Integrating physiology with remote sensing to advance the prediction of coral bleaching events.

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Highlights

- Widely-used satellite-based bleaching prediction tools use thermal dose and duration.
- Bleaching thresholds also depend on other factors such as local acclimation.
- Abiotic parameters that cause bleaching are measurable by satellite methods.
- A photophysiological bleaching prediction tool includes irradiance as a predictor.
- Light-at-benthos remote sensing products may advance coral bleaching prediction.

Abstract

Due to global climate change, very large areas of reef are susceptible to warming-induced coral bleaching, leaving coral reef stakeholders reliant upon remote sensing forecasts of coral bleaching for estimates of when and where bleaching will occur. Coral bleaching prediction methods, to date based on satellite sensed sea surface temperature, are being developed further to improve the accuracy of predictions. This review examines the coral physiological and bleaching forecasting literature to identify biological and geophysical parameters that explain variance in coral bleaching and knowledge gaps related to the application of this knowledge to bleaching prediction. Identified areas for the advancement of prediction methods include improvements in sea surface temperature product resolution and past datasets, incorporating the influence of UV irradiance on coral bleaching, and locally-varying thermal bleaching thresholds. More empirical data is necessary for some aspects of bleaching prediction development, though the potential exists for gains in predictive skill to be achieved through the implementation of current physiological and remote sensing knowledge.

1 Introduction

Coral reefs are ecosystems of high cultural, environmental and economic value, yet are one of the planet's most threatened ecosystems. The vast geographic extent of coral reefs, and the global nature of warming events that cause coral bleaching, has spurred the development of satellite remote sensing products for the prediction of coral bleaching. The main products, the NOAA National Environmental Satellite, Data, and Information Service (NESDIS) Coral Reef Watch product suite and the Australian Bureau of Meteorology (BOM) product suite, provide predictions based on sea surface temperature (Garde et al., 2014; Liu et al., 2006), and (more recently) solar irradiance (Skirving et al., 2018). These products have been highly utilised by reef managers and scientists since the 2000s. However, due to reasons such as the need for more sophisticated management to counter the upwards trend in coral bleaching severity, advancement in accuracy and precision of coral bleaching prediction is needed.

Effective stewardship of coral reefs is necessary to support the UN Sustainable Development Goal (SDG) 14, Life Below Water (UN, 2015). This SDG has targets to reduce marine pollution (14.1), manage, protect and restore marine and coastal ecosystems (14.2), address ocean acidification (14.3), sustainably manage fisheries (14.4), increase marine protected areas (14.5), regulate fisheries subsidies (14.6) and increase economic benefits of the ocean for small island or least developed States (14.7). Most other SDGs will require, as a prerequisite, the attainment of one or more SDG 14 targets. These SDGs include ending poverty (1), zero hunger (2), good health and wellbeing (3), decent work and economic growth (8), reduced inequalities (10), sustainable cities and communities (11), responsible consumption and production (12), climate action (13) and others (Singh et al., 2018). Coral reefs are substantial contributors to the values identified in the SDG 14 and related goals. Coral reefs support a level of biodiversity (SDG 14.2) that exceeds that of tropical rainforests (Reaka-Kudla, 1997; Small et al., 1998). Reefs protect coasts from erosion (SDG 13, 14.2 and 14.7), provide nursery habitat for fish recruits (SDG 14.4) and filter some pollutants from marine waters (SDG 14.1) (Moberg and Folke, 1999). They support commercial and artisanal fishing (SDG 1, 2, 8 and 14.4), tourism (SDG 8 and 11), drug discovery (SDG 3), the aquarium trade (SDG 14.4) and other biodiversity-based human industries (Cesar, 2000; Leal et al., 2014; Moberg and Folke, 1999).

The values and services provided by coral reefs are threatened by coral bleaching, an effect of the changing climate. Coral are animals that exist as colonies of polyps (phylum Cnidaria) and that excrete calcium carbonate skeletons, building mounds or branching structures that form the complex ultrastructure of coral reefs. They live in symbiosis with single-celled dinoflagellate algae of the family Symbiodiniaceae (the symbiont) that photosynthesise and are enclosed within the coral animal cells, and a bacterial community (the microbiome) (Knowlton and Rohwer, 2003). The phenomenon of coral bleaching is the loss of dinoflagellate cells from coral tissue (Goreau, 1964; Yonge and Nicholls, 1931), the loss of photosynthetic pigmentation from the dinoflagellate cells, or both (Kleppel et al., 1989). Loss of dinoflagellates and/or loss of pigments does occur as a necessary part of physiological adjustments made in response to natural cycles, such as seasonal changes in temperature or light (Fagoonee et al., 1999; Fitt et al., 2000; Secord and Muller-Parker, 2005). However the severity of the response is more extreme during prolonged periods of abnormally high sea temperatures and light levels, and these circumstances are becoming more frequent due to climate change (Hoegh-Guldberg et al., 2014).

Coral bleaching has a broad array of impacts on coral reef ecosystems and the human communities that depend on them. If the bleaching episode is prolonged, then mass coral mortality will result (Baird and Marshall, 2002), though if the event is short then surviving corals can recover (Szmant and Gassman, 1990). Other reef animals that eat or shelter on corals may die or decline after a mass coral mortality event (Iglesias Prieto et al., 2003; Pratchett et al., 2009). Fish communities may restructure as the ecosystem shifts from live coral-dominated to algae-covered coral skeletons (Graham et al., 2008). In the aftermath of a bleaching event, human communities that rely on reefs for cultural, economic or nutritional reasons are likely to be impacted. For instance, the diet of exploited fish populations are affected by the shift from coral to algae dominance due to bleaching, which in some cases affects the safety of fish protein for human consumption (Dunstan et al., 2018). In the long term, coral bleaching that happens more frequently than the recovery time of reefs (at least 5-10 years) will cause sustained reef degradation (Baker et al., 2008), eroding the wide range of values that coral reefs provide to human societies.

In this article, we review remote sensing products for the prediction of coral bleaching, examining their application to coral reef management and the SDGs, input data types, algorithm design, accuracy, and their basis in coral physiology. We explore some limitations of remote sensing input data types and mismatches between physiology and prediction methods. To assist in furthering the field of coral reef management and its contributions to the SDGs, we identify pathways for the future improvement of remotely sensed bleaching prediction methods.

2 Support of coral reef management through coral bleaching prediction

Effective management of coral reef ecosystems is a key method for supporting the ability of coral reefs to contribute to the ocean-related SDGs (UN Environment, ISU, ICRI and Trucost, 2018). Environmental managers cannot regularly visit all reef areas because most coral reefs systems are vast in size and remote, so effective remotely sensed bleaching prediction is a vital reef management tool. It has an impact on both long term planning to support reef conservation, and short term planning and responses to coral bleaching events (Maynard et al., 2009).

Several management options exist to reduce the immediate impacts of coral bleaching. As local actions cannot reduce the warming associated with climate change, management actions instead focus on local factors that affect coral bleaching severity, and on supporting coral recovery and long-term survival following bleaching events (Marshall and Schuttenberg, 2006; Maynard et al., 2009). Management responses that occur shortly before, during, or in the months after a bleaching event rely directly on knowledge of the extent and duration of that bleaching episode (McClanahan et al., 2007a). Restricting activities that physically injure corals during the bleaching episode helps to mitigate the lowered capacity that bleached corals have to repair their tissues (Marshall and Schuttenberg, 2006; Meesters and Bak, 1993). These activities include boat anchoring, anthropogenic sources of siltation such as dredging, the use of fishing gear types that pose a high risk of contact with the benthos, and some tourism activities (Cinner et al., 2009; Marshall and Schuttenberg, 2006). Temporary restrictions on catch of fish that assist in reef recovery, such as herbivores, can be implemented through gear restrictions and shifts in fishing grounds (Dunstan et al., 2018). Remotely sensed prediction of coral bleaching can provide estimates of the timeframe, location and magnitude of bleaching onset, mortality or recovery required to plan these immediate responses to a bleaching event.

Remote sensing-based predictions also assist in planning and funding surveys (via aircraft, diving, satellite photogrammetry, citizen science or otherwise) of coral bleaching that assist in documenting the scale of the event and improving the science and management knowledge base (Maynard et al., 2009). The difficulties of undertaking reconnaissance at regional scales (Baker et al., 2008) means that accurate predictions greatly improve the efficiency of survey effort. Predictions of the timing and spatial extent of mortality enable managers to plan the timing of reef surveys that conclusively link any mortality to the thermal anomaly. Surveys conducted too early may not observe mortality, whilst surveys conducted too long after mortality occurs carry the uncertainty that the observed mortality may have another cause (Marshall and Schuttenberg, 2006). Assessment of recovery from bleaching is important for determining the length of time that a reef is more sensitive to local anthropogenic stresses following a bleaching event, such as mechanical injury.

The benefits of satellite remote sensing-based coral bleaching predictions to the management of coral reefs have, to date, been realised in a number of reef regions (Table 1). Coral bleaching predictions may also aid managers in assessing the socioeconomic impacts of bleaching, and for the mitigation of socioeconomic impacts caused by management interventions. For instance, temporary restrictions on fishing may necessitate compensation of fishers or tourism operators (Marshall and Schuttenberg, 2006).

Remotely sensed prediction of coral bleaching can also contribute to marine protected area (MPA) design for reducing the effects of a changing climate on coral reefs. Marine protection (targeted for 10% of all marine and coastal areas under SDG 14.5) is recognised for its potential to reduce the marine impacts of climate change if projections are adequately considered in reserve design (Maestro et al., 2019). One strategy for selecting areas for coral reef protection is the identification of reefs at which climate impacts will be low. For instance, areas that have historically experienced less heat stress have been identified via remote sensing-based measures (HotSpot and Degree Heating Weeks) from the past (Beyer et al., 2018: heat stress under future climate projections was also assessed). Another framework for selecting a management strategy for reefs used remotely sensed heat stress measurements from the recent (2014–2017) global bleaching event to propose, for protection, those reefs that experienced the least climate disturbance (Darling et al., 2019).

Table 1: Illustrative examples where reef managers have used coral bleaching predictions to deliver valued outcomes that would not have otherwise been possible. Abbreviations: *AIMS*, Australian Institute of Marine Science; *CRW*, Coral Reef Watch; *JCU*, James Cook University; *GBRMPA*, Great Barrier Reef Marine Park Authority; *NOAA*, US National Oceanic and Atmospheric Administration; *WA*, Western Australia.

Location	**Time period of bleaching event**	**Prediction products**	**User**	**Use**	**Benefit of prediction**	**Reference**
Caribbean	Jun-Dec 2005	HotSpot, DHW	50 + Universities, Institutes and	Bleaching survey	Enabled bleaching documentation	Eakin et al. (2010a)

			Goverment Units.	planning in Caribbean	through 2575 surveys	
Western Australia	Jan-Mar 2011	DHW, ReefTemp	AIMS, WA Dept. Env. & Conserv., WA Dept. Fish.	Bleaching survey planning across 1200 km of coastline	Surveys coincided with thermal anomaly maxima	Moore et al. (2012)
Florida	August 2014	Not stated	Academic researchers	Local stressors (corallivores) reduced prior to thermal stress	Coral resilience to bleaching was enhanced	Shaver et al. (2018)
Great Barrier Reef	Feb-Apr 2016	Outlook	JCU, GBRMPA, AIMS	Bleaching survey planning	Enabled bleaching documentation over length of GBR	Hughes et al. (2018)
Maldives	2016	NOAA CRW product suite	Maldives Government	Capacity building and bleaching survey planning	Sufficient forewarning enabled 82 citizen scientists to be trained to conduct surveys	Ibrahim et al. (2017)
Palau	Future decades	Hydrodynamic modelling	Palau Government, NOAA	Identification of thermal refugia	Protected area system designed for resilience	Skirving et al (2010)

3 The biological basis of mass coral bleaching

Methods for remotely sensed prediction of coral bleaching are based, in part, on an understanding of the biological responses of corals to stressors. We focus on the stressors prevalent during the meteorological conditions that are typical during mass coral bleaching events: ocean warming, increased UV light intensity, and increased visible light intensity. During weather events featuring low wind and little cloud, clear skies permit large quantities of solar insolation to reach the ocean surface, thermally heating the water (Falter et al., 2014). The accompanying high visible and UV light intensities may penetrate to greater ocean depths as the low wind conditions promote thermal stratification, and increased clarity, of the water column (Heron et al., 2008; Jokiel, 2004; Strong et al., 2006). Through its effect on coral mitochondria and the symbiont photosystems, thermal stress or UV light may cause increased reactive oxygen species (ROS) production (Ferrier-Pages et al., 2007; Lesser et al., 1990; Nii and Muscatine, 1997). Elevated heat and elevated UV reduce the visible light intensity threshold for photoinhibition of the dinoflagellate symbionts (Hoegh-Guldberg, 1999) (Fig. 1).

For elevated temperatures, the mechanism can involve the suppression of the CO_2 fixation mechanism (Calvin-Benson cycle) of the symbionts, resulting in an over-reduced electron transport chain, a reduction in the ability of photosystem II (PSII) to photochemically utilise incoming photons, and production of ROS as a result (Jones et al., 1998; Buxton et al., 2012; Bhagooli, 2013; but see Leggat et al., 2004). Elevated temperatures may cause damage to the thylakoid membranes (Iglesias-Prieto et al., 1992), which may become energetically uncoupled but still able to evolve oxygen, some of which is converted into ROS by photosystem I (PSI) (Tchernov et al., 2004). Elevated temperatures may also damage PSII directly, inhibiting the protein synthesis-based repair of photo-damage to PSII and causing photoinhibition (Iglesias-Prieto, 1995; Takahashi et al., 2004; Warner et al., 1999, 1996). PSII may be damaged by high light at certain wavelengths, most strongly by UV (Nishiyama et al., 2006; Takahashi et al., 2010). Bleaching occurs because ROS triggers a number of pathways that result in the loss of symbiont cells from the coral, including apoptosis (programmed cell death) (Dunn et al., 2002), and/or because ROS damage to PSII decreases the pigment concentration in dinoflagellate cells (Takahashi et al., 2004). If not immediately ejected, the loss of photosynthesis may later cause the algal cells to cease contributing to the symbiosis, causing the coral host to then eject them (Dove et al., 2006; Dove and Hoegh-Guldberg, 2006; Iglesias-Prieto, 1995).

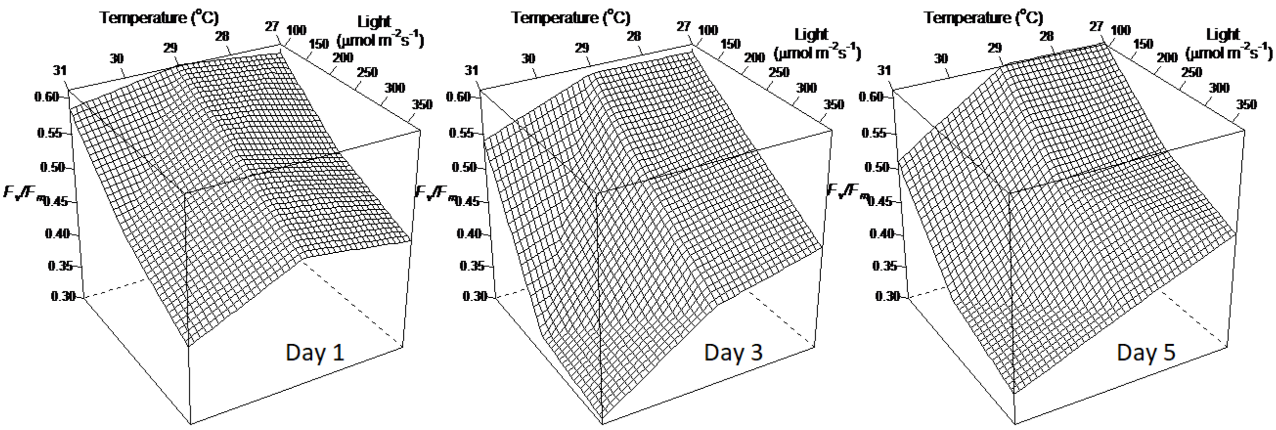

Fig. 1. High temperature reduces the light intensity threshold for photoinhibition of dinoflagellates in corals. In this graph, photosynthetic performance (F_v/F_m) declines with increasing temperature or increasing light, but the decline is more severe when both are combined, and with increasing length of exposure. The specimens are a mixture of *Porites* species exposed over a period of > 5 days. Experiment methods are described in Mason (2018a). The surface is a linear interpolation of F_v/F_m measurements at 27°C, 29°C and 31°C combined with 3 light levels (91 μmol m^{-2} s^{-1}, 226 μmol m^{-2} s^{-1} and 371 μmol m^{-2} s^{-1}).

When measuring coral bleaching, different proxies are used, depending on the scale of the observations. When a reef is observed by scuba or snorkel diving, several methods are in use, such as the visual assessment of coral colour compared to a colour scale on a reference card (Siebeck et al., 2006), or photographic assessment (Johnson and Goulet, 2007; Winters et al., 2009). In aquaria experiments on pieces of live coral, bleaching is usually measured as a statistically significant decline in symbiont cell density and/or chlorophyll content (per unit area or per symbiont cell). At a cellular level, processes that are attendant to coral bleaching, such as structural changes involved in cellular or organelle degradation, are often measured (Dunn et al., 2002; Gates et al., 1992).

Definitions of coral bleaching “severity” also involve different levels of resolution, depending on the scale of observations. Coral bleaching “severity” at a reef scale is often defined in a whole-of-benthos sense, such as the percent of corals that are totally white (Maynard et al., 2009), or the percent of corals displaying whiteness on at least part of the colony (Wooldridge and Done, 2004). In aquaria experiments, coral bleaching “severity” may instead refer to the proportion by which symbiont density, averaged over all fragments within one treatment, declines compared to a control treatment (Glynn and D’Croz, 1990). As the proxy for bleaching changes depending on the scale of observations, it can be difficult to apply results discovered at one scale to further the understanding of bleaching at a different scale. Nevertheless, the study and monitoring of coral bleaching require the synthesis of information obtained at different scales because of the huge geographic extent of reefs affected by bleaching and the fact that molecular or organism-scale processes can influence larger-scale patterns.

4 Remotely sensed data sources

4.1 Global sea surface temperature data

Remotely sensed sea surface temperature (SST) data is a key input for all bleaching nowcast prediction methods (Degree Heating Weeks [section 5.1], ReefTemp [section 5.1] and Light Stress Damage [section 6]). Prediction of bleaching via the Degree Heating Weeks product relies on a daily, global Level 4 (gap-filled) sea surface temperature product. At present, that product is the NOAA Geo-Polar Blended Global Sea Surface Temperature Analysis (Level 4), providing SST at a resolution of 0.05° (ca. 5 km) (Liu et al., 2017; NOAA, 2019). This product is built from radiometric measurements of sea surface temperature on polar-orbiting satellites (currently, the Suomi National Polar Orbiting Partnership and MetOp platforms) and geostationary satellites (GOES-East, GOES-West, Himawari-8, Meteosat-11 and Meteosat-8) (Maturi et al., 2017). Polar-orbiting observations are made at approximately 1–4 km spatial resolution, with the full earth imaged twice per 24 h. Full-disk geostationary observations are made at a 2–4 km (at nadir) resolution, at 10 min to 3 h intervals (satellite dependent), centred at the meridians of 140.7°E (Himawari-8), 75°W / 137°W (GOES-East / GOES-West) and 0° /41.5°E (Meteosat-11 / Meteosat-8) (Kurihara et al., 2016; Maturi et al., 2017; WMO, 2020). The SST product makes use of both polar-orbiting and geostationary data due to their distinct but complementary advantages: high spatial resolution and radiometric accuracy (polar-orbiting) *vs* high observational frequency (geostationary) (Maturi et al., 2017).

SST is retrieved from the polar-orbiting data using a regression of satellite *vs* in situ data, which inherently results in some biases in particular regions (Maturi et al., 2017; Petrenko et al., 2014). The regression method is limited in its ability to handle differences in atmospheric attenuation of signal due to view zenith angle, precipitable water vapour content of the atmosphere, and the like (Petrenko et al., 2014). However, the current regression algorithms, from the EUMETSAT Ocean and Sea Ice Satellite Application Facility (OSI-SAF), show much improved performance (reduction of bias) over previous regression methods (Petrenko et al., 2014).

Geostationary observations experience bias due to the same features of oceanic and atmospheric circulation always occurring within the same part of the stationary field of view of the sensor. Many biases have been reduced since 2013, when the retrieval method was switched from a regression against in situ method to a deterministic physical retrieval method (Koner et al., 2015). Currently, physical retrieval is used for three of the geostationary satellites and regression-based retrieval is used for the remaining two. Implementation of a physical retrieval method for polar-orbiting data is dependent on the further development of methods for correction of bias between the radiative transfer model predictions and actual observations, bias that is highly variable in space and time (Petrenko et al., 2014).

During construction of the Level 4 SST product, data from multiple sources need to be combined. To do so, generalised bias of one type against another type are first removed, by bias-correcting each type to an independent reference (Maturi et al., 2017). This reference is the National Centers for Environmental Prediction Real-time Global SST product, comprised of Advanced Very High Resolution Radiometer (AVHRR) SST retrievals with bias reduced via a physical stochastic retrieval method and in situ measurements from buoys (Maturi et al., 2017; Thiébaux et al., 2003). Next, optimal interpolation is used to gap fill, using the bias field as a reference (Maturi et al., 2017).

4.2 SST for the Australian region

The ReefTemp bleaching prediction method, which is operational for the Great Barrier Reef and Coral Sea, uses an SST product provided by Australia`s Intergrated Marine Observing System (IMOS). This agency produces a real-time daily SST product for waters surrounding Australia at ~2 km (0.018°) resolution from raw AVHRR SST received from NOAA polar orbiting satellites (Garde et al., 2014; Paltoglou et al., 2010). Once received at IMOS, the

AVHRR data are calibrated via regression against drifting buoy SST measurements from the Australian region (Paltoglou et al., 2010). The nighttime data from the individual AVHRR sensors in the NOAA satellite network are then collated and processed to remove observations affected by cloud cover, to form the IMOS L3S 1 day night-only SST product (Garde et al., 2014). Interpolation is not used to fill gaps due to cloud cover or missing data. To assist in nowcasting [section 5.1], a second SST product (the Reef Temp Next Generation (RTNG) 14-day mosaic) is created by filling gaps through finding all 1 day night-only SST observations for that pixel for the past 13 days, and using the latest observation (Garde et al., 2014). However, in areas where the latest observation for some pixels was a number of days ago and the temperature has changed since that time, artefactual SST gradients are created between gap-filled pixels and adjacent pixels with up-to-date SST (Garde et al., 2014). Furthermore, if high temperatures do not persist but the last observations for a pixel were taken during the high-temperature period, then the 14-day mosaic will artificially prolong high temperatures at that pixel. This may result in over-prediction of heat stress in those pixels by bleaching nowcast methods (Garde et al., 2014).

5 Methods for bleaching prediction

5.1 Nowcasts

Computational methods for predicting the global occurrence of coral bleaching from remotely-sensed data have been in use since 2001 (Table 2). Using global daily SST retrievals [section 4.1], now-casts (present-day predictions) of coral bleaching are made via NOAA`s Degree Heating Weeks (DHW) product (Wellington et al., 2001), which sums sea surface temperature anomalies (“HotSpots”) (Strong et al., 1997).

The DHW method, and other algorithms for bleaching prediction, rely on simplified models of coral bleaching responses under thermal stress. The DHW method is based on three assumptions: (1) temperatures of 1°C or more above the maximum monthly mean (MMM), will begin causing physiological stress; (2) the ability of any temperature ≥1°C above MMM to cause coral bleaching is dose dependent; and (3) the cumulative dose of all stressful temperatures within the previous 12 weeks is the determinant of bleaching (Gleeson and Strong, 1995; Strong et al., 2006). The MMM is defined as the mean temperature of the warmest month in the climatology of a location, and is derived from night-time satellite-detected sea surface temperatures for the years 1985–2012 (previously, the years 1985–1993 were used, excluding 1991–1992 that were cooled by the Mt. Pinatubo eruption: Liu et al., 2006). The SST dataset used for this archive does not have a consistent bias from 1985 to the present day, however work is underway to resolve this. The HotSpot is the number of degrees that the sea surface temperature exceeds the MMM at a given location (Liu et al., 2006). The DHW index is the weekly mean of the cumulative sum of every daily anomaly (HotSpot ≥1 °C) over the previous twelve weeks (84 days):

$$DHW_i = \sum_{n=i-83}^{i} \left(\frac{HotSpot_n}{7}\right), \text{where } HotSpot_n \geq 1\ °\text{C}$$

Field observations suggest that a DHW of 4 indicates significant bleaching in at least one coral species and that a DHW of 8 indicates significant bleaching in most species with mortality in at least one (Eakin et al., 2010b). However, Hughes et al. (2018) provided evidence that these impacts may happen at slightly lower DHW thresholds. DHW predictions are provided to any user in a value-added online format at the Coral Reef Watch Decision Support System (www.coralreefwatch.noaa.gov/satellite/index.php).

ReefTemp, an alternative algorithm for the Great Barrier Reef, uses the amount of heat stress accumulated, and the rate of heating, to calculate bleaching likelihood during the Austral summer period (December to March, inclusive). ReefTemp calculates Degree Heating Days (DHD), which is the sum, from the start of December up to the present day, of the positive anomalies of daily average SST (Garde et al., 2014):

$$DHD_i = \sum_{n=1Dec.}^{i} (SST_n - baseline_n),$$

$$\text{where } (SST_n - baseline_n) > 0°\text{C, 1 December} \leq i \leq \text{31 March}$$

The baseline for determining anomalies is the 2002–2011 mean temperature of the month the indexed day falls within, at a given location. ReefTemp then calculates the Mean Positive Summer Anomaly (MPSA), a measure of the mean severity of heating stress, which is the average rate of accumulation of Degree Heating Days over all days that have experienced a positive anomaly since the start of the summer period (Garde et al., 2014):

$$MPSA_i = DHD_i \div DHDcount_i$$

$$\text{where } DHDcount_i = \sum_{n=1Dec.}^{i} I_n,$$

$$\text{where } I_n = \begin{Bmatrix} 1 if (SST_n - baseline_n) > 0°C \\ 0 if (SST_n - baseline_n) \leqslant 0°C \end{Bmatrix}$$

The DHD and MPSA indices are individually used to predict the position of a reef on a graded scale of bleaching severity, for instance, under the 1-day ReefTemp SST product, moderate bleaching is predicted by a DHD threshold of 11.6 °C-days or an MPSA threshold of 1.4 °C (Garde et al., 2014). The graded scales of bleaching severity for given DHD and MPSA values (for the 14-day SST product) were calibrated using diver bleaching surveys for the Great Barrier Reef in 2002, followed by regression of 1-day DHD vs 14-day DHD (and likewise for MPSA) to obtain graded scales for the 1-day SST product (Garde et al., 2014; Maynard et al., 2008).

5.2 Forecasts

Other algorithms for bleaching prediction use ocean-atmosphere models to predict sea surface temperatures (Table 2), and these form important complementary products that are utilised alongside the now-casting methods. The Australian Bureau of Meteorology developed the Predictive Ocean Atmosphere Model for Australia (POAMA), an ocean-atmosphere computational model that predicts sea surface temperatures several months in advance (Spillman and Alves, 2009), which has recently been updated to the ACCESS-S model (Hudson et. al., 2017). These projections are made on a monthly rather than a weekly timeframe, so the near-future bleaching risk is calculated from these projections using Degree Heating Months (DHM) (Spillman et al., 2011). Using the fraction of an observed monthly average temperature that is above the MMM, the DHM algorithm operates by summing these fractions over a rolling three-month window and predicts bleaching onset when the total exceeds 1 (Donner et al., 2005). NOAA also produces a forecast product, Outlook, which applies a form of DHW to predictions of SST generated by the National Centres for Environment Prediction model, Climate Forecast System Version 2, to generate coral bleaching warnings 4 months in advance (Liu et al., 2018).

5.3 Resolution of finer-scale patterns

Hydrodynamic phenomena modulate the effect of weather and climate on sea surface temperature, and their evaluation could help downscale to SST-based bleaching now-casts. During "bleaching weather" (clear skies and low wind in summertime), the combination of solar heating and an absence of wind-induced mixing stratifies the water column, with a very warm surface layer (Skirving and Guinotte, 2000). Local processes that mix the water column will prevent this layer from occurring and thereby reduce the bleaching risk. Mixing can occur through swell waves, high-frequency currents (tides) and low frequency currents (such as the Gulf Stream) (Skirving et al., 2006). The effect of these features (other than swell) on vertical mixing can be modelled using the inputs of bathymetry of a reef system, low frequency current patterns (e.g. the NOAA Ocean Surface Current Analyses – Real time), tidal patterns (from tide gauge data) and water column temperature profile (Skirving et al., 2006). These spatial predictions of the amount of water column mixing allow the identification of areas of high and low thermal capacitance (those areas that will, respectively, heat slowly or quickly when heat is added to the system) (Skirving et al., 2010). Hydrodynamic predictions have a higher spatial resolution (e.g. 256.5 m) than current satellite SST products, and can be used to supplement satellite SST-based methods to better resolve patterns of heat stress at local scales (Skirving et al., 2006). This method has been used in Palau (Heron and Skirving, 2004), and has been developed in an initial form for the Great Barrier Reef.

Table 2: Methods for now-casting or forecasting of coral bleaching using satellite SST data or SST predictions from climate models. Abbreviations: *DHW*, Degree Heating Weeks; *MMM*, maximum monthly mean; *SST*, sea surface temperature

Analysis method	Description	Advantages	Limitations	References
HotSpot	The SST anomaly (difference between the SST and the MMM)	HotSpots > 0°C provide advance warning of possible heat stress conditions.	Indicates presence of stressful SST but not the amount of accumulated stress.	Strong et al. (1997)
Degree Heating Weeks	Rolling sum over 12 weeks of weekly SST anomalies above the MMM + 1°C.	Daily global now-casts of accumulated heat stress, provides important and	Forecast skill is limited in some situations. MMM calculations are	Liu et al. (2006)

		relevant information to environmental managers.	currently subject to some biases in the satellite SST record.	
ReefTemp	Sum, and mean rate of accumulation, of daily SST anomalies over summer period.	Takes rate of heating into account. May increase bleaching surveillance efficacy when used in conjunction with DHW.	Method for gap-filling of SST may introduce inaccuracies into predictions. Climatology period used is recent in time.	Garde et al. (2014)
Outlook (NOAA) and ACCESS-S (BOM)	Heat stress forecasts based on SST from a near-future ocean-atmosphere computational model	Provides time (> 1 month) for forward planning for probable bleaching events	Affected by uncertainty in underlying ocean-atmosphere model.	Liu et al. (2018), Hudson et al. (2017)
Hydrodynamic modelling	Modelling of water column mixing due to the interaction of currents and bathymetry	Supplements SST-based methods by identifying areas less susceptible to heat stress at a fine spatial resolution	Not yet developed for most coral reef regions. Needs extension to include the mixing effect of swell and the advection of cooled water.	Skirving et al. (2006)
Light Stress Damage product	Combines temperature anomalies and irradiance to nowcast bleaching.	Provides a more physiologically-complete method of predicting bleaching.	Still under development, in experimental use. Solar insolation products are currently not available for Himawari-8 or GOES-East.	Skirving et al. (2018)

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5.4 Accuracy of prediction of bleaching

Accuracy of bleaching prediction can be assessed against three aspects of the phenomenon: onset, severity and mortality. Onset prediction accuracy has been verified for DHW via the Peirce Skill Score (Hogan and Mason, 2012):

$$\text{Peirce Skill Score} = \frac{a}{a+c} - \frac{b}{b+d},$$

where a = number of correct predictions of bleaching

b = number of false predictions of bleaching

c = number of unpredicted bleaching events

d = number of correct predictions of no bleaching

For DHW, the Peirce Skill Score is 0.55 on average (van Hooidonk and Huber, 2009: anomalies were summed above MMM, not MMM + 1 °C). A maximum average score of 0.83 can be achieved if the DHW bleaching threshold is allowed to vary regionally, through an optimisation procedure, which compares favourably to the highest possible score of 1 (van Hooidonk and Huber, 2009). Based on surveys of bleaching, site-specific bleaching onset thresholds (as a function of temperature and duration of exposure) have been calculated for many sites on the Great Barrier Reef (Berkelmans, 2002) and in Florida (Manzello et al., 2007), and vary substantially among locations within both regions. Such differences among sites may be due, in part, to variation in coral community composition and differences among species in their susceptibility to bleaching and bleaching-associated mortality (Marshall and Baird, 2000). Thus, use of regionally-variant bleaching thresholds may improve bleaching onset predictive skill of DHW further.

The severity of bleaching typically has a positive correlation with DHW, but the strength of the correlation can vary substantially depending on the SST temperature product used (Table

3), providing scope for regional improvement of prediction of severity through continued improvement of satellite SST products.

Table 3. Correlations between remotely sensed bleaching predictions and observations of bleaching severity. Bars of grey at the left side indicate predictions made using two different sources of sea temperature by the same study. The r^2 in McClanahan et al. (2007b) also include a component for water depth. The *p* values are: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; N.S., not significant.

Bleaching algorithm	SST product	Ocean	Location	Year	r^2	Field observation type	*p* value of r^2	Reference
DHW	NOAA	Indian	East Africa	2005	0.36	Bleaching response index	***	McClanahan et al. (2007b)
DHW	JCOMM	Indian	East Africa	2005	0.56	Bleaching response index	***	McClanahan et al. (2007b)
DHW	ReefGIS	Indian	Andaman Sea	2010	0.11	Bleaching response index	N.S.	Wall et al. (2015)
DHW	In situ thermometer	Indian	Andaman Sea	2010	0.40	Bleaching response index	*	Wall et al. (2015)
HotSpot	AVHRR	Atlantic	Brazil	2010	0.96	Bleached corals (percent)	***	Ferreira et al. (2013)
DHW	NOAA	Pacific	N^{th} Mariana Islands	2014	0.41	Percent coral bleached	Not reported	Heron et al. (2016)

Similarly, the ability of the DHW index to accurately predict coral mortality is less than certain. DHW thresholds for bleaching-induced mortality that were established prior to 2010 appeared to underestimate mortality at 2 m depth in the 2016 bleaching event on the Great Barrier Reef (Hughes et al., 2018; see section 5.1). Furthermore, during this event, in-water observations suggested that some coral species died on exposure to high temperature without bleaching first (Hughes et al., 2018).

6 Incorporating irradiance into a bleaching prediction algorithm

Physiologically, thermal stress is known to cause bleaching through reducing the level of light stress required to cause photoinhibition (Hoegh-Guldberg, 1999), so ideally, satellite algorithms for bleaching prediction should include both light and temperature levels. Traditionally, light intensity has been measured from field station-based sensors (Hansen et al., 2002), limiting the scope for light intensity to be accurately measured over large areas of the oceans for the prediction of coral bleaching. However, approaches have recently been developed to retrieve shortwave radiation budgets from geostationary environmental satellites, resulting in a remotely sensed global irradiance product (Eakin et al., 2010b; Laszlo et al., 2008). Light Stress Damage (LSD) is an algorithm that uses satellite-derived irradiance (specifically, photosynthetically active radiation) and temperature to predict coral stress leading to bleaching and bleaching-induced mortality (Skirving et al., 2018). Bleaching nowcasts via LSD are provided experimentally by Coral Reef Watch for the Caribbean and Eastern Pacific (https://coralreefwatch.noaa.gov/satellite/lsd/index.php).

The LSD bleaching prediction algorithm (Skirving et al., 2018) is based on a physiological model of coral bleaching. Symbiont photosynthesis state can be rapidly determined by chlorophyll fluoresence. Photons received by light-harvesting complexes attached to photosystem II have three fates: usage to drive the electron transport chain (photosynthesis), dissipation through heat emission, or dissipation as chlorophyll fluorescence. Photosystem II capacity can be saturated through application of a bright pulse of light to a coral. Measurement of chlorophyll fluorescence under constant light prior to saturation (F_o) and following saturation (F_m) can be performed with a pulse amplitude modulated flurometer, after a period of dark adaptation (> 30 mins). Under the assumption that heat dissipation remains constant throughout, these measurements then give the proportion of photons whose energy may contribute to photosynthesis:

$$(F_m - F_o)/F_m = F_v/F_m$$

The LSD algorithm estimates F_v/F_m based on satellite-detected temperature and light and uses the sum of the change in this measure over an annual period as an index of physiological stress. Numerous physiological processes, termed *photoacclimation*, occur following a change in light level to optimise the efficiency with which the coral symbiosis utilises the available photosynthetically active radiation (Anthony and Hoegh-Guldberg, 2003). In the LSD product, relative F_v/F_m is determined by (a) excess excitation energy (*EEE*) in mol quanta day^{-1}, approximated as photosynthetically active radiation (PAR) today minus PAR in previous days adjusted for photoacclimation that has occurred; and (b) HotSpot (°C above MMM). The daily *EEE* is combined with the HotSpot to produce an approximation of the change in F_v/F_m (e.g. Fig. 2). Both *EEE* and SST anomaly can be derived from satellite maps of light intensity and temperature in near-real-time compared to the measurements of light over the preceding months and the climatological baseline of temperature for the location. To determine the relative F_v/F_m from both of these factors, physiological experiments were performed to measure the actual F_v/F_m in corals at many points along a continuum of anomalous temperatures and light levels (Scheufen et al., 2017). These experimental values are used as reference data to estimate the relative F_v/F_m for a given satellite-derived temperature anomaly and light level (Skirving et al., 2018).

F_v/F_m has a mechanistic link to, and is often a good proxy for, the onset of coral bleaching (Jones et al., 1998; Warner et al., 1999, 1996), and was chosen as the model output of the LSD algorithm as in situ measurements of F_v/F_m on corals are non-destructive, aiding field validation. The LSD algorithm is a conceptual advance over previous algorithms, which do not explicitly model a physiological variable that is mechanistically linked to bleaching onset. As F_v/F_m is the quantum efficiency of photosystem II when open, damage to PSII from the over-reduction of the electron transport chain (a symptom of heat- or light change-induced damage in the symbiont cells that presage bleaching) will register as a decline in F_v/F_m (Jones et al., 1998; Warner et al., 1999). It is important to note that declines in F_v/F_m can also indicate processes that are photoprotective, such as the dissipation, as heat, of excess light energy by aggregations of antenna complexes that are not linked to the electron transport chain (Matsubara and Chow, 2004; Takahashi and Badger, 2011). Thus, the decline of F_v/F_m in corals that are faced with thermal or light stress may not necessarily indicate physiological damage that will lead to coral bleaching. Furthermore, under some circumstances, physiological events that lead to coral bleaching originate in the coral animal tissue itself and not in the symbiont cells within the animal tissue (Gates et al., 1992), and it is unclear whether these mechanisms of coral bleaching will always cause immediate declines in F_v/F_m (Ainsworth et al., 2008). Nevertheless, F_v/F_m often correlates with symbiont cell density declines in coral bleaching experiments (Jones et al., 1998; Warner et al., 1996), supporting its use as a bleaching proxy in the LSD algorithm.

The LSD algorithm provides the possibility of prediction of the speed of coral recovery. Knowledge of the speed of coral recovery following bleaching events allows the planning of reef management responses to bleaching [section 2]. DHW reverts to zero once conditions conducive for recovery occur (twelve weeks of HotSpot < 1°C), providing no indication of recovery speed. In the LSD algorithm, the slope of the linear relationship between excess excitation energy and relative F_v/F_m becomes more negative as the thermal anomaly increases, allowing recovery to be estimated (Skirving et al., 2018). Some evidence suggests that, after the cessation of heat stress, this slope retains its steeper gradient for approximately 30 days, that is, the rate of repair (or repigmentation) of coral tissues is temporarily upregulated following heat stress (DeSalvo et al., 2010; Rodríguez-Román et al., 2006). Maintaining a more negative relationship between EEE and relative F_v/F_m for a temporary period following a return to non-stressful water temperatures may help to provide realistic estimates of the recovery rate of bleached corals (Skirving et al., 2018).

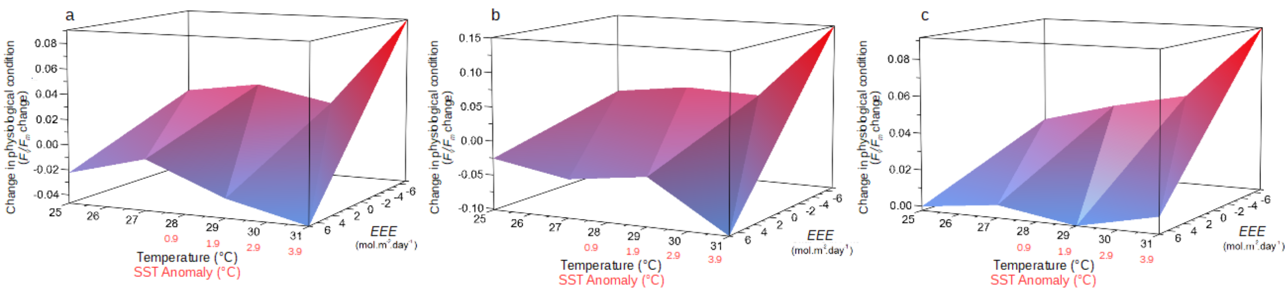

Fig. 2: The Light Stress Damage bleaching prediction method uses *EEE* (PAR today minus PAR yesterday) and SST anomaly (SST minus MMM) to approximate the change in F_v/F_m, depicted here for (a) *Acropora muricata*, (b) *Montipora monasteriata* and (c) a mixture of *Porites* species (note differing ranges on the vertical axes). These relationships may differ among coral taxa, and need to be determined through empirical measurements of F_v/F_m under actual *EEE* and SST anomalies. Experiment methods are described in Mason (2018).

7 Further development of remotely sensed bleaching prediction

More effective management of coral reefs is both an important end in itself and a means to contribute to the SDGs, including those of restoring marine ecosystems, increasing protected areas, and improving economic benefits to small island states. It is thus vital that remotely sensed bleaching prediction continues to be improved to increase prediction skill [section 5.4] and thereby to increase utility to reef management [section 2]. There are a number of avenues through which remotely sensed bleaching prediction could be improved, through better characterisation of the physiological response of corals under heat and light stress (Table 4). The first of these relates to improving the handling of light acclimation for irradiance-based bleaching prediction. To incorporate past light changes into the LSD index, these changes are scaled by a coefficient representing the daily light acclimation rate, and further empirical investigation of this rate is needed (Anthony and Hoegh-Guldberg, 2003; Skirving et al., 2018). A coefficient representing the daily light acclimation rate is used to calculate the component of light changes on all previous days that the coral has not yet fully acclimated to, which is then used to calculate *EEE*. (Skirving et al., 2018). However, changes of light in one direction may take longer to photoacclimate to than changes in the opposite direction. This is because changes in one direction may involve the building up of particular photosynthetic structures (e.g. pigment-protein complexes), whilst changes in the other direction may involve reducing the size or number of the same structures (Falkowski and Raven, 2007). When irradiance levels increase so much that they cause photodamage, the rate of repair of photosystems will influence *EEE*, and this rate needs determination in a range of symbiont species. Further questions include whether the magnitude of the light change (e.g. +1 versus +5 mol quanta$\cdot$m$^{-2}\cdot$day^{-1}) or the water temperature influences photoacclimation rate. The resolution of these questions is required in order to determine whether the acclimation rate used in the LSD algorithm must vary depending on the nature of the change in light intensity, or the water temperature.

A second challenge for the further development of the LSD algorithm is to identify, for different species, the threshold of F_v/F_m decline that indicates the onset of symbiont physiological damage that will lead to bleaching. The relationship between *EEE*, HotSpot and change in F_v/F_m may also vary among taxa, requiring investigation in a larger number of species.

Remotely sensed bleaching prediction that includes the impacts of UV light, which is often reported to be an important synergistic impact on thermal bleaching, may be possible in the future (Barnes et al., 2015; Kumagai and Yamano, 2018). Combining insolation products with sea level, ocean colour and surface reflectance could enable a remotely sensed benthic light product, predicting the irradiance of both the UV and visible components received at the sea floor (Barnes et al., 2015). As UV light is a powerful PSII inhibitor (Takahashi et al., 2010), the adjustment of *EEE* by applying a weighting factor to the UV component may account for its impact.

Some evidence suggests that temperature history and diurnal variation influence the thermal threshold for the onset of coral bleaching, and these features could be incorporated into future remotely sensed bleaching products. Increased resilience to high temperatures appears to be conferred by prior short-term temperature exposures that are slightly above maximum monthly averages, followed by a recovery period (lower temperatures) before high-temperature onset (Ainsworth et al., 2016; Bellantuono et al., 2012; Middlebrook et al., 2008, but see Middlebrook et al. 2012). The protective effect of this pre-warming is not yet incorporated into any bleaching prediction algorithms. Interestingly, pre-exposure to high visible light levels may also confer some protection against stress under subsequent high temperatures (Coles and Jokiel, 1978; Dunne and Brown, 2001). Finally, survival in environments with strong diurnal variation in temperature (>1°C) appears to raise the temperature threshold of bleaching (Safaie et al., 2018), and this may be an avenue for further improvement of bleaching prediction.

Table 4: Areas for remotely sensed bleaching prediction development.

Type of development	**Description**	**Section of paper**
Physical	Hydrodynamic models for thermal capacitance	5.3
Physical	Incorporate UV light into bleaching prediction by the development of a remote sensing product for the attenuation of UV and visible light at the sea bed	7
Physical	Continued development of satellite SST resolution	4, 5.4
Physical	Development of an SST product whose bias is consistent from the 1980s to the present day	5.1
Ecology/Physiology	Regionally-variant bleaching thresholds	5.4
Ecology/Physiology	Improve the accuracy of the photoacclimation rate used in Light Stress Damage algorithm	7
Ecology/Physiology	Determine F_v/F_m thresholds for bleaching in different coral species	7
Ecology/Physiology	Further research into the effect of pre-warming and high diurnal variation in temperature on bleaching thresholds	7

8 Summary and outlook

Coral reefs are an important contributor to many SDGs, for instance by providing artisanal fishing livelihoods, supporting small island nations, and providing material benefits of high biodiversity (e.g. new drugs). Remotely sensed bleaching prediction has a vital role to play in supporting these contributions of reefs, through facilitating management of coral bleaching impacts that threaten to cause severe reef degradation under climate change. Effective reef management can help to lessen bleaching impacts through preventing reef damage during vulnerable times, enhancing reef recovery ability, improved surveillance, limitation of socioeconomic impacts, and design of climate-resilient marine protected areas. Predictions of the timing, locations and magnitude of bleaching provide the knowledge required for these management activities, and improvements to prediction accuracy and precision thus directly contribute to better reef management.

Prediction of coral bleaching occurs, in near-real-time, through the DHW and ReefTemp satellite SST-based products, or as four-month forecasts through ocean-atmosphere models. The satellite SST-based methods effectively measure the cumulative dose of heat stress through time (and rate of heating, in the case of ReefTemp). As coral bleaching is usually the result of impacts of heat, light and UV on the photosystems of algal symbionts within the coral, the inclusion of light in bleaching prediction is a key area for development. The experimental product, LSD, uses a recently-developed satellite light product in conjunction with SST to predict coral bleaching, based on a model of physiological stress in the algal symbionts of corals. LSD provides a measure of the speed of coral recovery following bleaching, important knowledge for reef management that is not provided by other prediction methods.

Remotely sensed bleaching prediction methods can be improved, including through incorporating new physiological knowledge or acquiring further knowledge empirically. For SST-based prediction, areas for improvement include advances in satellite SST products, regional calibration of heat-stress thresholds for bleaching, and accounting for the apparent protective effect of pre-warming episodes. To improve bleaching prediction that uses irradiance, an understanding of how the rate of physiological adjustment to light change is influenced by several variables (e.g. light change magnitude) is needed. Expansion of irradiance-based prediction to include the UV region of the light spectrum is a further area for development.

Thanks to the development of SST products and heat stress algorithms by NOAA / NESDIS and the BOM, remotely sensed bleaching predictions are now available on a daily basis and their use is integrated into reef management practices. Further development of remotely sensed bleaching algorithms to improve predictions will enhance reef management and the monitoring of ecosystem services that reefs provide, and will contribute to advancement of the SDGs.

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R.A.B.M. wrote the first draft, W.J.S. and S.G.D. reviewed drafts.

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