Improved water quality can ameliorate effects of climate change on corals

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Abstract. The threats of wide-scale coral bleaching and reef demise associated with anthropogenic climate change are widely known. Moreover, rates of genetic adaptation and/or changes in the coral–zooxanthella partnerships are considered unlikely to be sufficiently fast for corals to acquire increased physiological resistance to increasing sea temperatures and declining pH. However, it has been suggested that coral reef resilience to climate change may be improved by good local management of coral reefs, including management of water quality. Here, using major data sets from the Great Barrier Reef (GBR), Australia, we investigate geographic patterns of coral bleaching in 1998 and 2002 and outline a synergism between heat stress and nutrient flux as a major causative mechanism for those patterns. The study provides the first concrete evidence for the oft-expressed belief that improved coral reef management will increase the regional-scale survival prospects of coral reefs to global climate change.

Key words: bleaching threshold; CO2 limitation; coral reef; dissolved inorganic nitrogen (DIN); Great Barrier Reef, Australia; zooanthellae species.

INTRODUCTION

In favorable environmental conditions, the obligate endosymbiosis between corals and dinoflagellate algae of the genus Symbiodinium (“zooxanthellae”) is characterized by an excess translocation of fixed-carbon photosynthetic products (photosynthates) from the zooxanthellae to the coral host (Fig. 1a; Muscatine 1990). Breakdown of the symbiosis (coral bleaching) occurs when a significant proportion of the zooxanthellae compliment is expelled from the coral animal (Brown 1997). Prolonged bleaching can be fatal to the coral host, and can devastate entire reef-scapes over vast areas of ocean (see, e.g., Sheppard 2003). The primary triggering condition for large-scale mass bleaching events is the combination of high solar irradiance and anomalously warm sea surface temperatures (SSTs; reviewed by Hoegh-Guldberg 1999). Such sensitivity makes coral reefs vulnerable to future climate change, with some scientists predicting that global warming trends could see the majority of the world’s coral reefs severely degraded or even transformed to non-coral-dominated states by as early as 2030 (see, e.g., Hoegh-Guldberg et al. 2006). However it is first necessary to briefly summarize our current understanding of warm water coral bleaching and DIN at organism, cellular and subcellular scales. A detailed account of the work summarized in the next paragraph is provided in Wooldridge (2009a).

The warm-water bleaching syndrome of the coral–algae endosymbiosis follows a sequence of algal photoinhibition, oxidative damage, and host cell membrane disruption (e.g., Gates et al. 1992, Lesser 1996, Jones et al. 1998, Warner et al. 1999). Wooldridge (2009a) proposes that the onset of this sequence is linked with a disruption to the “dark” photosynthetic reactions of the algal endosymbionts, implicating limited availability of CO2 substrate around the Rubisco enzyme (Fig. 1b). In this way, biophysical factors that cause CO2 demand to exceed CO2 supply within the coral’s intracellular milieu are identified as bleaching risk factors (Fig. 2). In terms of CO2 demand, an enlarged endosymbiont population increases the likelihood of CO2 becoming a
Figure 1. (a) Schematic overview of the internal carbon cycling that is maintained by the coral–zooxanthellae symbiosis. (b) Schematic representation of the breakdown of the symbiosis (=zooxanthellae expulsion), as triggered by a limitation of CO$_2$ substrate for the “dark” reactions of zooxanthellae photosynthesis. “P$_i$” indicates orthophosphate.

Figure 2. Schematic overview of the biophysical factors that interact to determine the demand- and supply-side dynamics for CO$_2$ substrate within the intracellular endosymbiont population. Factors that promote enlarged zooxanthellae densities increase CO$_2$ demand, while factors that promote fast zooxanthellae growth rates ultimately decrease CO$_2$ supply via ATP limitation of host “CO$_2$-concentrating mechanisms” (CCMs). Factors that can forestall ATP limitation help to maintain the CCMs. The notation $f$(factors) indicates a function of those factors; pCO$_2$ is partial pressure of CO$_2$. 

$\text{f}(\text{pCO}_2, \text{nutrients, morphology}) \rightarrow \text{f}(\text{solar irradiance, zooxanthellae density, CCM}) \rightarrow \text{CO}_2^{(\text{demand})} \rightarrow \text{CO}_2^{(\text{supply})}$

$\uparrow \text{CO}_2$ limitation

$\uparrow \text{Zooxanthellae expulsion \text{ ("bleaching")}}$

$\downarrow \text{Zooxanthellae (re)}\text{growth}$

$\downarrow \text{Photosynthate transfer}$

$\downarrow \text{ATP}_{\text{host}}$

$\downarrow \text{CCM}_{\text{host}}$

Self-enhancing “bleaching” response
limiting internal substrate during periods of peak photosynthesis (discussed by Dubinsky et al. 1990). Several factors promote enlarged endosymbiont populations (particularly on a per host cell basis), including DIN enrichment in the surrounding sea water (Muscatine et al. 1998), partial pressure of CO$_2$, pCO$_2$, enrichment in the surrounding sea water (Reynaud et al. 2003), and diffusive (i.e., branching) coral colony morphologies (Helmuth et al. 1997, Muscatine et al. 1998). Experimental manipulations confirm the higher number of zooxanthellae expelled during periods of high irradiance in corals exposed to DIN enrichment (Stimson and Kinzie 1991). However, since a coral’s total photosynthetic demand for CO$_2$ is determined by the rate of (re)growth (mitotic index, MI) (Goldman and Carpenter 1974, Strychar et al. 2004) and diffusive (i.e., branching) coral colony morphology (Wooldridge 2009a). The cellular energy (ATP) needed to activate the host CCMs is tightly coupled to the transfer of excess photosynthates from the zooxanthellae (Al-Horani et al. 2003). Subtly, this means that the zooxanthellae indirectly play a role in generating the CO$_2$ that they themselves require for photosynthesis. Therefore, should the flow of photosynthates from the zooxanthellae be disrupted, then the capacity of the coral host to energize the CCMs becomes limiting, leaving a proportion of the zooxanthellae vulnerable to CO$_2$ limitation (and expulsion); thereby further enhancing the reduction in photosynthetic flux. Wooldridge (2009a) proposes that the potential onset of this destructive self-enhancing feedback is ultimately determined by the rate of (re)growth (mitotic index, MI [%]) of the remnant zooxanthellae population following an initial irradiance-driven expulsion event. When a large number of zooxanthellae are expelled (per day) and then subsequently produced (per day), the increased respiratory cost of such turnover can lead to a negative autotrophic balance (see, e.g., Hoogenboom et al. 2006) where more carbon per day is directed into new cell production than is transferred to the coral host. This inverse relationship between photosynthetic transfer and symbiotic MI has been documented in corals, sea anemones, and jellyfish (Verde and McCloskey 1996, McGuire and Szmaint 1997, Sachs and Wilcox 2006). Hot water and high irradiance drive high zooxanthellae MI (Goldman and Carpenter 1974, Strychar et al. 2004) but only so long as DIN is not limiting to cell multiplication (Fitt 2000).

In this way, it is understood that upper thermal bleaching thresholds are not static, but rather, are directly related to the growth dynamic of the endosymbiont population. Thermal (kinetic) increases in MI are exacerbated by a surfeit of external seawater DIN, which leads to the entire bleaching syndrome at a lower temperature than would be the case in the absence of excess DIN. With that as our premise, we now consider its implications for populations, communities and reefscapes. First, we explore the hypotheses that, compared to analyses based on temperature alone, inclusion of DIN as a causative factor substantially increases the explained variability in complex patterns of coral bleaching documented on the GBR in 1998 and 2002. Second, we develop the proposition that substantial reduction of coastal DIN, as is currently being pursued for GBR waters, will have a serendipitous benefit of increasing the tolerance of corals to temperatures they currently find intolerable.

**METHODS**

We used a spatially explicit Bayesian belief network (BBN) model (Pearl 1988, Wooldridge and Done 2004) to investigate the benefits of inclusion of DIN in explaining and predicting variability in complex patterns of coral bleaching documented on the GBR in 1998 and 2002. The data set included (1) geographic patterns of coral bleaching observed during aerial surveys of ~1300 reefs (Berkelmans et al. 2004), (2) the maximum SST occurring at each reef over any three-day period (max3d) in those bleaching periods as a proxy for heat stress (Fig. 3c), (3) decadal average summer SST at each reef as a proxy for thermal history (Fig. 3a), and (4) an index of water quality at each reef based on the inverse risk of exposure to DIN-rich terrestrial runoff (Fig. 3b).

Further description of the methods of data collection, analysis, and proxy justification is provided as supplementary material (see Appendix B).

We used the Netica software package (Norsys Software, Vancouver, British Columbia, Canada) to build a BBN that describes how measurable attributes at each reef (max3d, water quality index, mean summer maximum SST), and inferred (bleaching resistance) reef attributes combine to influence bleaching status (i.e. presence/absence; Fig. 3e). The BBN visualizes the dependency relationships as arcs between our proxy indicator variables, which are represented in the BBN as multi-state nodes. The arcs connecting the nodes are directional and point from parent nodes to child nodes, i.e., the intuitive meaning of a directed link is that the parent node has a direct influence on the child node. The absence of a link between two variables indicates conditional independence between them. The strength (i.e., certainty) of the dependency link between a child and its parent node(s) is summarized through a conditional probability table (CPT). The CPT specifies the conditional probability of the child node being in a particular state, given the states of all of its parents (i.e., $P(\text{child} \mid \text{parent}_1, \text{parent}_2, \ldots, \text{parent}_n)$) and aims to reflect the fact that some states in the model domain will tend to occur more frequently when other states are also present.
Fig. 3. Data sets, tools, and predictions along the Great Barrier Reef (GBR). (a) Thermal history index based on the typical maximum summer sea surface temperature (SST). (b) Water quality index based on the inverse risk of exposure to terrestrial runoff that is rich in dissolved inorganic nitrogen (DIN). (c) Heat stress index based on maximum SST occurring over any three-day period (max3d) during summer of 1998. (d) Predicted areas of low resistance to coral bleaching (in red). (e) Bayesian belief network showing how (a), (b), and (c), were used to predict (d). (f) Temperature-dependent probability of coral bleaching in the “low resistance” (red) and “not low resistance” area (green) in (d). For any given temperature, improved water quality reduces the probability of bleaching ($P_{\text{bleaching}}$).
We populated the CPTs based on the ~1300 reef (bleaching) responses observed during 1998 and 2002 bleaching events on the GBR, and the measurable proxy variables of water quality, thermal history, and heat stress at each of those reefs. Bleaching resistance (Fig. 3e) is an “unobservable” attribute generated by the model using the expectation maximization (EM) algorithm (Dempster et al. 1977). Its bimodal behavior (high resistance; low resistance) was learned based on the conditional interactions between the measurable proxy variables and “bleaching” response, i.e., the EM algorithm searched over the CPTs to maximize the probability of the data (bleaching response) given the dependence-structured network. The calibrated BBN allowed our site-specific observations (i.e., parent states) to be propagated throughout the network via a probabilistic inference algorithm (Lauritzen and Spiegelhalter 1988), the key output being the likelihood of different states in our “bleaching” node (Fig. 3e). Finally, the bidirectional reasoning feature of the BBN was used to diagnose the most likely states of water quality and thermal history that lead to high or low bleaching resistance.

RESULTS

Previous analysis of the aerial survey data (Berkelmans et al. 2004) had shown that the max3d indicator of short-term heat stress alone was an excellent predictor of bleaching likelihood (presence or absence), with a predictive accuracy of 73% (SD = 2.0%). We improved this predictive capacity to 84% (SD = 1.41%) by inclusion in the BBN of water quality (Fig. 2b) and thermal history (Fig. 2a), the former of which is potentially amenable to local reef management. Within the BBN, the system states of water quality explained 68% of the (relative) belief variance of resistance while thermal history explained only 32%. The higher predictive significance of water quality is reflected in the spatially interpolated pattern of the bleaching resistance states. For example, zones with high probability (>0.55) of being classified low resistance (i.e., high sensitivity to heat stress) display strong spatial coherence with the low water quality state (Fig. 3d). However, back propagation of the BBN confirmed the subtle (conditional) importance of thermal history for classifying bleaching resistance, despite its relatively low explanatory power (32%) as a stand alone parent. For example, low resistance was found to be most probable at low water quality and high thermal history sites, whereas high resistance was most probable at high water quality and low thermal history sites. Spatial interrogation of the original (observed) bleaching response data from within (and outside) the zone of low resistance was used to generate functions of differential susceptibility to heat stress (Fig. 3f). These two-parameter Weibull functions show that the onset of bleaching occurs at a temperature ~1.0–1.5°C higher for reefs in the high resistance domain than those in the low resistance domain.

DISCUSSION

The coral-zooxanthellae endosymbiosis is highly adapted to clear, nutrient-poor (oligotrophic) waters, where the rate of proliferation of in hospite zooxanthellae populations is nitrogen limited (Hallock 2001). Nitrogen limitation ensures that photosynthetic carbon assimilation and its retention for zooxanthellae growth are sufficiently out of balance that there is a vitally important transfer of (excess) energy-rich photosynthates to the coral host, fueling its production of tissues, skeleton, and gametes (Dubinsky and Jokiel 1994, Dubinsky and Berman-Frank 2001). Moreover, the continuity in supply of metabolically cheap photosynthate represents a crucial element in forestalling the bleaching syndrome (Wooldridge 2009a). The progressive (self-enhancing) reduction in photosyntheate transfer caused by temperature- and irradiance-driven zooxanthellae turnover (i.e., expulsion and regrowth) is exacerbated by any surfeit of external seawater DIN that releases the zooxanthellae from their growth-limited state, and leads to the entire bleaching syndrome at a lower temperature than would be the case in the absence of excess DIN.

In our analysis, we showed that corals bathed in nutrient-rich coastal waters had a decreased bleaching resistance (per degree of heating) during the 1998 and 2002 bleaching events compared to reefs in oligotrophic oceanic waters, effectively lowering the upper thermal bleaching threshold by ~1.0–1.5°C (Fig. 3f). A complementary investigation suggests these figures could be as much as 2.0–2.5°C in the most DIN-enriched locations (Wooldridge 2009b). These findings are consistent observations that global reef locations that exhibit naturally high (>33°C) upper thermal bleaching thresholds generally have extremely low summer nutrient regimes (e.g., Red Sea; Genin et al. 1995). More importantly, the findings confirm that coral reef management interventions that seek to cause nutrients to become limiting to proliferation of benthic algae on reefs also have a strong rational basis as a bleaching prevention strategy.

Terrestrial runoff is not the only source of DIN that impacts upon the GBR, with periodic upwelling of deep (nutrient-rich) oceanic water often a dominating feature on the outer-shelf reefs (Andrews and Gentien 1982). Field observations from elsewhere around the world suggest that reefs which are exposed to nutrient upwelling also have enhanced thermal bleaching impacts (D’Croz et al. 2001). Clearly, the influence of oceanic (upwelled) DIN on bleaching sensitivity remains outside the realm of management, so coral reef management interventions will be most effective on the inner-shelf reefs of the GBR where terrestrial nutrients sources are most often the dominating influence (Wooldridge et al. 2006). However, a better understanding of the spatio-
temporal dynamics of DIN loading across the entire GBR is necessary for identifying those areas most vulnerable to heat stress. Within the GBR, DIN loading is typically highest at coastal locations that are exposed to terrestrial runoff, lowest at mid-shelf locations, and moderate at offshore (upwelling) locations (see, e.g., Sammarco et al. 1999). All things being equal, it is therefore predicted that the mid-shelf reefs of the GBR should display the highest resistance to heat stress.

However, all things are not equal, and we note in particular the existence of different zooxanthellae strains (clades) with different kinetic growth dynamics (Fitt 1985, Kinzie et al. 2001). The Wooldridge (2009a) model predicts that for maximum heat resistance it would be advantageous for the symbiosis to be dominated by zooxanthellae with a slow growth dynamic, such as clade D (M. J. H. van Oppen, unpublished data). The superior heat tolerance of corals that harbor clade D zooxanthellae (see, e.g., Berkelmans and van Oppen 2006) is therefore consistent with MI being an important consideration in defining upper thermal bleaching thresholds. It follows that areas exposed to high summer nutrient loads and heat stress should differentially favor the presence of clade D symbionts. Indeed, following the 2002 GBR bleaching event, the occurrence of clade D symbionts was highest on inshore reef sites that experience high nutrient loads, and extremely rare on the mid-shelf reefs (van Oppen et al. 2005). A similar spatial pattern has been noted in Panama (Caribbean Sea), where clade D symbionts dominate the coastal and deep offshore (potential upwelling) locations (Toller et al. 2001).

All is not equal also in relation to the specific risk of exposure to terrestrial runoff. In the present study, the calculation of this exposure risk was based on a quantitative expectation that flood plumes reach and deliver new nutrients to a reef (Devlin et al. 2003). This approach provides a useful indicator for the long-run-averaged summer condition, but the potential exists for this exposure risk to dynamically vary in response to flood-plume specific differences in the extent of cross-shelf dispersion. Furthermore, on the GBR the initial enriching impact of a flood plume is experienced as a short-term (days to weeks) pulse of high DIN water (Devlin and Brodie 2005). This flux of inorganic nutrients is subsequently recycled through pelagic food webs (e.g., via nitrification), which maintains a longer-term (weeks to months) persistence of the initial enriching impact, all be it at progressively lower levels of DIN availability (Alongi and McKinnon 2005). In this way, a coral’s bleaching resistance to heat stress may also display subtle temporal dynamics based on the specific timing of a flood in relation to a heat wave. The intensity of summer upwelling events on the GBR will vary on an annual basis. Clearly, the predictive capacity of the present BBN model for offshore sites could be improved by the development of a water quality index that captures the dominant GBR upwelling zones.

The thermal history of a site is often considered to be a fundamental determinant of a coral’s bleaching resistance to heat stress, with cooler-water acclimated corals often being more sensitive than warm-water acclimated corals (see, e.g., Coles and Brown 2003). For the present study, we observed the opposing outcome, with (1) the most bleaching-resistant corals being those that were acclimatized to cool, low-nutrient (oceanic) conditions and (2) the least bleaching-resistant corals being those that were acclimatized to warm, high-nutrient (coastal) conditions. Cooler conditions lead to lower zooxanthellae turnover and MI, which according to Wooldridge (2009a) better facilitates the accumulation of tissue stores that can be drawn upon to provide sustained offset to the autotrophic disruption that underpins the warm-water bleaching response (see Fig. 2). This is consistent with the higher bleaching resistance of corals that maintain thick tissue reserves (Loya et al. 2001). For reef sites that have upwelling as the dominant physical feature responsible for their cool summer thermal regime, we suggest that our generalized resistance response may be limiting.

The new conceptual picture that emerges from this paper is of the fundamental importance of nutrient loading, in particular DIN, in defining the bleaching resistance of corals to heat stress (Fig. 4). A federally funded program to reduce ambient DIN loads to reef waters is being implemented with a view to lessening the
fertilization of benthic algae and their propensity to overwhelm coral reefs (Anonymous 2007). With this analysis, we have shown that these actions also represent a rational strategy for ameliorating climate change effects on coral reefs, raising the temperature thresholds that cause corals to bleach, and reducing bleaching probability across the whole range of temperatures predicted for the inshore GBR by 2100.

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Literature Cited


APPENDIX A
Schematic overview of the active “CO₂-concentrating mechanisms” of the coral host (Ecological Archives A019-060-A1).

APPENDIX B
Development and justification of the proxy indicators used to describe Great Barrier Reef system dynamics (Ecological Archives A019-060-A2).