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Corresponding Author: Dr. Ove Hoegh-Guldberg,

Corresponding Author's Institution:

First Author: Ove Hoegh-Guldberg

Order of Authors: Ove Hoegh-Guldberg

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- Coral reefs are considered in the context of acclimatisation, evolution and migration.
- Evidence that these processes play a major role in reducing climate change is minimal.
- In contrast, coral reef ecosystems are rapidly declining across the world.
- Implementing solutions to local factors will buy important time and is essential.
- Future sustainability of coral reefs depends on a rapid decrease in CO_2 emissions.

Title:

Coral reef sustainability through adaptation: Glimmer of hope or persistent mirage?

Short title:

Coral reef adaptation: glimmer of hope or mirage?

Author, affiliation and permanent address:

Ove Hoegh-Guldberg*

Global Change Institute

Building 20, University of Queensland

St Lucia 4072 Queensland, Australia

Ph: +61 7 3365 1156

Email: oveh@uq.edu.au

**Corresponding author*

Abstract:

Coral reefs are highly threatened by human activities at both global (ocean warming and acidification) and local scales (overfishing, pollution, and physical destruction) as current rates of environmental change exceed those seen for tens of millions of years. Recent authors, however, have suggested that coral reefs might increase their tolerance to these rapid environmental changes through acclimatisation, genetic adaptation, and migration. While there is evidence of all three responses acting within coral populations, there is little basis for the conclusion that reef-building corals and coral reefs will become more sustainable and resilient over time. Most studies that make the latter claim have correctly identified components and mechanisms but have otherwise incorrectly extended evidence that is otherwise *necessary but not sufficient* to support the conclusion that coral reefs will survive to their ability to acclimatise, adapt and/or migrate to the current rapid environmental changes.

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Keywords:

Coral reefs, sustainability, acclimatisation, evolution, migration, global climate change, ocean warming, ocean acidification

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Introduction

The distribution and abundance of coral reef ecosystems is declining rapidly in response to rapid changes to the environment that surrounds them. It has been Proposed [1] that "evidence for the ability of individuals or communities to adaptively respond to thermal stress suggests that bleaching thresholds may increase in response to climate warming". This is an important statement in that it implies we may have more time with respect to the pressures that coral reefs and related ecosystems. At its heart, is the notion that reef building corals might become partly or fully sustainable on their own to rapid global change through evolutionary processes, despite the unprecedented rates of environmental change in today's oceans. As will be argued here, however, evidence for evolutionary adaptation is scant when compared to the much more abundant evidence of rapidly declining coral populations and associated coral reef ecosystems.

Coral reefs are found throughout the world's tropics and can be separated into two broad categories based on whether or not their calcium carbonate skeletons build up over time to create the complex three-dimensional structures that typify carbonate coral reefs. Carbonate coral reefs are found in the region from 30° north or south of the equator where local physical and chemical conditions are favourable [2]. At the fringe of this distribution (in addition to regions affected by equatorial upwelling), there are often dense populations of reef-building corals that don't build carbonate reef structures [3]. While both coral reef ecosystems are typified by high levels of biological diversity, carbonate coral reefs are among the most diverse ecosystems on the planet with an estimated 1 – 9 million species [4]. Both types of reef systems provide ecosystem goods and services to human populations through support of fisheries, tourism and broader benefits such as the protection of coastal areas from waves and storm impacts [5,6].

Local and global pressures

In addition to being important in terms of their biological diversity and contributions to humanity, coral reef ecosystems are among the most highly threatened ecosystems, with coral reefs and human activities tending to collide along tropical coastlines across the world [7,8]. Currently there are at least 500 million people living along tropical coastal areas with the number expected conservatively to double by the end of century. As coastal populations have increased, coastlines have been modified, fisheries overexploited, and levels of pollution have increased rapidly [7,9,10]. Looking across the world's coral reefs, 75% are threatened [7] and as much as 95% may be in danger of being lost by mid-century [11,12]. These numbers have been reinforced by numerous analyses of literature which document rapid decreases in the size of coral populations. In Southeast Asia and the Western Pacific, coral reefs have declined by 50% since the early 1980s [13,14]. In the Caribbean, dramatic declines of well over 90% since the 1970's have been documented for coral cover on Jamaican reefs [15] and the wider Caribbean [16,17]. Similar reports exist for the Indian Ocean and other sites [18].

Carbon dioxide arising from the burning of fossil fuels as well as changes to land use have driven atmospheric concentrations of carbon dioxide to levels that have not been seen for tens of millions of years [19]. These changes have increased the retention of heat, consequently driving up planetary temperatures [Hansen et al. 2013]. At the same time, CO_2 has entered the ocean in increasing amounts leading to rapidly declining pH and carbonate ion concentrations [19-21]. These changes are occurring at a rate which is unprecedented in 65 Ma if not 300 Ma [22].

In addition to increasing coral mortality, human influences can also result in a series of cumulative impacts on fundamental parameters such as coral growth, calcification and reproduction. Reef-building corals are vulnerable to changes in the temperature and carbonate chemistry of seawater [12,23-25]. Small changes in temperature over the summer maxima (under normal light levels) will disrupt the mutualistic symbiosis between reef building corals and symbiotic dinoflagellates from the genus *Symbiodinium*, resulting in a sudden whitening of their tissues as the brown symbionts leave (i.e. bleaching, [12]). If the levels of thermal stress are small (1°C) and short-lived (3-4 weeks), bleached corals will recover over the months that follow a heat stress event [25-27]. However, if conditions of warmer (+2-3°C above the long-term summer maxima) for longer (> 6 weeks) corals will starve, suffer disease and/or die in great numbers [26,28]. Since the first reports in the 1980s, mass coral bleaching and mortality has affected the majority of coral reefs in the world often with transformative impacts on coral populations and ecosystem structure [18].

While coral bleaching, disease and mortality are significant endpoints of thermal stress, there is additional evidence of impacts on the growth and reproduction of corals. Reduced growth from thermal stress [20] and also significantly reduced reproduction of corals that experience thermal stress and bleaching [30] is reported. Changes to the carbonate chemistry of seawater as a result of ocean acidification also have impacts on growth, calcification and possibly reproduction as pH and carbonate ion concentrations decrease, with impacts have a number of life history stages of corals and related tropical organisms [23,24,31].

Previous studies of the impact of these changes on coral reefs have focused on short-term experimental exposures to changes in temperature or CO_2. Very few experiments (exception, [32], however, have involved attempts to expose communities or ecosystems to elevated temperature and CO_2, limiting our understanding of how reefs might change under future conditions that involve changes to both ocean warming and acidification. Experiments have also tended to exclude natural variability in conditions that ultimately may have significant implications for the interpretation of responses. For example, the partial pressure of CO_2 in waters flowing around Heron Island on the southern Great Barrier Reef experience increases to 450 ppm in the summer due to changing rates of reef photosynthesis and calcification [B. Tilbrooke, CSIRO *in* Dove et al 2013]. Consequently, experiments that set their CO_2 levels at constant partial pressures of 450 ppm in order to explore lower IPCC scenarios such as SRES-B1 or RCP4.5 are actually only exploring conditions typical of summer under today's conditions.

<Insert Figure 1 here>

Taking these issues on board, [33] exposed coral communities within mesocosms to replicated changes in both temperature and CO_2 levels, while at the same time incorporating diurnal and seasonal variability. The computer controlled system involves multiple replicate flow-through mesocosms which contain a small section of coral reef and which are designed to approximate the density and mix of corals and other organisms found on nearby reef crest communities at Heron Island (Figure 1). After acclimatisation, conditions in some of these 6000 L mesocosms are adjusted to different offsets across the treatments for long periods of time (3 – 24 months). The treatments investigated included Preindustrial, Control (today) as well as future scenarios SRES-B1 (~RCP4.5) and SRES-A1FI (~RCP8.5), with levels of variability that approximate those typical of a reef crest communities at Heron Island. Under preindustrial and Control (today) conditions, corals grew significantly during the experiment and the composition of the coral communities remain more of less unchanged. Under B1 (RCP4.5) and A1FI (RCP8.5) treatments, however, branching corals such as *Acropora formosa; Seriatopora hystrix; Stylophora pistillata, Montipora* sp., bleached and died by the end of the experiment. Calcification also showed significant trends with corals from B1 and A1 FI slowing to near zero in the initial part of the experiment (prior to mortality, [33]). Community calcification also declined but differed in that it decreased well below zero in the A1FI treatment. While dead coral skeletons were dissolving in these treatments, it appeared that carbonate sediments within the experiment experienced some of the largest losses of carbonate within this experiment [33]. The increase in the rate of decalcification matches the results of other experiments on two important bio-eroders, excavating sponges [34] and endolithic microalgae [35] with decalcification rates being driven up by warmer and more acidic conditions.

Responses of corals to hostile conditions: acclimatisation, evolution or migration

One way out of the dilemma that reef-building corals face is to either adjust their physiology (acclimatise), evolve via natural selection (adapt) and/or migrate as conditions become more and more hostile. In this regard, there are some interesting possibilities as to how reefs are likely to respond to rapid changes in the environment that surrounds them.

a. Acclimatisation to stress (modification of the phenotype)

Acclimatisation occurs when the phenotype of an organism is adjusted over time to better fit a change in the environment. In this way, organisms may acclimatise to new conditions which occur in a wide variety of organisms [36] including reef building corals [37]. While there is evidence that corals can adjust their thermal tolerance within their normal environmental range [38,39], there is little evidence that acclimatisation has resulted in a shift or extension of the upper thermal tolerance of reef-building corals [40]. Simply put, if acclimatisation were occurring perfectly, then corals would not be experiencing the current extensive bleaching and mortality in response to thermal stress as they would have adjusted their physiology to suit the new conditions. Some evidence exists for corals which shift the relative concentration of different clades of symbiotic dinoflagellates in order to better suit the environment [41] although these studies have shown that shifts in the proportion of symbionts may be accompanied by costs in terms of growth and relative competitiveness [42]. Recent evidence suggests that the thermal threshold used by satellites to project when and where mass coral bleaching is likely to occur may have increased over time [1]. This study is complicated by the fact that these measurements are at the community level and hence are most likely due to the loss of fragile species as opposed to acclimatisation and/or adaptation of individual species. This has been pointed out for other studies [43] that have claimed to have demonstrated shifts in tolerance due to acclimatisation or adaptation

[44]. Trans-generational acclimatisation [45], where organisms (in this case on coral reef fish) inherit greater tolerance from parents who have been previously exposed to stress (in this case higher CO_2 and lower pH), presents some interesting mechanisms for some organisms. These experiments have not been attempted with corals (which tend to have long generation times from 5 to 100 years) or with the combination of factors (i.e. ocean acidification as well is warming) that are likely to occur under future ocean warming and acidification. Nonetheless, transgenerational acclimatisation remains an intriguing area for further investigation.

b. Evolution of stress tolerance (genetic adaptation)

Evolution by natural selection has also been as a mechanism by which thermal and chemical limits of current populations may shift to become more tolerant as oceans warm and acidify. Given time, corals, like any organism are likely to adapt to local conditions, which is reflected in the widespread evidence that corals are locally adapted to temperature, be that at local [46] or geographic [47-49] scales. However, the rate of environmental change as well as extent to which stabilisation of environmental conditions occurs or not are critical factors determining whether or not the evolution of corals, and marine life in general, is likely to keep pace with anthropogenic ocean warming and acidification. The biological characteristics of the community and species are also important. In this respect, generation times as well as the amount of genetic variability within a population are critical factors determining the ability of locally adapted populations to increase their thermal tolerance. There is little doubt that organisms such as bacteria, which have short generation times (minutes to hours) and high mutation rates will be able to keep up changes to ocean conditions, even if current rates of change are unprecedented in the past 65 Ma if not 300 Ma [22]. Corals, on the other hand, have generation times from 4 to over 20 years for most corals [50] and hence do not have demographic characteristics that favour rapid evolution. The hypothesis that reef-building corals may be able to swap their symbionts for more thermally adapted varieties [51] has not been supported by the sizeable number studies that have sought to show that corals can take on truly novel symbionts that enable them to survive higher sea temperatures. These studies have also suffered from a number of other issues including the assumption that the dinoflagellate symbionts are the only factor determining the overall thermal tolerance of the mutualistic symbiosis [43,52-54].

While the evidence for the rapid evolution of corals is virtually nonexistant, there is substantial evidence for why the rapid evolution of tolerance to future environmental conditions is unlikely to occur. Firstly, the rates of environmental change exceed those seen over the past hundreds of thousands if not tens of millions of years [12,22,55]. Secondly, the generation time of organisms such as reef building corals is relatively long [50]. The third, which is often overlooked is that conditions with respect to ocean warming and acidification are set to change continuously for hundreds of years under our current emission pathway [56]. That is, we are imposing conditions that change continuously and which are not the 'step change' which would otherwise enable populations and communities to 'catch up' with the change once conditions stabilise once again. The last issue is that adaptation to thermal stress is unlikely to be simple and is likely to involve scores of genes and cellular processes that need to be adjusted [57]. Consequently, evolution of tolerance to changing temperatures and sea water chemistry is unlikely to be a simple selection process (i.e. the change in a single gene) but rather a complex set of changes across multiple genes. The probability of suitable combinations decreases geometrically as the number of genetic changes required increases.

Not surprisingly, the distribution and abundance of coral populations is decreasing rapidly in most parts of the world [13-17] under increasing levels local and global drivers of stress. This problem is exacerbated by the fact that anthropogenic ocean warming and acidification is unlikely to stabilise for many hundreds of years under current scenarios for the emission of CO_2 and methane. Until this happens, adaptation might arise within a population of corals but will not have the time required for it to spread given that the same adaptation will quite rapidly become unfit as ocean temperatures and sea water chemistry continue to change.

c. Migration of reefs to higher latitudes

The warming of ocean waters at higher latitudes is shifting the range of marine organisms from plankton to fish [58]. As waters warm at higher latitudes, conditions as far as temperature is concerned are becoming increasingly favourable for reef building corals in the short-term. This has led to the proposal at coral reefs may shift to higher latitudes over time, more or less compensating for their losses at lower latitudes. Consistent with this is evidence that the distribution of coral reefs has varied with relatively small shifts in average global temperature on the paleontological past [59,60]. There are also a number of recent observations of reef building corals showing shifts too high latitude locations (up to 14 km yr^{-1}; [59-61] in many areas of the world.

It is important to note that both pieces of evidence are *necessary but not sufficient* to support the idea that coral reef ecosystems will or are moving to higher latitudes. Paleontological examples involve warming over hundreds if not thousands of years, mostly involve situations in which reefs did not experience changes at the same time in pCO_2, pH or carbonate ion concentrations [12]. Given that anthropogenic ocean warming and acidification will involve simultaneous changes in all three parameters, the degree to which examples from the past are useful proxies for the future is at least questionable. Secondly, the degree to which the movement of coral species to higher latitudes is evidence that entire coral reef ecosystems will shift to higher latitudes is also questionable. The movement of coral reef ecosystems to higher latitudes requires a shift in the distribution and abundance of thousands of species as well is the movement of complex ecological relationships and processes. These changes also have to occur over very short periods of time. In a simple example, the Great Barrier Reef ecosystem would have to travel at the speed of 15-20 km per year to keep up with a 2°C change over the next 100 years [43]. There is no evidence of this scale of movement of a coral reef ecosystem anywhere in the literature, and certainly no evidence of the extension of the southern end of the Great Barrier Reef by 600 km, which should have already occurred given that the Great Barrier Reef waters have warmed by 0.4°C since 1950 [62].

Shifts in the distribution of coral populations depend on dispersal and the existence of heat tolerant individuals at lower latitudes that are ready to migrate into areas as they warm. As raised by BM Riegl, et al. [49], we may be approaching the limits in terms of thermal tolerance of individuals in some areas of the world such as the Arabian Gulf, where corals experience some of the highest sea temperatures globally. There are no obvious sources of more thermally tolerant corals to replace those in this area of the world as oceans warm rapidly over the coming decades and century.

Requirements for sustainability via adaptation?

In exploring the requirements for adaptation to play a role in establishing a more sustainable future for marine ecosystems such as coral reefs, it is important to consider the implications of future climate trajectories. Of the four major scenarios of the fifth assessment report of the IPCC, for example, only the scenario RCP 3.0 exhibits the stabilisation of planetary temperature over the mid to late part century. As this is a requirement for adaptation to play a role, this is the only scenario where coral reefs (indeed many other ecosystems) have a chance of persisting beyond the middle of this century. All of the other models are characterised by conditions that continue to change hence imposing rapidly changing selection pressure over time. As evolutionary rates are many organisms including reef-building coral are likely to be severely constrained by their life history characteristics (i.e. long generation times, reduced variability), the distribution and abundance of corals and coral reefs is likely to continue to decline rapidly.

Achieving sustainability through adaptation will also depend on a rapid reduction of drivers other than ocean warming and acidification. Increasing the management of local stresses such as overfishing, for example, can enhance the resilience of coral populations to climate related phenomena such as thermal stress. TP Hughes, et al. [63], for example, demonstrated that bleached coral reefs on the central Great Barrier Reef which had healthy populations of grazing fishes, for example, recovered from coral bleaching related mortality three times faster than reefs where access by grazing fishes to damaged reefs had been prevented. Exploring the possibilities of how one can boost the resilience of coral reefs and buy important time while global society deals with enhanced greenhouse warming and acidification of our planet will become increasingly important as the current century progresses.

Conclusion

It is very clear that were entering to a period in which a lack of action on local and global drivers of stress will lead to conditions and impacts on these valuable ecosystems which will take thousands of years to reverse. Evidence that corals and other organisms are, and can acclimatise, adapt and/or migrate successfully to the unprecedented rapid rates of environmental change is sparse and in the minds of some circumstances be seen as a persistent mirage. In this regard, evidence that corals will autonomously evolve into the resilience state (i.e. benefiting efforts to achieve sustainability) under the current rapid changes to the environment is not supported by the literature. On the other hand, evidence of corals are ‘losing the fight’ is widespread and is on the increase, with most long-term studies showing declines of around 50% since the early 1980s. Given the dependence of human communities on coral reefs for food, livelihoods, coastal protection and other services, these changes are likely to have serious long-term consequences for people, communities and nations. Given the long-term commitment that these changes involve, it is an imperative that we rapidly involve a global strategy in which we rapidly reduce both local and global drivers of change and thereby avoid future in which we experience the semi-permanent or permanent loss of centrally important ecosystems such as coral reefs.

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Title:

Coral reef sustainability through adaptation: Glimmer of hope or persistent mirage?

Short title:

Coral reef adaptation: glimmer of hope or mirage?

Author, affiliation and permanent address:

Ove Hoegh-Guldberg*

Global Change Institute

Building 20, University of Queensland

St Lucia 4072 Queensland, Australia

Ph: +61 7 3365 1156

Email: oveh@uq.edu.au

**Corresponding author*

Abstract:

Coral reefs are highly threatened by human activities at both global (ocean warming and acidification) and local scales (overfishing, pollution, and physical destruction) as current rates of environmental change exceed those seen for tens of millions of years. Recent authors, however, have suggested that coral reefs might increase their tolerance to these rapid environmental changes through acclimatisation, genetic adaptation, and migration. While there is evidence of all three responses acting within coral populations, there is little basis for the conclusion that reef-building corals and coral reefs will become more sustainable and resilient over time. Most studies that make the latter claim have correctly identified components and mechanisms but have otherwise incorrectly extended evidence that is otherwise *necessary but not sufficient* to support the conclusion that coral reefs will survive to their ability to acclimatise, adapt and/or migrate to the current rapid environmental changes.

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Keywords:

Coral reefs, sustainability, acclimatisation, evolution, migration, global climate change, ocean warming, ocean acidification

Highlights:

- Coral reefs are considered in the context of acclimatisation, evolution and migration.
- Evidence that these processes play a major role in reducing climate change is minimal.
- In contrast, coral reef ecosystems are rapidly declining across the world.
- Implementing solutions to local factors will buy important time and is essential.
- Future sustainability of coral reefs depends on a rapid decrease in CO_2 emissions.

Introduction

The distribution and abundance of coral reef ecosystems is declining rapidly in response to rapid changes to the environment that surrounds them. CA Logan, et al. [1], however, propose that "evidence for the ability of individuals or communities to adaptively respond to thermal stress suggests that bleaching thresholds may increase in response to climate warming". This is an important statement in that it implies we may have more time with respect to the pressures that coral reefs and related ecosystems. At its heart, is the notion that reef building corals might become partly or fully sustainable on their own to rapid global change through evolutionary processes, despite the unprecedented rates of environmental change in today's oceans. As will be argued here, however, evidence for evolutionary adaptation is scant when compared to the much more abundant evidence of rapidly declining coral populations and associated coral reef ecosystems.

Coral reefs are found throughout the world's tropics and can be separated into two broad categories based on whether or not their calcium carbonate skeletons build up over time to create the complex three-dimensional structures that typify carbonate coral reefs. Carbonate coral reefs are found in the region from 30° north or south of the equator where local physical and chemical conditions are favourable [2]. At the fringe of this distribution (in addition to regions affected by equatorial upwelling), there are often dense populations of reef-building corals that don't build carbonate reef structures [3]. While both coral reef ecosystems are typified by high levels of biological diversity, carbonate coral reefs are among the most diverse ecosystems on the planet with an estimated 1 – 9 million species [4]. Both types of reef systems provide ecosystem goods and services to human populations through support of fisheries, tourism and broader benefits such as the protection of coastal areas from waves and storm impacts [5,6].

Local and global pressures

In addition to being important in terms of their biological diversity and contributions to humanity, coral reef ecosystems are among the most highly threatened ecosystems, with coral reefs and human activities tending to collide along tropical coastlines across the world [7,8]. Currently there are at least 500 million people living along tropical coastal areas with the number expected conservatively to double by the end of century. As coastal populations have increased, coastlines have been modified, fisheries overexploited, and levels of pollution have increased rapidly [7,9,10]. Looking across the world's coral reefs, 75% is threatened [7] and as much as 95% may be in danger of being lost by mid-century [11,12]. These numbers have been reinforced by numerous analyses of literature which document rapid decreases in the size of coral populations. In Southeast Asia and the Western Pacific, coral reefs have declined by 50% since the early 1980s [13,14]. In the Caribbean, dramatic declines of well over 90% since the 1970's have been documented for Jamaican reefs [15] and the wider Caribbean [16,17]. Similar reports exist for the Indian Ocean and other sites [18].

Carbon dioxide arising from the burning of fossil fuels as well as changes to land use have driven atmospheric concentrations of carbon dioxide to levels that have not been seen for tens of millions of years [19]. These changes have increased the retention of heat driving up planetary temperatures [Hansen et al. 2013]. At the same time, CO_2 has entered the ocean in increasing amounts leading to rapidly declining pH and carbonate ion concentrations [19-21]. These changes are occurring at a rate which is unprecedented in 65 Ma if not 300 Ma [22].

In addition to increasing coral mortality, human influences can also resulted in a series of cumulative impacts on fundamental parameters such as growth, calcification and reproduction. Reef-building corals are vulnerable to changes in the temperature and carbonate chemistry of seawater [12,23-25]. Small changes in temperature over the summer maxima (under normal light levels) will disrupt the mutualistic symbiosis between reef building corals and symbiotic dinoflagellates from the genus *Symbiodinium*, resulting in a sudden whitening of their tissues as the brown symbionts leave (i.e. bleaching, [12]). If the levels of thermal stress are small (1°C) and short-lived (3-4 weeks), bleached corals will recover over the months that follow a heat stress event [25-27]. However, if conditions of warmer (+2-3°C above the long-term summer maxima) for longer (> 6 weeks) corals will starve, suffer disease and/or die in great numbers [26,28]. Since the first reports in the 1980s, mass coral bleaching and mortality has affected the majority of coral reefs in the world often with transformative impacts on coral populations and ecosystem structure [18].

While coral bleaching, disease and mortality are significant endpoints of thermal stress, there is additional evidence of impacts on the growth and reproduction of corals. T Goreau and A Macfarlane [29] reported reduced growth from thermal stress while AM Szmant and NJ Gassman [30] demonstrated that the reproduction of corals was significantly reduced in corals that experience thermal stress and bleaching. Changes to the carbonate chemistry of seawater as a result of ocean acidification also have impacts on growth, calcification and possibly reproduction as pH and carbonate ion concentrations decrease, with impacts have a number of life history stages of corals and related tropical organisms [23,24,31].

Previous studies of the impact of these changes on coral reefs have focused on short-term experimental exposures to changes in temperature or CO_2. Very few experiments (exception, [32], however, have involved attempts to expose communities or ecosystems to elevated temperature and CO_2, limiting our understanding of how reefs might change under future conditions that involve changes to both ocean warming and acidification. Experiments have also tended to exclude natural variability in conditions that ultimately may have significant implications for the interpretation of responses. For example, the partial pressure of CO_2 in waters flowing around Heron Island on the southern Great Barrier Reef experience increases to 450 ppm in the summer due to changing rates of reef photosynthesis and calcification [B. Tilbrooke, CSIRO *in* Dove et al 2013]. Consequently, experiments that set their CO_2 levels at constant partial pressures of 450 ppm in order to explore lower IPCC scenarios such as SRES-B1 or RCP4.5 are actually only exploring conditions typical of summer under today's conditions.

<Insert Figure 1 here>

Taking these issues on board, S Dove, et al. [33] exposed coral communities within mesocosms to replicated changes in both temperature and CO_2 levels, while at the same time incorporating diurnal and seasonal variability. The computer controlled system involves multiple replicate flow-through mesocosms which contain a small section of coral reef and which are designed to approximate the density and mix of corals and other organisms found on nearby reef crest communities at Heron Island (Figure 1). After acclimatisation, conditions in some of these 6000 L mesocosms are adjusted to different offsets across the treatments for long periods of time (3 – 24 months). The treatments investigated included Preindustrial, Control (today) as well as future scenarios SRES-B1 (~RCP4.5) and SRES-A1FI (~RCP8.5), with levels of variability that approximate those typical of a reef crest communities at Heron Island. Under preindustrial and Control (today) conditions, corals grew significantly during the experiment and the composition of the coral communities remain more of less unchanged. Under B1 (RCP4.5) and A1FI (RCP8.5) treatments, however, branching corals such as *Acropora formosa; Seriatopora hystrix; Stylophora pistillata, Montipora* sp., bleached and died by the end of the experiment. Calcification also showed significant trends with corals from B1 and A1 FI slowing to near zero in the initial part of the experiment (prior to mortality, S Dove, et al. [33]). Community calcification also declined but differed in that it decreased well below zero in the A1FI treatment. While dead coral skeletons were dissolving in these treatments, it appeared that carbonate sediments within the experiment experienced some of the largest losses of carbonate within this experiment [33]. The increase in the rate of decalcification matches the results of other experiments on two important bio-eroders, excavating sponges [34] and endolithic microalgae [35] with decalcification rates being driven up by warmer and more acidic conditions.

Responses of corals to hostile conditions: acclimatisation, evolution or migration

One way out of the dilemma that reef-building corals face is to either adjust their physiology (acclimatise), evolve via natural selection (adapt) and/or migrate as conditions become more and more hostile. In this regard, there are some interesting possibilities as to how reefs are likely to respond to rapid changes in the environment that surrounds them.

a. Acclimatisation to stress (modification of the phenotype)

Acclimatisation occurs when the phenotype of an organism is adjusted over time to better fit a change in the environment. In this way, organisms may acclimatise to new conditions which occur in a wide variety of organisms [36] including reef building corals [37]. While there is evidence that corals can adjust their thermal tolerance within their normal environmental range [38,39], there is little evidence that acclimatisation has resulted in a shift or extension of the upper thermal tolerance of reef-building corals [40]. Simply put, if acclimatisation were occurring perfectly, however, then corals would not be experiencing the current and extensive bleaching and mortality in response to thermal stress as they would have adjusted their physiology to suit the new conditions. Some evidence exists for corals which shift the relative concentration of different clades of symbiotic dinoflagellates in order to better suit the environment [41] although these studies have shown that shifts in the proportion of symbionts may be accompanied by costs in terms of growth and relative competitiveness [42]. Recent evidence suggests that the thermal threshold used by satellites to project when and where mass coral bleaching is likely to occur may have increased over time [1]. This study is complicated by the fact that these measurements are at the community level and hence are most likely due to the loss of fragile species as opposed to acclimatisation and/or adaptation of individual species. This has been pointed out for other studies [43] that have claimed to have demonstrated shifts in tolerance due to acclimatisation or adaptation

[44]. Trans-generational acclimatisation [45], where organisms (in this case on coral reef fish) inherit greater tolerance from parents who have been previously exposed to stress (in this case higher CO_2 and lower pH), presents some interesting mechanisms for some organisms. These experiments have not been attempted with corals (which tend to have long generation times from 5 to 100 years) or with the combination of factors (i.e. ocean acidification as well is warming) that are likely to occur under future ocean warming and acidification. Nonetheless, transgenerational acclimatisation remains an intriguing area for further investigation.

b. Evolution of stress tolerance (genetic adaptation)

Evolution by natural selection has also been as a mechanism by which thermal and chemical limits of current populations may shift to become more tolerant as oceans warm and acidify. Given time, corals, like any organism are likely to adapt to local conditions, which is reflected in the widespread evidence that corals are locally adapted to temperature, be that at a local [46] or geographic [47-49] scales. However, the rate of environmental change as well as extent to which stabilisation of environmental conditions occurs or not are critical factors determining whether or not the evolution of corals, and marine life in general, is likely to keep pace with anthropogenic ocean warming and acidification. The biological characteristics of the community and species are also important. In this respect, generation times as well as the amount of genetic variability within a population are critical factors determining the ability of locally adapted populations to increase their thermal tolerance. There is little doubt that organisms such as bacteria, which have short generation times (minutes to hours) and high mutation rates will be able to keep up changes to ocean conditions, even if current rates of change are unprecedented in the past 65 Ma if not 300 Ma [22]. Corals, on the other hand, have generation times from 4 to over 20 years for most corals [50] and hence do not have demographic characteristics that favour rapid evolution. The hypothesis that reef-building corals may be able to swap their symbionts for more thermally varieties [51] as not been supported by the sizeable number studies that have sought to show that corals can take on truly novel symbionts that enable them to survive higher sea temperatures. These studies have also suffered from a number of other issues including the assumption that the dinoflagellate symbionts are the only factor determining the overall thermal tolerance of the mutualistic symbiosis [43,52-54].

While the evidence for the rapid evolution of corals is virtually nonexistence, there is substantial evidence for why the rapid evolution of tolerance to future environmental conditions is unlikely to occur. Firstly, the rates of environmental change exceed those seen over the past hundreds of thousands if not tens of millions of years [12,22,55]. Secondly, the generation time of organisms such as reef building corals is relatively long [50]. The third, which is often overlooked is that conditions with respect to ocean warming and acidification are set to change continuously for hundreds of years under our current emission pathway [56]. That is, we are imposing conditions that change continuously and which are not the 'step change' which would otherwise enable populations and communities to 'catch up' with the change once conditions stabilise once again. The last issue is that adaptation to thermal stress is unlikely to be simple and is likely to involve scores of genes and cellular processes that need to be adjusted [57]. Consequently, evolution of tolerance to changing temperatures and sea water chemistry is unlikely to be a simple selection process (i.e. the change in a single gene) but rather a complex set of changes across multiple genes. The probability of suitable combinations decreases geometrically as the number of genetic changes required increases.

Not surprisingly, the distribution and abundance of coral populations is decreasing rapidly in most parts of the world [13-17] under increasing levels local and global drivers of stress. This problem is exacerbated by the fact that anthropogenic ocean warming and acidification is unlikely to stabilise for many hundreds of years under current scenarios for the emission of CO_2 and methane. Until this happens, adaptation might arise within a population of corals but will not have the time required for it to spread given that the same adaptation will quite rapidly become unfit as ocean temperatures and sea water chemistry continue to change.

c. Migration of reefs to higher latitudes

The warming of ocean waters at higher latitudes is shifting the range of marine organisms from plankton to fish [58]. As waters warm at higher latitudes, conditions as far as temperature is concerned are becoming increasingly favourable for reef building corals in the short-term. This has led to the proposal at coral reefs may shift to higher latitudes over time, more or less compensating for their losses at lower latitudes. Consistent with this is evidence that the distribution of coral reefs has varied with relatively small shifts in average global temperature on the paleontological past [59,60]. There are also a number of recent observations of reef building corals showing shifts too high latitude locations (up to 14 km yr^{-1}; [59-61] in many areas of the world.

It is important to note that both pieces of evidence are *necessary but not sufficient* to support the idea that coral reef ecosystems will or are moving to higher latitudes. Paleontological examples involve warming over hundreds if not thousands of years, mostly involve situations in which reefs did not experience changes at the same time in pCO_2, pH or carbonate ion concentrations [12]. Given that anthropogenic ocean warming and acidification will involve simultaneous changes in all three parameters, the degree to which examples from the past are useful proxies for the future is at least questionable. Secondly, the degree to which the movement of coral species to higher latitudes is evidence that entire coral reef ecosystems will shift to higher latitudes is also questionable. The movement of coral reef ecosystems to higher latitudes requires a shift in the distribution and abundance of thousands of species as well is the movement of complex ecological relationships and processes. These changes also have to occur over very short periods of time. In a simple example, the Great Barrier Reef ecosystem would have to travel at the speed of 15-20 km per year to keep up with a 2°C change over the next 100 years [43]. There is no evidence of this scale of movement of a coral reef ecosystem anywhere in the literature, and certainly no evidence of the extension of the southern end of the Great Barrier Reef by 600 km, which should have already occurred given that the Great Barrier Reef waters have warmed by 0.4°C since 1950 [62].

Shifts in the distribution of coral populations depend on dispersal and the existence of heat tolerant individuals at lower latitudes that are ready to migrate into areas as they warm. As raised by BM Riegl, et al. [49], we may be approaching the limits in terms of thermal tolerance of individuals in some areas of the world such as the Arabian Gulf, where corals experience some of the highest sea temperatures globally. There are no obvious sources of more thermally tolerant corals to replace those in this area of the world as oceans warm rapidly over the coming decades and century.

Requirements for sustainability via adaptation?

In exploring the requirements for adaptation to play a role in establishing a more sustainable future for marine ecosystems such as coral reefs, it is important to consider the implications of future climate trajectories. Of the four major scenarios of the fifth assessment report of the IPCC, for example, only the scenario RCP 3.0 exhibits the stabilisation of planetary temperature over the mid to late part century. As this is a requirement for adaptation to play a role, this is the only scenario where coral reefs (indeed many other ecosystems) have a chance of persisting beyond the middle of this century. All of the other models are characterised by conditions that continue to change hence imposing rapidly changing selection pressure over time. As evolutionary rates are many organisms including reef-building coral are likely to be severely constrained by their life history characteristics (i.e. long generation times, reduced variability), the distribution and abundance of corals and coral reefs is likely to continue to decline rapidly.

Achieving sustainability through adaptation will also depend on a rapid reduction of drivers other than ocean warming and acidification. Increasing the management of local stresses such as overfishing, for example, can enhance the resilience of coral populations to climate related phenomena such as thermal stress. TP Hughes, et al. [63], for example, demonstrated that bleached coral reefs on the central Great Barrier Reef which had healthy populations of grazing fishes, for example, recovered from coral bleaching related mortality three times faster than reefs where access by grazing fishes to damaged reefs had been prevented. Exploring the possibilities of how one can boost the resilience of coral reefs and buy important time while global society deals with enhanced greenhouse warming and acidification of our planet will become increasingly important as the current century progresses.

Conclusion

It is very clear that were entering to a period in which a lack of action on local and global drivers of stress will lead to conditions and impacts on these valuable ecosystems which will take thousands of years to reverse. Evidence that corals and other organisms are, and can acclimatise, adapt and/or migrate successfully to the unprecedented rapid rates of environmental change is sparse and in the minds of some circumstances be seen as a persistent mirage. In this regard, evidence that corals will autonomously evolve into the resilience state (i.e. benefiting efforts to achieve sustainability) under the current rapid changes to the environment is not supported by the literature. On the other hand, evidence of corals are ‘losing the fight’ is widespread and is on the increase, with most long-term studies showing declines of around 50% since the early 1980s. Given the dependence of human communities on coral reefs for food, livelihoods, coastal protection and other services, these changes are likely to have serious long-term consequences for people, communities and nations. Given the long-term commitment that these changes involve, it is an imperative that we rapidly involve a global strategy in which we rapidly reduce both local and global drivers of change and thereby avoid future in which we experience the semi-permanent or permanent loss of centrally important ecosystems such as coral reefs.

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Figure-1

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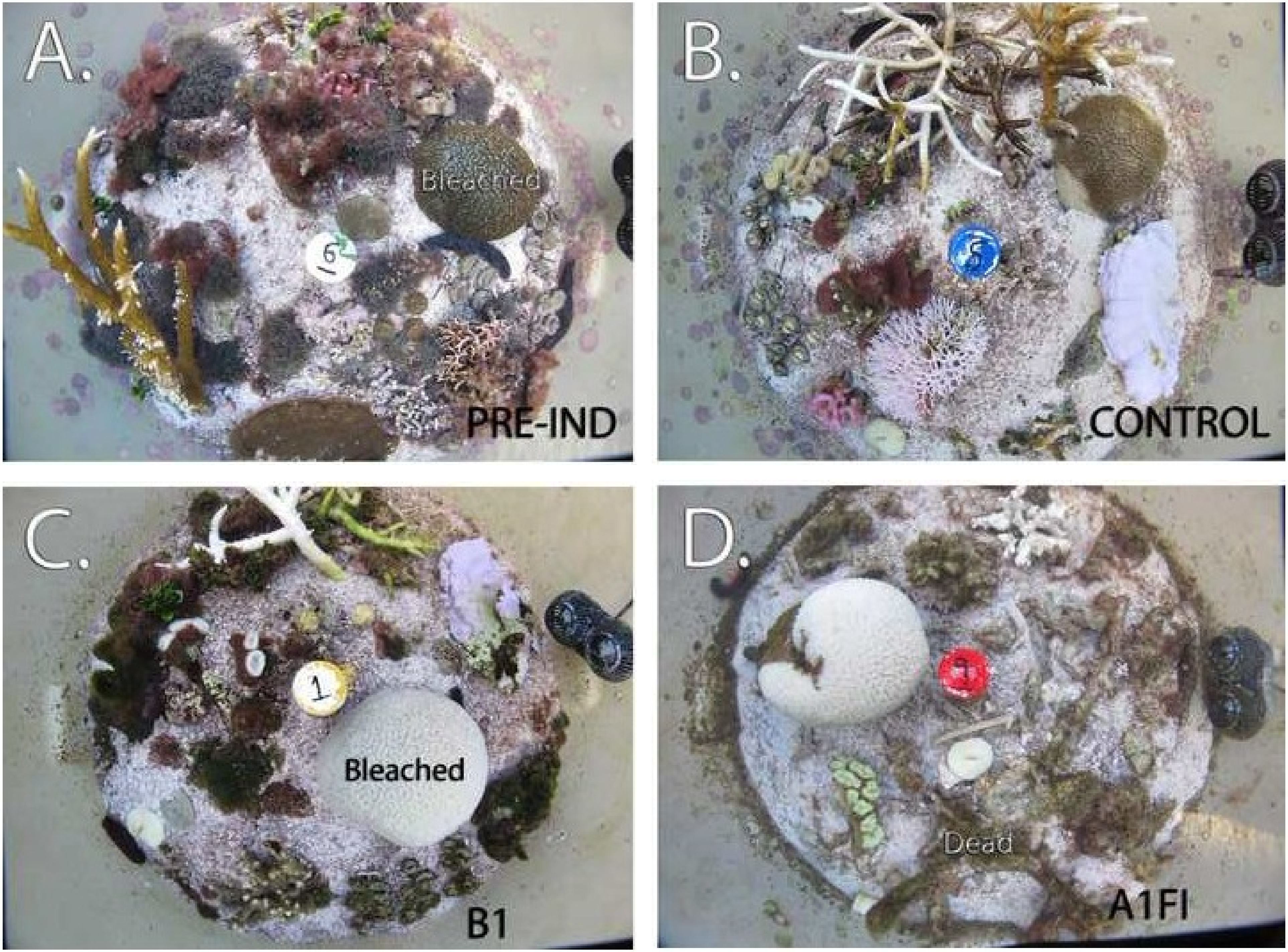

Legend

Figure 1. Photographs of the final condition within mesocosm tanks from three-month experiment run by Dove et al (2013). A. Preindustrial conditions (atmospheric CO_2 concentration: 280 ppm, - 1°C), B. Control (today) conditions (atmospheric CO_2 concentration: 396 ppm, +0°C), B1 (atmospheric CO_2 concentration: 570 ppm, + 2°C), and A1FI (atmospheric CO_2 concentration: 972 ppm, +4°C). Normal: Coral with typical concentrations of symbiotic dinoflagellates (brown colour). Bleached: coral where symbiotic dinoflagellates have left tissues. Dead: examples where coral has died and has been overgrown by microalgae. Full details are available in Dove et al. (2013).