopes exposed to off-reef waters have greater coral cover than back reefs and lagoons. This occurs because as water moves across the reef, nutrients and organic matter are taken from the water, leaving the waters above back reefs extremely poor in nutrients (Baird et al., 2004). Thus, large backreef areas such as on Cockburn Reef, which the analysis here considers feasible from

the standpoint of high residence time and change in reactive oxygen species under reduced solar radiation, are unlikely to have high coral cover.

Over time, the model compensates for the poor initial equal distribution of corals (obtained from the coarse 1km configuration), as can be seen by the development of higher coral cover on the rims of Otter Reef (Figure 31). The problem of erroneously high backreef coral cover can be overcome by either running the high-resolution models for longer or initialising them with realistic initial coral distributions (Roelfsema et al., 2018), or both.

Comparison with shading experiments

Coelho et al., (2017) undertook shading experiments on three species under high light and thermally stressful temperature. They found light reductions up to 75 percent decreased the bleach rate, although this varied between the three species. Comparison with these experiments will require a better quantification between reactive oxygen species build-up and bleaching.

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APPENDIX A – RRAP DOCUMENT MAP



Reef Restoration and Adaptation Program, a partnership

Reef Restoration and Adaptation Program

GBRrestoration.org

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Reef Restoration and Adaptation Program, a partnership:



Great Barrier
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