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COMMENT/RESPONSE

Climate change and coral reefs: Trojan horse or false prophecy?

A response to Maynard et al. (2008)

O. Hoegh-Guldberg

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Abstract Maynard et al. (Coral Reefs 27:745–749, 2008a) claim that much of the concern about the impacts of climate change on coral reefs has been "based on essentially untested assumptions regarding reefs and their capacity to cope with future climate change". If correct, this claim has important implications for whether or not climate change represents the largest long-term threat to the sustainability of coral reefs, especially given their ad hominem argument that many coral reef scientists are guilty of "popularising worst-case scenarios" at the expense of truth. This article looks critically at the claims made by Maynard et al. (Coral Reefs 27:745–749, 2008a) and comes to a very different conclusion, with the thrust and veracity of their argument being called into question. Contrary to the fears of Grigg (Coral Reefs 11:183–186, 1992), who originally made reference to the Cassandra syndrome due to his concern about the sensationalisation of science, the proposition that coral reefs face enormous challenges from climate change and ocean acidification has and is being established through "careful experimentation, long-term monitoring and objective interpretation". While this is reassuring, coral reef ecosystems continue to face major challenges from ocean warming and acidification. Given this, it is an imperative that scientists continue to maintain the rigour of their research and to communicate their conclusions as widely and clearly as possible. Given the shortage of time and the magnitude of the problem, there is little time to spare.

Keywords Climate change · Ocean acidification · Corals · Fish · Bleaching · Cassandra syndrome

Introduction

Cassandra, the Princess of Troy, was so beautiful that the god Apollo gave her the gift of prophecy in return for her love. Things did not work out though, and Apollo was dumped, spurring him to punish Cassandra by proclaiming her prophecies as false. Cassandra, however, would foresee the destruction of Troy and desperately try to warn the Trojans of the perils of the wooden horse. They did not listen, and the city of Troy was destroyed. Deriving from myth, the term 'Cassandra syndrome' is used to describe people who see the future but are not believed or are powerless to act. Grigg (1992) used the Cassandra syndrome to warn our profession of the pitfalls of sensationalising science over and above the evidence. It is an important point, especially given the history of some research areas (e.g., *Acanthaster*) where sensational claims have been made but clearly have not come to pass (Grigg 1992).

Grigg wrote the original perspective over his concern that the growing alarm over the potential destruction of coral reefs by global warming might travel a similar road to that associated with the sensational claims with respect to the *Acanthaster* issue. At the time Grigg penned his opinion piece, coral bleaching had not been reported in his home state of Hawaii, and catastrophic events such as the worldwide episode of coral bleaching in 1997–1998 had not yet occurred. Grigg was also sceptical, as were many,

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O. Hoegh-Guldberg (✉)
Centre for Marine Studies, ARC Centre for Excellence for Coral Reef Studies, St. Lucia, QLD 4072, Australia
e-mail: oveh@uq.edu.au

O. Hoegh-Guldberg
Coral Reef Targeted Research Project, The University of Queensland, St. Lucia, QLD 4072, Australia

over the linkage between global warming and atmospheric CO_2. Since that time, however, our understanding of the threats to coral reefs by a rapidly changing climate and acidifying ocean has grown enormously and considerable amounts of experimental and field evidence has accumulated (Hoegh-Guldberg and Smith 1989; Glynn 1996; Brown 1997; Jones et al. 1997; Hoegh-Guldberg 1999; Berkelmans 2002; Douglas 2003; Raven et al. 2005; Kleypas and Langdon 2006; Bruno and Selig 2007; Hoegh-Guldberg et al. 2007; Lesser 2007) These perspectives have led to the widely held conclusion that the future of coral reefs as functional ecosystems is in doubt if oceans continue to warm and acidify at rates which are unprecedented in the past 420,000 years at least (Hoegh-Guldberg et al. 2007).

Maynard et al. (2008a) pick up on Grigg's concern and challenge key propositions underpinning the conclusion that the future of coral reefs is in doubt in a business-as-usual high CO_2 world. In reference to the many scientists who have concluded this, they ask, "are they, like Cassandra, correct, or are these the false prophets that Grigg (1992) warned us of 15 years ago?" To answer this question, Maynard et al. (2008a) reviewed four key propositions, and claim that the available evidence does not support the notion that coral reefs face functional extinction from rapid climate change. They suggest that a number of alternative viewpoints can be supported instead.

The present article explores the evidence and conclusions of Maynard et al. (2008a) and finds both wanting. It also finds the supposition that the current climate projections for coral reefs are "either unsupported by existing data or have yet to be thoroughly tested" to be poorly supported. While more research is always desirable, a broader examination of the literature strongly supports the notion that coral reefs are rapidly facing conditions which may soon remove them as functional ecosystems within tropical oceans.

Proposition 1. All corals are living close to their upper thermal limits

One of the key characteristics of reef-building corals is their sensitivity to small increases above the summer maximum temperature at any one location. This tight causal relationship is epitomised by the fact that the 'Hotspot' program at National Oceanic and Atmospheric Administration (Toscano et al. 2000) accurately predicts coral bleaching when sea temperatures rises 1°C above the long-term summer sea surface temperature. Coral bleaching at this stage usually involves a visible number of corals. While occasionally these predictions may fail for reasons associated with variability in other secondary factors such as light (Mumby et al. 2001), the relationship delivers accurate information more than 90% of the time. Further increases in sea temperature will trigger larger bleaching responses, with 2°C for 4 weeks or more causing most species of coral to bleach. Given the small size of the thermal anomalies (1–2°C) that will result in widespread coral bleaching, it seems hard to dispute the conclusion that most corals are living close to their thermal limits. It is important to be mindful, however, that the general reef-scale responses inherent in the current reporting of bleaching events do not represent the complete set responses of corals and that some few coral species may not bleach when the majority of the community do. Some corals may also persist in sub-habitats that may experience higher temperatures (e.g., warm intertidal pools) and hence have higher thermal thresholds. Whether these normally rare physiological types can play a role in the rapid evolution of coral reef communities is uncertain at best.

Maynard et al. (2008a) focused on the differences between species, presumably to show that some species of corals are not living close to their upper thermal thresholds. The variability of corals with respect to thermal stress has been reported numerous times (Hoegh-Guldberg and Salvat 1995; Marshall and Baird 2000; Loya et al. 2001) and shows a consistent pattern whereby corals such as *Acropora* and *Stylophora* are among the first to bleach while other corals such as *Porites* are usually able to survive slightly higher sea temperature (usually another 1–2°C) before bleaching becomes visible. These differences between species are small, however, compared with projections of future sea temperatures (IPCC 2007). As part of this discussion, Maynard et al. (2008a) state that in the absence of an adaptive response, a change in the relative abundance of species is a far more likely outcome of climate change than the disappearance of reef corals. This agrees with the sentiments of Hoegh-Guldberg et al. (2007) and others who have concluded that projected scenarios of climate change will result in different yet less diverse reef communities in the short-term, with the important caveat that these changed reef communities will eventually disappear if sea temperatures continue to rise rapidly. The key point here is that species extinction and the loss of biodiversity are not adaptive strategies per se. It is also important to note that while corals can survive acute short-term exposures over a few hours (Hoegh-Guldberg and Smith 1989; Takahashi et al. 2004) there are no examples of coral species or genotype that can survive chronic exposures to 3–6°C increases above the summer sea temperature for more than a month at a particular site. Given that average sea temperatures surrounding coral reefs are projected increase by 3–6°C by the end of the century (IPCC 2007), this level of variability in thermal stress tolerance will not be enough for coral communities to survive current business-as-usual greenhouse scenarios. As a final point, the small-scale variability in thermal tolerance among corals due to sub-habitat differences (e.g., in exceptionally warm intertidal pools or back reef areas) does not necessarily resolve the problem that corals face given that elevated temperatures will be relative to the temperature of the sub-habitat that corals experience. These warmer than normal environments tend to also increase by a set amount above 'ambient' during warm periods, placing these corals under more or less the same stress to those in more average reef sub-habitats.

Proposition 2. Corals cannot adapt or acclimate to projected rates of change

A key issue that is raised continuously but has minimal relevance in discussions of corals and their ability to tolerate future climates is that of acclimatisation ('acclimate', Maynard et al. 2008b). Acclimatisation is a form of phenotypic plasticity whereby organisms such as corals and their symbionts can optimise their physiological performance in response to environmental changes within their tolerance range (Coles and Brown 2003). There are a growing number of studies that have shown that corals will have slightly higher thermal tolerances if they are exposed to several weeks of higher temperatures prior to the temperature stress event (e.g., Middlebrook et al. 2008). Crucially, however, acclimatisation does not give an organism a completely new set of capabilities, or improve its ability to deal with conditions outside its thermal tolerance range. Consequently, it is not part of the micro-evolutionary mechanisms that are required for adjusting the reactive norm to the novel conditions imposed by climate change, as emphasised by Visser and others (2008). As a result, further discussion here will focus on the ability of corals to genetically adapt rather than acclimatise to projected rates of change.

With respect to the ability of corals to adapt to higher temperatures, Maynard et al. (2008a) point to the geographical variability in bleaching thresholds as circumstantial evidence of the ongoing evolution of temperature tolerance in both coral species and communities. This feature of coral populations has never been disputed before (e.g., "different thermal optima and maxima suggests that corals have adapted genetically to different thermal regimes", Hoegh-Guldberg 1999; see also other work by Berkelmans 2002 and others) and was first experimentally documented by Coles et al. (1976). The problem of using these geographical differences as evidence that coral populations can evolve to keep pace with climate change, however, is that the rate at which these evolutionary changes have occurred is unknown (and likely to be long given the complexity of adapting to elevated temperature). As discussed below, evidence that evolution can demonstrably keep up with the rate of climate change is lacking or ambiguous at best.

In *lieu* of having measures of the evolutionary rate of corals, Hoegh-Guldberg et al. (2007) discuss a number of life history and biological constraints that are likely to limit the rate at which corals can evolve. One of the key obstacles to rapid evolution in reef-building corals is their relatively long generation times as compared with other organisms such as bacteria (~20 min) and *Drosophila* (7 days at 29°C). Maynard et al. (2008a) take issue with this position and point to the fact that the age of first fecundity of some corals (in their single example, *Stylophora pistillata*) occurs at the end of the first year. Closer inspection of the literature reveals that most corals have generation times longer than 3 years (e.g., *Acropora*, (Wallace 1985), with a large number having generation times between 33 and 37 years (Babcock 1991), and some having generation time of over 100 years, e.g., *Porites* (Potts et al. 1985). These estimates include the complication that reproductive condition and hence gamete output is highly dependent on colony size; hence major reproductive contributions to coral populations by new arrivals or naturally selected genotypes may not occur until many years or decades later. These characteristics do not favour rapid evolutionary change in response to rapidly changing sea temperatures especially where many generations are required to significantly shift the reactive norm (>10 generations; Skelly et al. 2007). Consequently, the geographical differences in thermal tolerance are unlikely to have arisen over the short timescales required to keep pace with climate change.

The migration of corals and their symbionts (i.e. gene flow) has also potential to influence the genetic makeup of a population at a particular location. Ultimately, the migration or dispersal of corals depends on two issues. First, localised recruitment is required for local adaptation of coral populations. Second, dispersal distances are critically important in estimates of how far genotypes can travel each generation; a factor determining ultimately how far corals are likely to be able to migrate over time. Most of the evidence suggests that dispersal distances are of the order of 5–100 km (Underwood et al. 2007), supporting the idea that local adaptation can occur to physical variables such as temperature. The issue of dispersal distances not being as large as originally thought (Hughes et al. 1992; Hughes 2000) also constrains the speed with which corals can migrate from one area to another. Given the importance of understanding whether organisms can migrate in response to climate change, it becomes apparent that these shorter distances present problems with respect to the flow of potentially warm adapted genotypes to higher latitudes. Latitudinal gradients in temperature are in the vicinity of 1.5°C per thousand kilometres, which suggests considerable distances (over 20 km) need to be travelled by genotypes each year to keep pace with projected changes in sea temperatures of 3°C over the next 100 years. Add to this, the impacts of thermal stress reducing reproductive output and hence gamete production (Szmant and Gassman 1990; Lasker and Coffroth 1999; Baird and Marshall 2002) and the idea of a rapid movement of warm genotypes to higher latitudes in time for the current projected changes of 3–6°C (IPCC 2007) become highly unlikely. As discussed by several authors (Guinotte et al. 2003; Hoegh-Guldberg et al. 2007), the associated decrease in carbonate ion concentrations at higher latitudes as atmospheric carbon dioxide spirals upwards makes any significant poleward migration of reef-building corals unlikely.

In a final attempt to demonstrate that corals can adapt quickly enough to climate change, Maynard et al. (2008a) point to two studies which they say demonstrate that bleaching mortality rates have declined and thermal tolerance has increased in some regions. The first is Glynn et al. (2001) which Maynard et al. (2008) claims demonstrate that fewer corals died in the 1997–1998 mass bleaching event than the one in 1982–1983 because corals had become more tolerant to thermal stress. A detailed reading of the Glynn et al. (2001)'s excellent article, however, reveals a complex range of factors that vary between the two events, a situation which led Glynn et al. (2001) to state that they were not in a position to (and correctly did not do so as a result) conclude that there had been a widespread change in thermal tolerance of corals in the region. The second piece of evidence, Maynard et al. (2008a) use as evidence of the coral thermal tolerance evolving with sea temperature, is the observed decrease in the sensitivity of corals between 1998 and 2002. This article is a useful contribution but lacks the necessary precision given that corals are only distinguished to the level of two genera *Acropora* and *Pocillopora* (Maynard et al. 2008b). Consequently, the conclusions are confounded by the possibility of species-specific mortality within two genera leading to community change rather than evolutionary adaptation. Given that there is considerable variation within these genera with respect to thermal tolerance, it is not possible to separate individual species impacts from more general shift in the sensitivity of coral communities to thermal stress.

The observations of Maynard et al. (2008b) that different responses of communities of corals are not surprising (as discussed earlier), and are useful in understanding of the sorts of changes that are occurring in the early stages of major climate change (Maynard et al. 2008b). There is little doubt that microevolution is and will occur as a result of global climate change (Visser 2008). The important issue here, however, is whether the observed shifts in allele frequencies within a population are due to new genes arising from mutation and/or migration, or to the elimination of alleles from population. Under the first set of processes, populations could potentially continue to increase their thermal thresholds in situations where the changes are fast enough to keep up with the rate of change. Under the current very rapid rates of climate change (100–1,000 times that of the most rapid environment of changes over the past 420,000 years at least; Hoegh-Guldberg et al. 2007), these slow rates of evolutionary change are unlikely to keep pace. Within the second set of processes, sensitive genotypes will be lost from the population, narrowing genetic diversity and shifting allele frequencies to fewer more tolerant types. This type of change has its downsides, however, in terms of reducing the resilience of populations to other factors such as disease and competition. Also, as argued above, temperature increases are likely to continue, resulting in a continual narrowing of genes frequencies over time until the variability within the population has been exhausted and corals disappear. It is important to remember that corals that can survive chronic long-term changes that are 3–6°C above long-term summer temperature maxima are extremely rare and have not been observed despite a considerable number of experiments investigating thermal thresholds (Hoegh-Guldberg and Smith 1989; Jones et al. 1998; Hoegh-Guldberg and Jones 1999; Berkelmans and van Oppen 2006; Ulstrup et al. 2006; Middlebrook et al. 2008; Oliver et al. 2009). This would suggest that the ability of coral populations to shift to future sea temperatures of this magnitude (expected by the end of the century under the current greenhouse trajectory; IPCC 2007) is extremely limited or nonexistent.

Proposition 3. Trade-offs resulting from ocean acidification lead to reduced fecundity

Ocean acidification represents an additional stress for corals to cope with in addition to the unprecedented changes in sea temperature. Coral reefs are already in novel circumstances with respect to temperature and carbonate ion concentrations that are outside those that they have experienced for the past 420,000 years at least (Hoegh-Guldberg et al. 2007). The projected changes in acidification will continue to affect growth, calcification and a range of other physiological processes as a result of changes in the carbonate ion chemistry and pH of seawater (Raven et al. 2005; Kleypas and Langdon 2006; Portner and Farrell 2008). Recent evidence has demonstrated that ocean acidification is likely to increase the sensitivity of reef-building corals to elevated temperature, reducing the temperature thresholds quite dramatically (Anthony et al. 2008). While we are unsure of the entire range and intensity of impacts arising from ocean acidification, they are likely to add rather than remove stress from reef-building corals (as claimed by Maynard et al. 2008a). This is supported by direct evidence from in situ records of coral calcification, which show an abrupt downturn in calcification and linear extension of massive corals on the Great Barrier Reef (Cooper et al. 2008; De'ath et al. 2009) and in Thailand (Tanzil et al. 2009) over recent decades. Whilst Maynard et al. (2008a) further suggest that high initial energy levels may reduce mortality risk from bleaching (Anthony et al. 2007), recent research shows that ocean acidification causes significant decreases in productivity and increases coral sensitivity to bleaching (Anthony et al. 2008), further impacting upon the energy reserves of corals.

Whilst mesocosm experiments suggest that gametogenesis and recruitment are not significantly impacted upon under projected pCO_2 conditions (Fine and Tchernov 2007; Albright et al. 2008; Kuffner et al. 2008), post-settlement skeletal extension is reduced by over 50% (Albright et al. 2008). More recent experimental results suggest that ocean acidification impacts a range of reproductive stages, including the suppression of egg production in marine shrimp (Kurihara et al. 2008) and significant reductions in hatching success in copepods (Mayor et al. 2007). The absence of evidence on this issue is largely due to a lack of research rather than confirmation that ocean acidification does not compromise the physiology and energetics of corals. Reviews such as those undertaken by Raven et al. (2005), Kleypas and Langdon (2006) and Portner and Farrell (2008) conclude the exact opposite to Maynard et al. (2008a).

Proposition 4. Climate induced coral loss leads to widespread fisheries collapse

This proposition is not essential for us to conclude that coral reefs face an uncertain future. It has, however, important implications for how the loss of reef structure will impact other organisms such as fish and is worth responding to for these reasons alone. Despite admitting that there is considerable uncertainty, Maynard et al. (2008a) state that only a few (10–12%) species of fish that are reliant on corals for food and shelter will be affected, and that none of these are important fishery species. The latter conflicts directly with the importance of benthic reef fish, which are not involved formally in a fishery per se, but that are crucially important for tens of millions of subsistence fishers throughout the tropics (FAO 2001). Maynard et al. (2008a) concede the importance of reef rugosity to fish abundance and diversity, but conclude that decreases in the rugosity of reefs “do not always occur, and depend on relative contributions of contemporary coral growth versus erosion of the underlying reef framework”. Given that there are serious threats to coral abundance (discussed above), and a host of examples of where corals have, and are disappearing as reef calcifiers disappear and where reef rugosity is clearly under threat (see studies referenced by Bruno and Selig 2007), this conclusion seems out of step with most of the evidence. Maynard et al. (2008a) also neglect to appreciate the important contributions of non-coral calcifiers on coral reefs (e.g., calcareous algae), and their relative sensitivity to ocean acidification (Anthony et al. 2008; Kuffner et al. 2008). In addition to this, there is growing evidence that bioerosion (the other side of the reef carbonate equilibrium) increases as pH decreases (Przeslawski et al. 2008) further tipping the balance towards crumbling reef frameworks. There are plenty of examples from the Eastern Pacific that illustrate the outcome for reef structures if calcifiers such as corals and red coralline algae are reduced in number (Glynn 2000; Manzello et al. 2008). Ultimately, the loss of calcifiers for long periods under high levels of atmospheric CO_2 suggest that reef structures are vulnerable in the longer term (century), irrespective of whether they survive at shorter timescales (decadal). These examples and conclusions conflict with the inference of Maynard et al. (2008a) that reef structures are somehow immune to the impacts of rapid global change, and hence their loss does not represent a threat to fish, fisheries and people.

The role of science in a rapidly changing world

Cassandra's prophecy warned of the dangers of the Trojan horse yet was ignored with tragic consequences for Troy and its people. Similarly, many scientists are warning of the consequences for key ecosystems such as coral reefs if we continue down the pathway of unrestrained growth in atmospheric CO_2 (Glynn 1996; Brown 1997; Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2007; IPCC 2007). Grigg (1992) warned of the need to explore the issues associated with coral bleaching and global warming using “careful experimentation, long-term monitoring and objective interpretation”. Contrary to the opinion of Maynard et al. (2008a), this has been the *modus operandi* and our understanding of the drivers and the impacts associated with global climate change has made impressive and rigorous progress over the past 15 years. While more research is certainly needed to fill the gaps and uncertainties with respect to how the next few decades and century will unfold, there is little support for the conclusion that coral reefs will survive atmospheric carbon dioxide levels of 600–1000 ppm and increases in ocean temperatures of 2–6°C. For this reason, and the fact that we are currently on a pathway headed towards 1,000 ppm and beyond, we must also strive to communicate the extreme urgency of the situation to the broader scientific and non-science community, and to urge the international community to rein in the emission of carbon dioxide and other greenhouse gases. This will take measures that go far beyond those that have been proposed so far by the international community and will only come about if governments understand the dire circumstances that the world faces if we lose coral reefs and other critically important parts of the biosphere. Hopefully, a clear, objective and coherent voice from the coral reef community will be listened to. We can only hope.

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