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Excess seawater nutrients, enlarged algal symbiont densities and bleaching sensitive reef locations: 2. A regional-scale predictive model for the Great Barrier Reef, Australia

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ABSTRACT

A spatial risk assessment model is developed for the Great Barrier Reef (GBR, Australia) that helps identify reef locations at higher or lower risk of coral bleaching in summer heat-wave conditions. The model confirms the considerable benefit of discriminating nutrient-enriched areas that contain corals with enlarged (suboptimal) symbiont densities for the purpose of identifying bleaching-sensitive reef locations. The benefit of the new system-level understanding is showcased in terms of: (i) improving early-warning forecasts of summer bleaching risk, (ii) explaining historical bleaching patterns, (iii) testing the bleaching-resistant quality of the current marine protected area (MPA) network (iv) identifying routinely monitored coral health attributes, such as the tissue energy reserves and skeletal growth characteristics (viz. density and extension rates) that correlate with bleaching resistant reef locations, and (v) targeting region-specific water quality improvement strategies that may increase reef-scale coral health and bleaching resistance.

1. Introduction

There is growing need among managers, policy makers and stakeholders for spatially-explicit information on the risk that climate-related ‘coral bleaching’ impacts pose at the local management scales of reefs and regions (Marshall and Schuttenberg, 2006). The value in such information lies in its potential to: (i) identify reef locations that exhibit greater (or lower) resistance to thermal bleaching, (ii) explain the interacting determinants responsible for such reef-scale variability, and where possible (iii) draw attention to local adaptation actions that may help to mitigate the risk.

The modern availability of remotely-sensed products that can identify areas of anomalous sea surface temperature (SST) greatly improves capacity to develop localised (<5 km) predictions of heat stress and potential bleaching impacts. For example, the widely employed NOAA Coral Reef Watch Program (CRW) bleaching prediction method uses a thermal stress algorithm based on satellite-derived SST. This method is based on empirical evidence that corals bleach when exposed to ~ 1 °C above their historical summertime maximum SST for several weeks (Liu et al., 2003). Weekly thermal anomalies > 1 °C above a climatology (maximum monthly mean SST) are summed over a 12 week period to produce a ‘Degree Heating Week’ (DHW) metric (Liu et al., 2003); a DHW > 4 °C-weeks predicts a “likely bleaching event”. Application of this DHW metric for the two largest mass bleaching events on the Great Barrier Reef (GBR, Australia), which occurred during the austral summers of 1998 and 2002 (Berkelmans et al., 2004), demonstrates its utility for predicting the presence/absence of reef-scale bleaching; in this case with an accuracy of ~60% (Fig. 1). However, such SST-derived products (alone) are unable to provide important insight as to why some reef locations exhibit lower (or higher) resistance to thermal bleaching (Case 2 and Case 3; Fig. 1).

Reef locations which display higher bleaching resistance (Case 3; Fig. 1) may become important reservoirs of abundance and biodiversity on the GBR (and elsewhere) in the coming decades, especially given the prospect of an increased frequency of anomalous heating events. In an

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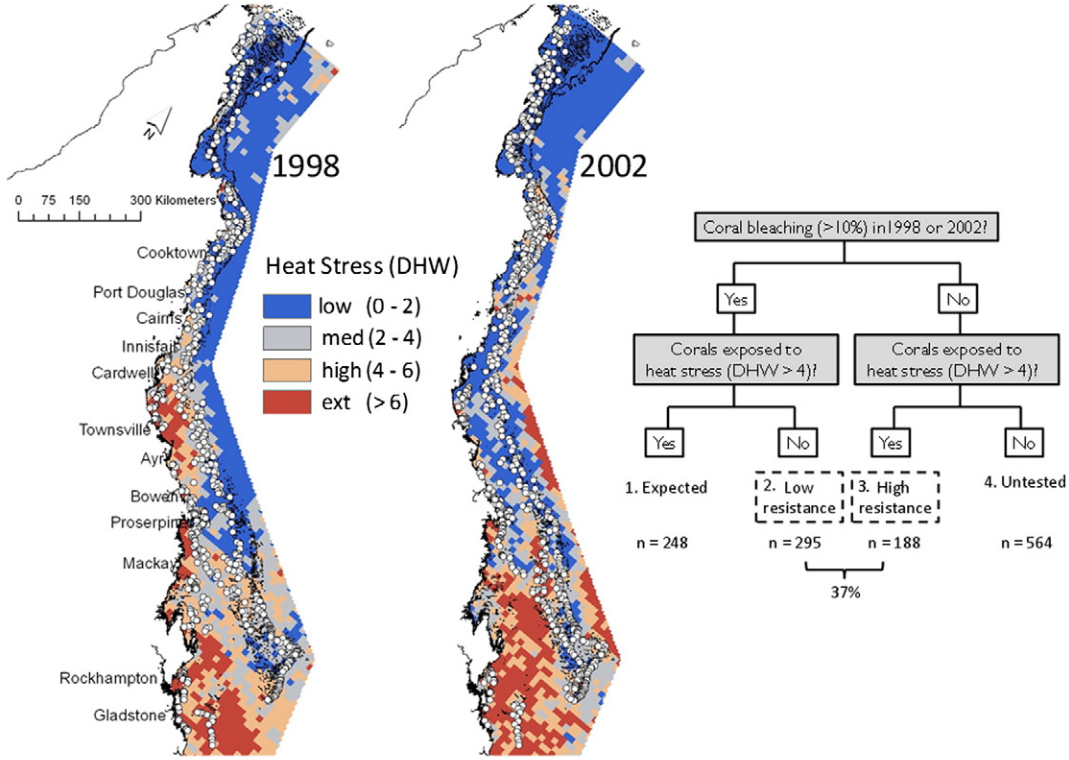

Fig. 1. Aerial surveys (circles) conducted during the summers of 1998 (n = 654) and 2002 (n = 641) highlighted that the GBR suffered widespread, but very patchy, coral bleaching on reefs scattered over many thousands of square miles. Heat stress (DHW) alone predicts presence/absence of bleaching with an accuracy of ~60%. The unexplained variability confirms the existence of areas with comparatively low or high resistance to thermal bleaching. Supplementary Appendix A provides additional details that underpin the aerial bleaching observations and DHW predictions.

ideal world, such reef locations would be key 'source' reefs within a managed network of Marine Protected Areas (MPAs) that aim to mitigate coral bleaching impacts (Done, 2001; Game et al., 2008; Mumby et al., 2011). Equally, such locations represent ideal sites for long-term capital investment in ecologically sensitive day-tourism facilities (Zell, 1999; Amelung and Nicholls, 2014).

The challenge for scientists and reef managers is to develop the capacity to reliably identify bleaching resistant reef locations and to differentiate them from locations that have not bleached only because they were not exposed to thermal stress – just "lucky so far" (Case 4; Fig. 1). This latter case would only be an appropriate choice for enhanced protection (or long-term tourism investment) if the non-bleaching could be shown to have been due to a reliable oceanographic feature such as current or upwelling that makes prolonged exposure of anomalous SST unlikely, even in a warmer world. It would not be appropriate if such cooling was not a reliable oceanographic feature.

A number of environmental factors, at a variety of observational scales, are potentially important in conferring the desired attribute of thermal bleaching resistance (reviewed by West and Salm, 2003). At regional scales, poor water quality, particularly an excess availability of bioavailable dissolved inorganic nitrogen (DIN = nitrate + nitrite + ammonium), is an increasingly identified feature linked with low resistance to thermal stress (Wooldridge, 2009a; Wagner et al., 2010; Wiedenmann et al., 2012; Vega-Thurber et al., 2014; Wooldridge et al., 2015; Wooldridge, in press). DIN concentrations affect the stability and functioning of the coral-algae symbiosis. For example, DIN enrichment can enhance the risk of intracellular phosphorus becoming a limiting nutrient, which has been linked to lower thermal resistance (Wiedenmann et al., 2012). Elevated DIN concentrations can also prevent the coral host from maintaining demographic control of its algal symbionts, resulting in an enlarged symbiont population (see e.g., Dubinsky et al., 1990; Stimson and Kinzie, 1991). In a companion paper, Wooldridge (in press) demonstrated how exceeding seawater nutrient thresholds that permit ambient zooxanthellae densities to proliferate beyond species-specific 'optimal' levels (e.g., ~1.5–2.0 × 10^6 cells cm^{-2} for thin tissue branching *Acropora* spp.) can limit the capacity of the host coral to build tissue energy reserves needed to combat periods of thermal stress. For the central GBR, this nutrient threshold was linked with seawater chlorophyll-*a* >0.45 $\mu g \cdot L^{-1}$, a threshold previously shown to correlate with a significant loss in species for hard corals and phototrophic octocorals on the central GBR (De'ath and Fabricius, 2008; Great Barrier Reef Marine Park Authority, 2010).

In addition to limiting host energy reserves, an excess of algal symbionts has been theoretically predicted (Wooldridge, 2009b, 2012, 2013a) and experimentally demonstrated (Nesa and Hidaka, 2009) to enhance the basal-rate of oxidative damage to host cells during periods of thermal stress (see also Cunning and Baker, 2013). Considered together, these risk factors help to make sense of the growing number of observations that reveal nutrient-enriched coral reefs to have: (i) lower thermal bleaching thresholds (Wooldridge, 2009a; Wooldridge and Done, 2009; Wiedenmann et al., 2012; Wooldridge, in press), and (ii) enhanced thermal bleaching impacts (Wagner et al., 2010; Vega-Thurber et al., 2014). Notably, both the theoretical predictions and field-based studies support the existence of species-specific 'optimal' symbiont densities, at which significant bleaching is best resisted at presently accepted upper natural limits for temperature and irradiance (Wooldridge, 2012; Cunning and Baker, 2013; Wooldridge, in press).

In this paper, we develop a spatial risk assessment model for the GBR, wherein reef-scale 'bleaching risk' is separated into explicit components of 'hazard exposure' (= the heating stress) and 'sensitivity' (= resistance to the heating stress). In this way, we test the benefit of indentifying reefs wherein the corals are most likely to have enlarged (suboptimal) symbiont densities, and thus have lower resistance to heating stress. We highlight the utility of this modelling framework for: (i) improving early-warning forecasts of summer bleaching risk, (ii) explaining historical bleaching patterns, (iii) testing the bleaching