Effects of Acclimatization on Coral Heat Stress Tolerance

by

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Abstract

A systematic literature review was conducted to determine whether acclimatization, an assisted evolution technique, can be used to mitigate the impacts of increased ocean temperatures on coral reef systems due to the global climate crisis. The review examined the relationship between acclimatization and changes in heat stress tolerance of corals. Targeted online database searches were used to identify 2000-2020 peer-reviewed research, which was used as the main source of reference data.

Results of the study show that acclimatization does occur for discrete species of coral under specific conditions. However, parameters are not standardized across studies, which creates inconsistent results. It is evident that much more research needs to be conducted to identify coral species with a thermal tolerance amenable to acclimatization, specific environmental conditions that will facilitate the acclimatization process, and over what temporal scales the conditions need to be applied.

While most research has been focused on intra-generational acclimatization, there is evidence emerging that trans-generational acclimatization may be possible. Research indicates coral larvae brooded under predicted environmental conditions will physiologically perform better under similar conditions than coral larvae that were not exposed. Continuing research into the potential of acclimatization as a coral reef management tool is necessary across all facets of this adaptation technique.

The study results provide insight into an adaptation strategy that could assist in coral reef management and allow humans to help coral reef systems adapt to predicted environmental conditions. While the study is a systematic literature review, and novel research was not conducted, the goal is to inspire readers to continue research and mitigative efforts to preserve coral reef systems for future generations.

Table of Contents

List of Tables

List of Figures

List of Acronyms

CBASS – Coral Bleaching Automated Stress System

CDC – Centers for Disease Control and Prevention

DHW – Degree heating week

DNA – Deoxyribonucleic acid

ENSO – El Niño Southern Oscillation

EPA – Environmental Protection Agency

F_M – Maximum fluorescence

F_V – Variable fluorescence

GBRMPA – Great Barrier Reef Marine Park Authority

GEB – Gene expression biomarkers

GHG – Greenhouse gas (expressed in $CO_{2\text{ equivalent}}$)

IPCC – Intergovernmental Panel on Climate Change

MHW – Marine heat wave

MMM – Multi-model mean

NASA – National Aeronautics and Space Administration

NHGRI – National Human Genome Research Institute

NOAA – National Oceanic and Atmospheric Administration

RCP – Representative Concentration Pathway

SST – Sea surface temperature (expressed in °C or °F)

TEEB – The Economics of Ecosystems and Biodiversity

TOPT – The Ocean Portal Team

UNDP – United Nations Development Programme

UNEP – United Nations Environment Programme

USGS – United States Geological Survey

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Chapter 1: Introduction

A variety of human activities have been linked to the degradation of coral reef systems and coral mortality events. Even before the effects of the global climate crisis became noticeable, coral reef systems around the world had been coming under an increasing number of local anthropogenic stressors such as overfishing, destructive fishing practices, pollution, and coral mining. While these threats were regional, some discrete coral reef areas were disproportionately impacted due to the cumulative effects of threats, with severe losses seen in some regions. For example, Caribbean coral declines are widespread, and attributed to local stressors. A study using palaeoecological, historical, and survey data, found that declines from the prehuman period began in the 1950s and 1960s, earlier than previously thought (Cramer et al., 2020). Interestingly, these declines began many years before bleaching events and disease began impacting the Caribbean corals.

An issue in determining the overall decline of coral reef systems is the lack of historical baseline information. A review by Bruno (2011) looked at the difficulties in establishing a historical baseline at the Great Barrier Reef for comparison purposes. One reason for the lack of baseline information is that coral reef systems only became the target of monitoring programs after noticeable declines in their health had already occurred. Many studies (Eddy et al., 2018; Bruno, 2013; McClenachan et al., 2017) that attempt to provide a historical baseline of global reef systems for comparison with current conditions rely on meta-analysis data obtained through electronic and manual literature searches and personal communication with experts and historians. As such, this leaves the results open to interpretation as differing methods are used to survey the quantity and quality of reef ecosystems in addition to the intrinsic subjective nature of some observations. Consequently, there is a great deal of uncertainty attached to the results.

The most significant global threats to coral reef systems are linked to the effects of climate change, specifically changes in ocean temperature, chemistry, and depth. Increasing ocean temperatures are resulting in mass bleaching and mortality events (Hughes et al., 2018). Changes to the chemistry of the ocean are threatening the ability of coral to produce the skeletal calcium carbonate building blocks of a reef’s structure (Eyre et al., 2018). With sea level rise, there is increased wave energy which results in greater sediment mobility, destructive impacts to coral reef structures (Perry et al., 2018), and impediments to sunlight reaching coral (Webster et al., 2004). Sunlight is crucial for coral survival as it fuels the photosynthetic reactions of zooxanthellae, microscopic photosynthetic algae that reside within coral polyps, and provide the necessary sustenance for coral to survive (NOAA, n.d.-b).

One of the main drivers of coral bleaching events is anomalous sea surface temperatures (SSTs). When seawater temperature is increased, coral become stressed due to the abnormal thermal conditions which can lead to mortality (Hughes et al., 2017). Thus, scientists are interested in determining if the heat stress tolerance of corals can be modified, if there is an upper limit to thermal adaptation, and how quickly discrete species of coral can adapt to novel thermal conditions.

Identifying potential mitigation and adaptation strategies and determining their efficacy and feasibility of implementation is essential for supporting the survival of coral reef systems. Even if the production of greenhouse gases (GHGs) was stopped today, there is a latency period between cause and effect (Ricke & Caldeira, 2014); thus, impacts from global warming and climate change will continue to be magnified in the foreseeable future. One such strategy, assisted evolution, which aims to accelerate naturally occurring evolutionary processes in corals, uses four main approaches: acclimatization, modification of microbial symbiont communities, evolution of *Symbiodinium*, and selective breeding.

This research project focuses on the potential of utilizing acclimatization to modify the heat stress tolerance of corals, which could allow them to survive in the hotter ocean environment that is predicted (IPCC, 2019). The acclimatization approach uses natural adaptation processes to increase coral thermal stress tolerance by exposing coral to anticipated environmental conditions. Reviewing this promising adaptation strategy may inspire further research and provide much-needed attention to arguably the greatest threat that coral reefs face.

1.1 Background

1.1.1 Ecosystem Services and Oceanic Biodiversity

The importance of coral reefs to oceanic biodiversity and the ecosystem services that they offer cannot be overstated. Healthy coral reef systems provide ecosystem services, defined by TEEB (2010) as the direct and indirect contributions of ecosystems to human well-being, that benefit the environment, human health, and underpin many economies. These ecosystem services include food production, carbon sequestration and storage, raw materials and medicinal resource creation, extreme event moderation, ecosystem resident habitat formation, genetic diversity preservation, biological control facilitation, and tourism generation (TEEB, 2010). Also, ecosystem services provided by coral reef systems were estimated to have an average annual value of $172 billion globally (Diversitas, 2009).

Coral reefs are diverse ecosystems that occupy a mere one tenth of one percent (0.1%) of the earth's seascape; however, an estimated 25% of marine species, are supported by coral reef systems at some point during their lifecycle (Scripps Institution of Oceanography, 2020). In fact, new marine species and habitats are still being discovered and surveyed (Richards & Day, 2018) with more than one million species of plants and animals estimated to be part of coral reef ecosystems (NOAA, n.d.-e).

Scientists have found that ecosystems with greater diversity in the foundation species, such as trees in a forest, or in this case, corals in a reef system, tend to be healthier and provide a higher output of ecosystem services (Gamfeldt et al., 2013). As such, coral could be seen as being in a mutually beneficial relationship with biodiversity. Coral reefs provide the setting for ecosystem biodiversity to flourish, and in turn, biodiversity allows corals to thrive.

In order to provide evidence to support this supposition, native coral gardens were created and placed in a degraded reef environment during a study conducted by Clements and Hay (2019). Single-species coral gardens were then compared to mixed-species coral gardens over time (16 months) with respect to coral tissue death, weight, and colonization of harmful seaweeds within the garden plots. The sample results seen in figure 1 show the mixed-species coral gardens consistently outperformed the single-species gardens.

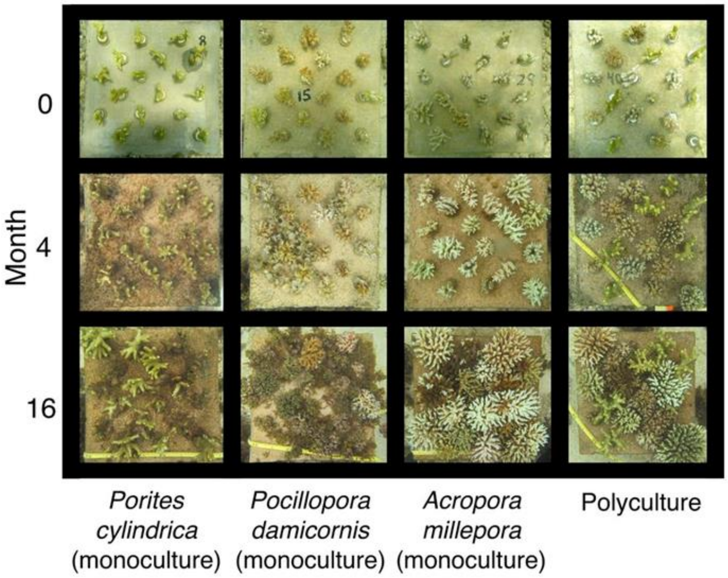

Figure 1 – Results of single and mixed-species coral garden growth (Reproduced from Clements & Hay, 2019)

The change in coral mass at the four-month mark was 24% greater in the polycultures than the best-performing monoculture, and 61% greater than the aggregate across monocultures. At 16 months, coral growth in polycultures was 67% greater than the average across all monocultures and about on par with the best-performing monoculture. Furthermore, tissue mortality among monocultures was consistently greater than polycultures throughout the duration of the experiment except for *Acropora millepora*, the best-performing monoculture, which was statistically indistinguishable. Finally, macroalgal biomass development was inhibited significantly in the polycultures and the best-performing monoculture as low mortality limited the opportunity for macroalgal growth. The results give credence to the hypothesis that foundation species diversity promotes healthy growth, recovery from disturbances, and by extension, increased ecosystem services.

A study conducted by Kiessling et al. (2010) provides insight into how important coral reefs are to oceanic biodiversity. Benthic marine invertebrate genera were considered eligible for the study if they spanned more than one geological period and the environment of origin could be identified. The study results showed 21.6% of candidate genera were positively identified as originating in a reef environment. Additionally, the study found that reefs are a significant net exporter of biodiversity, as species that originate within the ecosystem migrate to new locations of residence or pursue a nomadic existence. Thus, the findings indicate that reef environments are cradles of biodiversity as they function to produce, support, and export a large portion of overall marine biodiversity.

The findings of these studies indicate that oceanic biodiversity is created, exported, and perpetuated by corals and the reef ecosystems that they create. The health of coral reefs, which is inextricably connected to biodiversity, can arguably be seen as a reflection of the health of our oceans, and is being threatened by the global climate crisis. Ecosystem services that coral reefs provide, and millions of people rely on every day, are directly affected by their inherent diversity and health; consequently, the continued existence of coral reef systems is crucial, with far-reaching impacts derived from their demise.

1.1.2 The Global Climate Crisis

The global climate crisis is a phrase which encapsulates both global warming and global climate change. These global issues are measured in terms of a departure from baseline temperatures and natural climate cycles. Global warming is defined as the gradual increase of the mean global temperature of the lower atmosphere, typically measured from surface temperatures, over a 30-year period (IPCC, 2018). Global warming is the result of an increase in heat-trapping greenhouse gas (GHG) concentrations in the atmosphere causing an imbalance in the earth's energy budget. The earth's energy budget consists of the balance between energy radiated by the sun into the earth's atmosphere versus the amount of energy radiated from earth's atmosphere back into space (NASA, 2017).

Climate change is the long-term change in average weather patterns which can occur on local, regional, and global scales. According to a report released by the IPCC (2014), anticipated consequences of climate change include the following:

- Global mean sea level rise
- Ocean warming
- Ocean acidification
- Longer and more frequent droughts and heat waves
- Extreme precipitation events occurring with more intensity and frequency
- Ice-free summer months in the Arctic Ocean
- Greater intensity and frequency of hurricanes

While the heat stress of corals due to ocean warming will be the focus of this study, it should be noted that ocean acidification works synergistically with ocean temperature rise to drive coral bleaching events (Anthony et al., 2008), which can lead to coral mortality. As such, an overview of ocean temperature rise, ocean acidification, and coral bleaching is warranted.

1.1.2.1 Ocean Temperature Rise

Global warming is leading to an increase in the average sea surface temperature (SST) as atmospheric concentrations of carbon dioxide (CO_2) are increased due to anthropogenic activities such as fossil fuel combustion. As CO_2 emissions continue to increase for the foreseeable future, mitigation of potential increases in SST below levels that significantly impact coral reef systems appears untenable.

Species of reef building coral are extremely sensitive to fluctuations in temperature with a narrow range of global annually averaged temperature tolerance of 21.7 – 29.6°C (71.1 – 85.3°F) (Guan et al., 2014). As such, a rise of just one degree Celsius from normal conditions for a four-week period can trigger bleaching in coral, depending on the discrete species of coral being stressed. If ocean temperatures remain high for eight weeks or longer, the coral cannot recover and begins to die. The severity of the bleaching event will depend on both the magnitude of temperature above the long-term average and length of the perturbation. Of note, it is possible for coral to perish without ever bleaching if the imposed heat stress is too severe. Additional threats to coral reef ecosystems created by warming oceans include hypoxia and increased disease outbreaks (IPCC, 2019).

1.1.2.2 Ocean Acidification

Since the beginning of the industrial era in 1750, anthropogenic activities have contributed massive amounts of CO_2 to the atmosphere, whose concentration affects the earth's energy budget (EPA, n.d.-b; NASA, n.d.). Thankfully, there are natural carbon sinks, or reservoirs that absorb more carbon from the atmosphere than they release. The ocean is the world's largest natural carbon sink which helps to reduce the atmospheric concentration of CO_2, a GHG that traps heat in the atmosphere and drives global warming. However, this natural phenomenon comes at the cost of a changing ocean chemistry due to the massive uptake of CO_2 and the resulting chemical reactions that change the natural equilibrium, making oceans more acidic (NOAA, n.d.-f; Watson et al., 2020).

Currently, the ocean is absorbing approximately 22 million tons of CO_2 per day, or roughly 30% of CO_2 emitted to the atmosphere, and has absorbed an estimated 525 billion tons of CO_2 since the industrial revolution commenced (The Ocean Portal Team [TOPT], 2018). The transfer of atmospheric CO_2 to absorbed CO_2 at the air-ocean interface, and vice versa, is regulated by one of the equilibrium reactions that make up the carbonate system. The carbonate system is a series of reversible chemical reactions that serve to buffer fluctuations in species concentration while regulating pH levels and flow of CO_2 between the atmosphere, hydrosphere, biosphere, and lithosphere. As the pH in the ocean decreases due to increased CO_2 uptake, the presence of additional hydronium ions will cause a much greater amount of carbonate to react and produce bicarbonate which significantly reduces the carbonate species available in seawater (*Ocean Chemistry & Acidification*, 2018).

Calcium carbonate ($CaCO_3$) minerals are the fundamental structural materials for marine organisms to produce shells and other skeletal structures of biogenic carbonate including coral skeleton formation. Having fewer carbonate species available for biomineralization imparts a greater physiological burden on coral polyps as they try to produce their skeletal structures (Byrne & Fitzer, 2019). Corals are composed of a framework of aragonite bundles, the calcium carbonate polymorph vital for their skeletons, that provide structural stability against perturbations and build a platform upwards towards the sunlight they need for energy

(Lippsett, 2018). Based upon the current rate of CO_2 being absorbed by the world's oceans the aragonite saturation of seawater is projected to steadily decrease until it reaches a tipping point where net accretion of calcium carbonate will be taken over by net dissolution (Eyre et al., 2018).

1.1.2.3 Coral Bleaching

Coral bleaching occurs when coral polyps expel their colourful resident algae, zooxanthellae, which leaves the coral a striking white colour, as seen in figure 2, and is an indicator that the coral is under stress. Corals are not killed instantly, but by expelling their zooxanthellae, they are essentially starting a countdown to their demise, as most depend on the algae to obtain their essential nutrients through photosynthesis. The longer that stressors, such as ocean acidification and thermal anomalies, are impacting coral reefs, and polyps are unable to recruit new zooxanthellae, the more susceptible they become to mortality (NOAA, n.d.-b).

Figure 2 – Corals during a bleaching event (Reproduced from Gorse, 2019)

A study by Eakin et al. (2018) looked at mass bleaching events where hundreds of kilometres or more of coral reefs are affected. Mass bleaching events are primarily driven by global threats including prolonged anomalous SSTs and increased ocean acidification. Global bleaching events take place when mass bleaching events occur within all three ocean basins, being the Atlantic, Pacific, and Indian Oceans, during a given year. The most recent global bleaching event, occurring between 2014 and 2017, was atypical for a couple of reasons. The duration, spanning three years, was an unusually long interval of continuous anomalous SSTs as compared to previous events. Also, enough heat stress was present to trigger a global bleaching event prior to the onset of El Niño which had not been previously observed. During the 36-month duration of the most significant global bleaching event ever recorded, 75% of reefs throughout the world were impacted, half being impacted twice, with an overall mortality of approximately 30%.

Furthermore, the rate of incidence of global bleaching events is increasing dramatically. In the 1980s, bleaching events of this magnitude were occurring at a rate of once every 25 – 30 years. As of 2018, the estimated rate of occurrence is once every six years and is expected to continue decreasing as these events are driven by global ocean warming (Hughes et al., 2018).

1.1.3 Mitigation of Global Climate Crisis Impacts to Coral Reef Systems

Mitigation of global climate crisis impacts to coral reef systems can not be accomplished by any singular approach. Various methodologies need to be employed concurrently, including adaptation and restoration strategies, to offset the adverse impacts imposed by this crisis. While some strategies such as reef restoration have been used for many years, emerging approaches in adaptation are continuing to evolve and show promise.

Coral reef restoration aims to restore damaged, degraded, or destroyed reefs to the healthy functioning ecosystems that they once were. Research conducted by Smith and McLeod (2018) indicates that there have been three distinct periods when different approaches in reef restoration have emerged since the 1970s. The first period, beginning during the 1970s, involved the addition of artificial reef structures and transplanting of coral. The second period, spanning from approximately 2000-2010, concentrated on both the addition of habitat and removal of invasive algae and predators such as the crown-of-thorns starfish. Finally, the current period, beginning in 2016, has been focussing on incorporating advances in technology into reef restoration efforts. Reef restoration strategies that have been applied over time can be seen in figure 3.

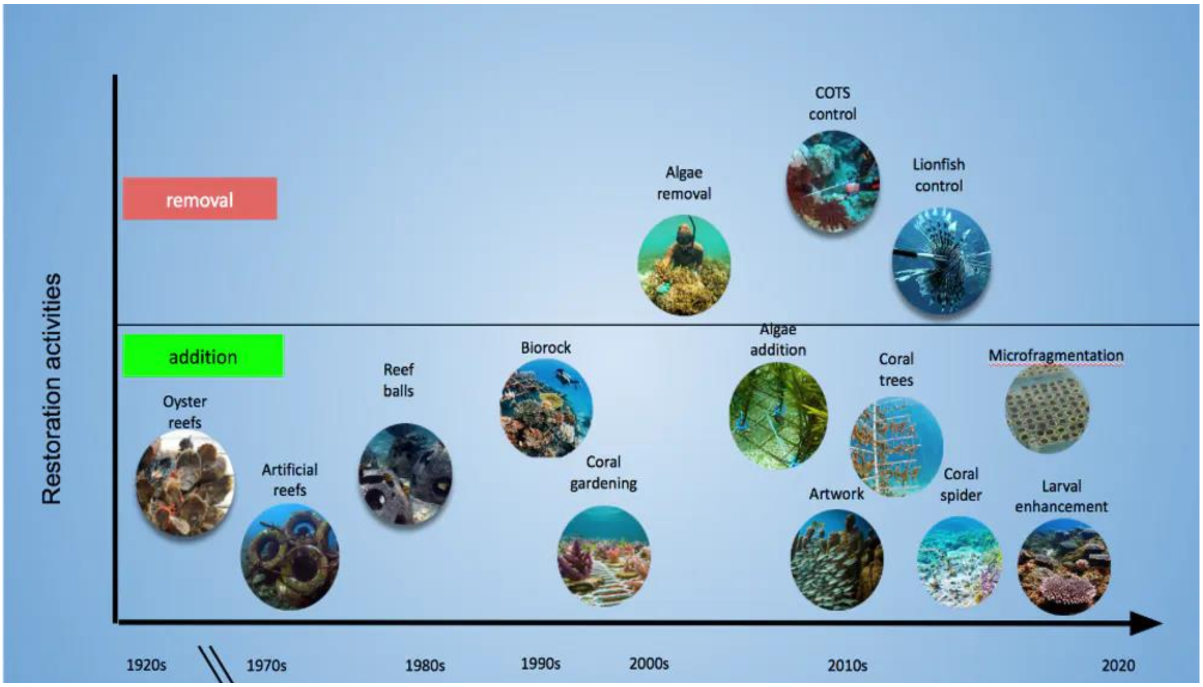

Figure 3 – A timeline of coral reef restoration techniques (Reproduced from Smith & McLeod, 2018)

One traditional approach to coral reef restoration is through coral aquaculture, otherwise known as coral gardening or coral farming. In-situ and ex-situ methods are both employed where coral fragments of healthy populations are cultivated in nurseries before being explanted onto reefs with degraded coral cover (Reef Resilience Network, n.d.-a).

A company that is furthering the effectiveness of this approach, Coral Vita, has developed innovative micro-fragmenting technology that is shown to increase the natural growth rate of corals by 50 times (United Nations Environment Programme [UNEP], 2019). Using this breakthrough technology has reduced reef restoration times from decades to months. According to a study conducted by Boström-Einarsson (2019), other restoration methods and techniques include:

- Larval enhancement
- Substratum stabilization
- Substratum enhancement with electricity

To ensure the continued survival of coral reef systems in the face of challenges posed by the global climate crisis, scientists are researching a variety of tactics to try and augment the stress tolerance of corals and help acclimatize these marine animals to their changing environment. Acclimatization is a phenotypic response of an organism, not involving genetic change, to adjustments in the exposed environment that alters the organism’s performance.

For example, a research study by Liew et al. (2018) looked at how DNA methylation, which is described as a biological process by which methyl groups are added to the DNA molecule, affects coral's stress tolerance. Evidence of DNA methylation has been observed in corals (Li et al., 2018; Diamond & Roberts, 2015) and is thought to be associated with phenotypic plasticity upon exposure to varying environmental conditions. Phenotypic plasticity is the ability of one genotype to express varying phenotypes which are the observable characteristics or traits of an organism. After growing colonies of the globally distributed scleractinian cauliflower coral *Stylophora pistillatal* in seawater aquariums for two years in varying levels of acidity, the genomes of the corals were sequenced to determine any changes in methylation patterns.

The results showed increased DNA methylation occurred in corals growing in environments with increased acidity. Genes with increased methylation were related to cell growth and stress response and consequently, polyp and cell size increased with acidity. Since coral polyps reside in cavities called calyxes, which offer polyps a protective sanctuary, bigger polyps result in bigger calyxes. A larger calyx means less skeleton needs to be produced by the coral to continue to grow at the same pace. The result is significant since ocean acidity can impair skeletal production and corals need to maintain their growth rate as they compete for light as sea levels rise. Thus, growing corals under future seawater conditions, a process known as environmental hardening or acclimatization, could help them flourish in the novel environmental conditions by taking advantage of natural mechanisms of adaptation. However, the study recognized that further understanding of mechanisms of coral resilience is necessary to identify additional avenues for reef restoration.

Modification of symbiont communities is the process of adjusting the composition of coral-associated microbes, within their endosymbiotic communities to increase the stress tolerance of the symbionts. *Symbiodinium* evolution, where *Symbiodinium* are colloquially called zooxanthellae, looks to modify the algae through mutagenesis and/or selection processes in a laboratory setting (van Oppena et al., 2015). Selective breeding involves identifying desirable traits in parent corals that can be bred to produce offspring with these desirable characteristics. For example, selecting heat-tolerant species of coral, breeding them to produce offspring with this desired trait, and adding them to a reef can increase the stress tolerance of the entire reef system as the coral propagate (Albright, 2018).

Genetic traits have been modified or enhanced for commercial purposes, such as herbicide resistance for crops, and the same concept can be applied in marine biotic propagation. However, genetic enhancement is not without its potential pitfalls (Snow et al, 2005; Prakash et al., 2011) as a species can be given a competitive advantage through the genetic manipulation process which may upset the naturally occurring equilibrium of the ecosystem. Also, assisted evolution of coral species may not be successful in introducing enough stress tolerance for all species to endure predicted environmental conditions, with potentially only a small number of species being able to survive and thrive. The result would be severely reduced natural biodiversity and the potential to affect the overall function of the ecosystem (Baker, 2020).

Research into assisted evolution techniques is still ongoing with many unanswered questions remaining such as assessments of the efficacy and feasibility of these methods, risk assessment of each option, and the evaluation of benefits from these approaches. Also, time and resources need to be expended to better establish historical baseline information, reduce uncertainties, and determine quantitative threshold information to increase the accuracy in predictive modelling (van Oppena et al., 2015).

1.2 The Research Problem Statement

Numerous stressors are causing widespread degradation and mortality of coral reef systems around the world with the global climate crisis having the greatest impact. The magnitude and frequency of stressors such as anomalous SSTs and ocean acidification are projected to increase significantly under a business-as-usual scenario (IPCC, 2019). While evidence suggests that corals have naturally had some success in adapting to rising ocean temperatures, there is uncertainty whether corals have the capacity to adapt at the rate necessary to survive in predicted temperature conditions (Coles et al., 2018). As such, research is being conducted in various approaches to try and increase the heat stress tolerance of corals. This project will seek to determine the efficacy of acclimatization as an adaptation measure to heat stress.

The reality is we do not know the extent of impacts that a potential collapse of global coral reef systems could have on present and future marine biodiversity, global food chains, and the way of life for millions of humans. There are varying degrees of negative outcomes that are projected, and the potential for a catastrophic collapse of a natural resource that has been taken for granted for too long cannot be ruled out.

The main research question of this proposed project is:

Can acclimatization mitigate impacts of increased ocean temperatures on coral reef systems due to the global climate crisis?

1.3 Project Objectives

The primary objective of this project is to determine whether research suggests acclimatization has the potential to be an effective adaptation strategy to mitigate impacts of the global climate crisis, specifically increased ocean temperature, on coral reef systems. While this project does not provide any unique research outcomes and is a literature review examining how acclimatization can help coral reef systems to adapt to novel environmental conditions in the future to survive, hopefully it informs and inspires, providing motivation to help solve this often-overlooked global dilemma. The more pressure that the public and industry professionals can apply to their respective governments, the greater probability that the necessary resources and international cooperation will be extended to combat this significant global challenge.

1.4 Project Scope

This systematic literature review project focuses on whether research indicates that acclimatization, an assisted evolution technique, can be utilized to increase the heat stress tolerance of corals. The systematic review process identified published literature that provide an understanding of our current state of knowledge. Literature was analyzed and synthesized to derive a conclusion as to the efficacy and feasibility of utilizing acclimatization as an adaptation strategy. While there are other assisted evolution techniques currently being researched, this systematic literature review project is constrained to evaluating acclimatization as a coral reef management tool.

Chapter 2: Methods

The literature search was conducted exclusively through internet databases as the current Covid-19 situation removed physical search of material at a library as an option. Background reference material was sourced applying two different methods. First, topics such as coral reefs and the climate crisis, that are well documented by reputable institutions and the scientific community, were sourced through webpage searches utilizing the Google search engine and the keywords listed below. Preference was given to websites of government institutions such as NASA and NOAA. Dedicated coral conservation and research entities (e.g., Reef Resilience Network) were also given preference.

Second, topics that have less documentation and unique research studies were sourced through online database searches. Publications included in the search consisted of books, journal articles, research reports, dissertations, and review articles. The following databases containing relevant material were utilized during the search process:

- BCIT Library Catalogue
- JSTOR
- Science Direct
- PubMed
- ProQuest
- Google Scholar

Searches were initially restricted to the year 2000 and later as the information could potentially be more relevant due to new technologies and/or analysis techniques being employed. Also, search results were initially filtered for peer review status (when the option was available) as it can lend credibility to findings within the publications. Candidate publications were then targeted using the following key words to identify sources focused on background information for the research topic:

- Climate crisis
- Biodiversity
- Coral reefs
- Assisted evolution
- Ecosystem services

Finally, a manual review of the remaining candidate literature was conducted. Sources determined eligible for contribution were appraised, abstracted, and aligned through the addition to a literature review matrix. The literature review matrix allows for source literature to be documented, analyzed, and readily available for potential reference use in the completion of the systematic literature review project.

Discussion section resource literature has a narrower focus than the background reference material as it is specific to the research question. As such, utilizing the aforementioned databases was the only approach applied to the literature search for the Discussion section. Search was restricted to the year 2000 and later as much of the research pertaining to assisted evolution, and specifically, acclimatization, is quite novel. Search results were also filtered for peer review status (when the option was available). Candidate publications were then targeted using the following key words to identify sources focused on discussion information for the research topic:

- Marine heat waves
- Acclimatization
- Coral heat stress

A manual review of the remaining candidate literature was conducted, and sources determined eligible for contribution were added to a literature review matrix.

Targeted searches for published literature to support the Discussion section were performed that built upon information found in eligible literature derived from “Acclimatization” keyword searches. Using the same parameters to filter the results, searches were conducted using the following keywords:

- Intra-generational acclimatization
- Trans-generational acclimatization

These keywords were used as eligible literature identified from the “Acclimatization” keyword search indicated these were inherently two different avenues of research. Intra-generational acclimatization research looks at the ability of coral to acclimatize within their lifespan, while trans-generational acclimatization focuses on the heritable potential of acclimatization.

Further targeted searches for supplemental literature to support the Discussion section, that did not include the year 2000 date restriction, were conducted using the following keywords:

- Historical coral heat tolerances
- Coral heat stress monitoring

A manual review of the remaining candidate literature was conducted, and sources determined eligible for contribution were added to a literature review matrix.

Eligible publications, 63 in total, were evaluated and prioritized by a few different methods. Publication date was a parameter employed as recent publications likely include innovative technologies and research that advances previous research. Also, acclimatization studies that include more than one species of coral that are ubiquitous to coral reef systems were given priority as the results will be a better indicator of global efficacy. Finally, literature written by frequently cited authors from studies in the field of coral heat stress research was also given precedence.

The literature review matrix was utilized to aid in the writing process through the completion of row and column analyses. By moving down columns, the column analyses highlighted patterns across literature sources such as similarities and contrasts between sources and gaps in knowledge. By moving across rows, the row analyses highlighted the contributions of singular published literary articles to the field which helped identify the 37 primary research and case study articles that are referenced in the project.

Information derived from the literature review matrix analyses was used to form the basis of the introduction, methodology, results and discussion, and conclusions sections of the systematic literature review study. A summary of the literature review matrix entries that supported the study can be seen in Appendix A.

The results of this systematic literature review are presented through a synthesis of selected case studies that explore research into intra-generational and trans-generational acclimatization.

Chapter 3: Results and Discussion

Results of the systematic literature review are presented and discussed through synthesis of published research and case studies. First, projected marine heat waves are examined to provide insight into the intensity and spatial scale of anomalous SSTs over various temporal scales. Subsequently, heat stress thresholds of corals and heat stress identification and monitoring are reviewed. Finally, acclimatization is discussed in detail through case studies of both intra-generational acclimatization and trans-generational acclimatization. Findings of the case studies provide the basis to derive conclusions as to the feasibility of utilizing acclimatization as a coral reef management strategy.

3.1 Projected Marine Heat Waves

As a result of the global climate crisis, marine heat waves (MHWs) are occurring with greater intensity, have become longer lasting, are more extensive, and becoming more frequent due to climate change. In fact, the IPCC's *Special Report on the Ocean and Cryosphere in a Changing Climate* (2019) reported that, over the period 1982 – 2016, the frequency of marine heat waves has doubled. Moreover, they conclude it is very likely that 84 – 90% of these heat waves occurring between 2006 – 2015 are attributable to increases in heat caused by anthropogenic activities.

A study by Oliver et al. (2019) sought to determine the projection of MHWs to the end of the 21st century using multi-model mean (MMM) analysis outputs from seven models. Emissions inputs were used from two anthropogenic emission scenarios being Representative Concentration Pathways (RCP) 4.5 and 8.5. RCP 4.5 assumes anthropogenic emissions of GHGs peak in 2040 while RCP 8.5 assumes anthropogenic emissions of GHGs continue to rise throughout the 21st century. A MHW was defined as "periods when daily temperatures were above a threshold based on the seasonally varying 90th percentile[1] for at least five consecutive days". The baseline used to define temperature anomalies for each model was determined from the analysis of a base period of 1982 – 2005 from that model. The modeling results of MHW intensity and annual number of days, where the purplish shading represents natural variability, can be seen in figure 4.

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[1] The 90th percentile of a set of data is the value at which 90 percent of the data is below it. (Taylor, 2019)

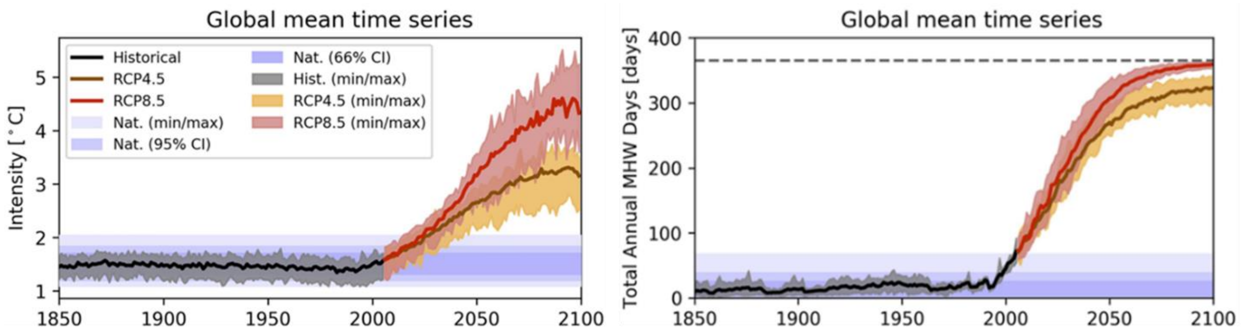

Figure 5 – MHW intensity and annual number of days projected through the 21st century (Adapted from Oliver et al., 2019)

Global mean MHW intensity will exceed natural variability for RCP 4.5 in the year 2044 and the year 2033 for RCP 8.5. Moreover, the results predict that globally, there will be MHWs 365 days a year under RCP 8.5 by the year 2100. These results paint a grim picture of what the future may hold depending on the degree to which we mitigate anthropogenic forcings and should impart a sense of urgency given the current trends. The spatial distribution of predicted SST anomalies under RCP 8.5 as compared to a historical baseline of 1961 – 1990 can be seen in figure 5.

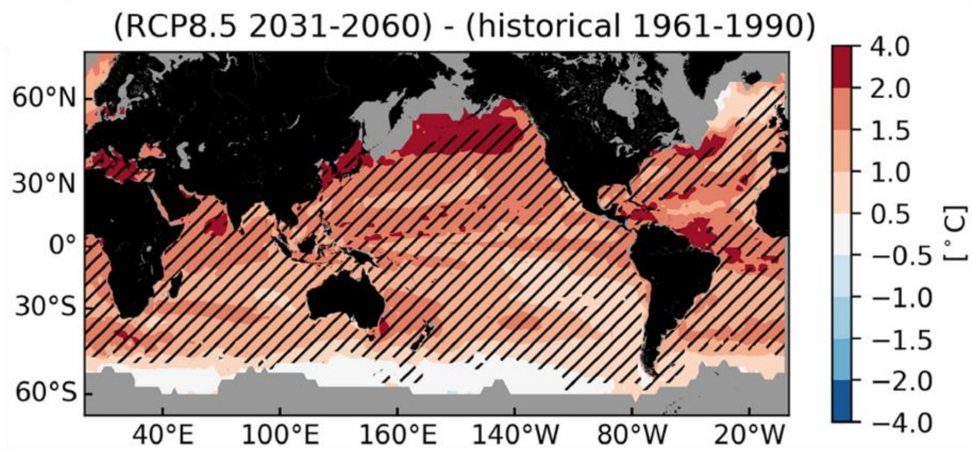

Figure 4 – Spatial distribution of predicted SST anomalies (Adapted from Oliver et al., 2019)

As figure 5 illustrates, there will be an uneven spatial distribution of SST anomalies which will necessitate the need for greater adaptation depending on geographical location. Regardless of the anthropogenic emissions scenario used, there will be a growing need for marine biota to adapt to novel environmental conditions or face the negative consequences.

3.2 Heat Stress Thresholds

Various research carried out during the 1970s (Jokiel & Coles, 1977; Coles et al., 1976) determined heat stress temperature thresholds that induced bleaching in corals. Coral studied at Kānéohe Bay, Hawaii, was compared to coral of the same species and genus located at Eniwetok Atoll in the Marshall Islands. The research was novel at the time and suggested that coral live in environments near the upper boundary of their current heat stress tolerance threshold globally, typically within 1-2°C of the geographical summer mean water temperature. This conclusion has been observed throughout environments around the world in which corals live, even though the summer maximum varies widely between 25°C in Rapa Nui to 34°C in the Arabian Gulf (Coles & Riegl, 2013).

As SSTs have continued to increase, corals are living in seawater that is in increasingly closer proximity to their thermal limit in the summer months (Hoegh-Guldberg, 1999). If there are no mechanisms to acclimatize to new environmental conditions, or if acclimatization can not occur concurrently at a similar rate to SST warming, survival of coral is put into question. As such, based on MHW predictions, significant effort and resources must be expended expeditiously to identify and implement adaptation strategies if we are to limit mass bleaching, degradation, and mortality.

A study by Schoepf et al. (2015) looked at two species of coral, *Acropora aspera* and *Dipsastraea*, located in the naturally thermal extreme environment of the Kimberley region in northwest Australia. The study included intertidal corals, or corals exposed to extreme diurnal heat fluctuations when exposed during low tide, and subtidal coral which inhabit a much more thermally stable environment. Interestingly, the findings indicate coral subject to a wider range of diurnal temperature fluctuation had a higher threshold to heat stress.

Recently, the Coral Bleaching Automated Stress System (CBASS), a portable experimental system, was developed by researchers to facilitate short-term acute heat stress assays (Voolstra et al. 2020). The development of CBASS technology is significant as it allows flexibility to test the heat tolerance of in-situ discrete colonies of coral in a very short period of time (18 hours). Conversely, traditional methods require extensive field preparation, equipment, and monitoring over extended periods or require a laboratory setting. The utilization of CBASS has the potential to speed up heat stress threshold research, identify thermally resistant species of coral, and assist in the prioritization of coral reefs for restoration efforts.

There are many challenges attached to heat stress tolerance research in corals. For example, heat stress tolerance thresholds are specific to discrete coral and can vary for each species, geographical location, and even across colonies due to physiological variations (Reef Resilience Network, n.d.-b). As a result, it would be difficult to generate a heat stress index with a high degree of accuracy. Also, there are approximately 6,000 species of coral (National Geographic, n.d.-c) , which means much more research is needed to identify heat stress resistant candidates and how heat stress thresholds vary within a distinct species. If only a small number of coral species can survive in projected environmental conditions, it will significantly reduce the biodiversity of coral reef with cascading impacts.

3.3 Heat Stress Identification and Monitoring

Heats stress monitoring has evolved as technologies have advanced with the goal of providing more precise, predictive, and moving toward proactive monitoring techniques. Heat stress monitoring in corals historically relied on physical observation of stressed corals once coral bleaching occurred which is reactive in nature.

Once remote satellite sensing was developed, it provided an opportunity to identify areas at risk of bleaching due to anomalous SSTs on a global scale at near-real-time. Over the last couple of decades, a key tool in heat stress monitoring has been the degree heating week (DHW) product of the NOAA Coral Reef Watch which uses remote sensing information. This product facilitates the measuring, comparing, and predicting of accrued heat stress of coral reef environments referenced to the warmest period of the year based on historical data. DHWs are a thermal stress index that represents the accumulation of thermal anomalies, considering both the magnitude and duration of thermal stress, experienced by corals across a three-month period. DHW values reaching 4°C-weeks and 8°C-weeks are associated with mild bleaching events and severe bleaching with widespread mortality, respectively. Therefore, the induction of a heat stress response in coral can be inferred based upon the geographical location of accumulated heat in a water body over a relatively long period (Liu et al., 2006).

A 2016 review by Louis et al. looked at the state of knowledge pertaining to potential gene expression biomarkers (GEBs) linked to heat stress in scleractinian coral. GEBs, biological markers identified through large-scale gene expression profiling (Stransky & de Souza, 2013), are characteristic biological properties or molecules that can be detected and measured in parts of an organism. GEBs have the potential to be utilized by reef managers as a tool to link organism physiology with large-scale climatic conditions. Also, GEBs have the potential to be used to detect sublethal stress, in-situ, before visible signs of stress are observed. Therefore, this emergent technology that utilizes organism analysis at the molecular level, can theoretically be used in a proactive manner to warn of impending heat stress tolerances being exceeded and the imminent bleaching event that may follow.

Research into gene expression patterns, in terms of coral, only began in the early 2000’s (Louis et al., 2016), thus, is still in its infancy. Potential GEB candidates linked to heat stress in scleractinian coral include heat shock protein genes, ion transport genes, oxidative stress genes, metabolic genes, immune response genes, and structural genes. Research in this field of heat stress detection is ongoing and no universally accepted biomarker of heats stress has been identified at this point.

The study found gaps in the current research of gene expression biomarkers that include a lack of biomarker research in *Symbiodinium*, the algal symbionts, a lack of field studies and field test kits, and the significant variation in study results of gene expression levels between species, location, and within colonies. More research needs to be conducted to address these gaps and increase our limited comprehension of the molecular responses of coral and symbiont to heat stress. As gaps in our knowledge are filled in, this promising approach to heat stress monitoring can be utilized to identify sub lethal heat stress in discrete organisms and inform management decisions.

3.4 Acclimatization

Acclimatization describes phenotypic changes by an organism to perturbations of typical conditions experienced in the natural environment which results in the adjustment of an individual organism's tolerance levels to the perturbation. Acclimatization is one of the primary avenues of research into measures that can help coral reefs adapt to predicted environmental changes and help ensure their survival and continuation of the associated benefits. Research is ongoing to determine the potential limits to acclimatization, the temporal scales attached to the phenomenon, and the species that have the capacity to acclimatize to predicted environmental conditions.

An interesting study by Schoepf et al. (2019) not only looked at long-term acclimatization capacity of the coral *Acropora aspera*, but also the heat stress response upon successful acclimatization to a cooler environment (~3-6°C). *Acropora aspera*, common reef building coral, were sourced from shallow reefs at the Kimberley region in northwest Australia where they are the dominant species at the study site. Coral fragments were placed in thermally controlled mesocosms with temperature regimes that simulated the native environment, a heated environment (+1°C) for approximately six months, and the cooler environment for approximately nine months. Additionally, iterations of both constant and fluctuating (~4°C) diurnal temperatures were established for each temperature regime.

Upon completion of the nine-month preconditioning phase, a 13-day heat stress test was conducted and Fv/Fm, the photochemical efficiency of the coral, being the fraction of light energy converted into chemical energy during photosynthesis, was measured. Heat stress causes irreversible damage to photosystem II (Fv/Fm) in affected symbiotic dinoflagellates that reside within coral polyps during a bleaching event. Thus, heat stress causes dysfunction that has been shown to decrease variable fluorescence and maximum fluorescence (Fv/Fm) (Warner et al., 1999). A photochemical efficiency of approximately 0.6 has been shown to be a good indicator of healthy coral (Schoepf et al., 2019). Photochemical efficiency results from the heat stress test can be seen in figure 6.

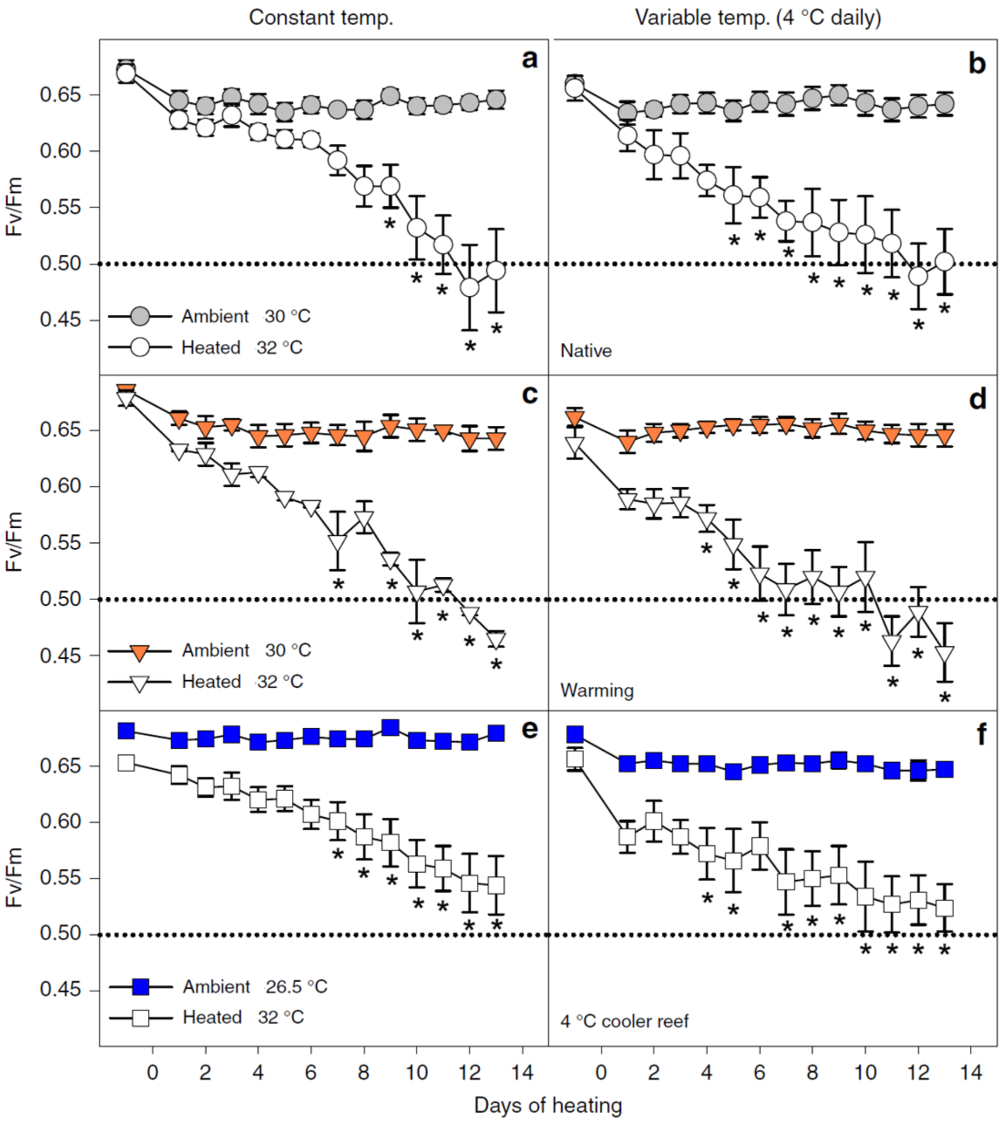

Figure 6 – Photochemical efficiency results from heat stress testing (Adapted from Schoepf et al., 2019)

Figure 6a,b shows results from the native preconditioning temperature regime (circles), figure 6c,d the warmer preconditioning (triangles), and figure 6e,f the cooler preconditioning (squares). Asterisks indicate a statistically significant difference between corals preconditioned in the ambient or elevated heat temperature regimes.

The results show *Acropora aspera* coral that has been preconditioned to a higher than ambient temperature for six months bleached more quickly and with greater severity during the heat stress test as compared to the control coral (ambient temperature regime). During the preconditioning phase, the temperature of the heated mesocosms had to be reduced as seasonal temperature fluctuation caused the onset of bleaching. Coral health was recovered during the next three months before heat stress testing was conducted. Conversely, coral that had been subject to a cooler preconditioning temperature regime showed heat stress tolerance similar to the control coral. Initially, upon exposure to cooler temperatures, low temperature bleaching was induced; however, the physiological function of the coral quickly normalized to be within healthy parameters.

However, previous similar studies have produced results that contradict these findings of a reduced heat tolerance after preconditioning to an elevated temperature environment. For example, a study by Middlebrook et al. (2008), involving the same species of coral, *Acropora aspera*, found that preconditioning prior to a simulated thermal stress event significantly increased thermal tolerance. It is important to note that there were many differences in variables that could potentially affect results across these two studies such as ambient temperature, elevated temperature, geographical location, and preconditioning timescale. More research would need to be conducted to potentially identify the variables that contributed to these contested results.

Some intriguing inferences can be derived from the findings of the Kimberley region study (Schoepf et al., 2019). First, the results indicate that *Acropora aspera* do not have the capacity to increase their heat stress tolerance when subject to preconditioning over this timescale (six months). This may indicate that there is a rigidity to the upper boundary of heat stress tolerance in corals living in a naturally extreme heat environment. The author postulates that coral living in naturally extreme environments such as this may have evolved their heat tolerance at the expense of acclimatization capacity. More research would need to be carried out to verify such a claim.

Second, the results suggest that coral may retain the upper boundary of their heat stress tolerance after acclimatizing to a cooler environment. The implications for use as an adaptation management strategy, at least in the short term, are quite encouraging. Human-assisted transplantation could be utilized to seed cooler reefs with coral species that have been preconditioned or from more heat resistant natural environments. Time could be bought for coral reef systems to naturally acclimatize to predicted environmental conditions without ecosystem collapse while research continues and technology advances. Of note, this is a snapshot of a discrete species of coral under a specific set of experimental conditions. Therefore, the results may be specific to this species of coral, the experimental preconditioning timescale used, or the temperature regimes that were utilized.

For a coral reef to benefit from the effects of heat stress preconditioning, large-scale transplantation would likely be necessary throughout the ecosystem. Upon review, studies into the large-scale application of intervention measures for the effects of increased frequency of heat waves could not be identified. This is not surprising due to the relatively novel research into the preconditioning of corals and results that are not always consistent between studies. Large-scale studies will need to be conducted to identify potential risks that may not be anticipated. For example, if there is not enough diversity in the species of thermally resistant coral introduced to a reef through transplantation, overall biodiversity may suffer which could degrade ecosystem health and reduce the output of ecosystem services.

However, climate change adaptation projects are emerging, such as the United Nations Development Programme (UNDP) supported project in Mauritius and Seychelles that was approved in 2018 (Adaptation Fund, n.d.). The six-year project focuses on the restoration of degraded reefs where live coral cover has declined by 70 and 50-90%, in Mauritius and Seychelles respectively, over the last couple of decades. Corals that are resistant or resilient to bleaching will be propagated in nurseries before being transplanted onto the degraded reefs. Studying projects such as this will provide insight into the effects of large-scale preconditioning of coral reefs, the benefits that can be gained, and potential risks that could be mitigated.

3.4.1 Intra-generational Acclimatization

Intra-generational acclimatization is a rapid-response mechanism where phenotypic changes occur in an organism during its lifetime due to imparted stresses (van Oppena et al., 2015). The result is a readjustment of the organism’s threshold to stressors such as heat. This approach is a more viable adaptation strategy in organisms that are long-lived, such as coral, that have a lifespan of up to 5,000 years, making them the longest living animals on earth (NOAA, n.d.-g). Corals' long lifespan allows time for acclimatization to be realized with the benefits lasting into the future.

A study by Coles et al. (2018) conducted an experiment in Kānéohe Bay, Hawaii, where the open ocean water temperature has increased by approximately 1°C over the last 50 years, during which three major bleaching events occurred. Since thermal tolerance data was acquired through experimentation at this location in 1970, along with the conditions described, it provided ideal circumstances to replicate the 1970 experiments and compare the results for evidence of acclimatization. The researchers increased the precision of experiment reproduction and the validity of their comparisons by ensuring the same location, methodology, seawater system, and observer were used across both iterations.

The experiment involved exposing the same three species of coral, being *Montipora capitata*, *Pocillopora damicornis*, and *Lobactis scutaria* to identical heat stress conditions, being ambient and 2.8°C above ambient SST. The ambient temperature condition in 1970 was 26.4°C as compared to 28.6°C in 2017. A total of 480 colonies were used within six mesocosms where subject corals were randomly placed within shaded and unshaded sections (50/50), with the shaded section simulating a water depth of approximately 2.5m. The mean temperatures maintained within the mesocosms during the experiment were 28.62 ± 0.015°C (ambient) and 31.40 ± 0.015°C (heated) with no statistical significance between mesocosms.

Readings and observations were obtained across a 31-day heating phase followed by a 28-day recovery phase. Coral survivorship was determined by the number of individuals that remained alive throughout both phases. Visual observations of pigmentation and mortality were completed by the collaborator synonymous with both experiments to retain any subjective bias. During the heated phase, visual observations were taken 2-3 times a week for the first two weeks, two times a week during the third week, and once during the fourth week. During the recovery phase, visual observations were conducted once per week. The frequency of observation in 2017 was consistent with that of the 1970 experiment. The results of survivorship and visual health assessments can be seen in figure 7.

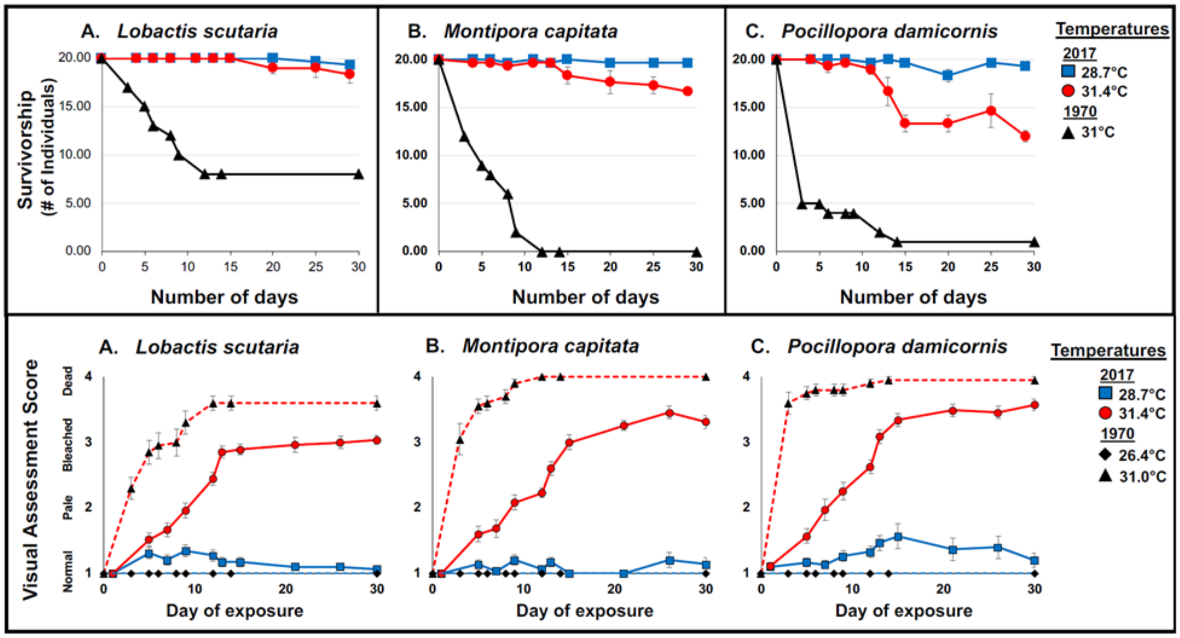

Figure 7 – Survivorship results of each coral species included in both experiments (Adapted from Coles et al., 2018)

Although the baseline had shifted between experiments conducted in 1970 versus 2017, the survivorship results clearly show a much higher proportion of survivorship in the 2017 iteration for all species involved. A numerical summary can be seen in table 1.

Table 1 – A numerical comparison of survivorship results

Species	1970	2017
Montipora capitata	0%	83%
Pocillopora damicornis	5%	60%
Lobactis scutaria	40%	92%

Visual assessments scores, meant to describe mean health, showed results similar to survivorship in that heat stressed coral in 2017 had been impacted to a lesser degree as compared to 1970. The onset of bleaching was postponed for a number of days and the overall severity of effects, such as mortality, were reduced. The author of this study states that this experiment is the first to provide evidence of acclimatization to increased SSTs occurring over the last 50 years for the same coral species at the same location.

The results of this study provide evidence that acclimatization in these species of coral does occur under specific conditions. What is unclear is the effect the individual mechanisms that induced acclimatization have, if they are more effective when applied in tandem, and the extent of the timescale necessary to produce desired results. For example, what effect of acclimatization would be achieved if elevated SSTs or multiple bleaching events were applied individually, how do the results differ from the concurrent application of influences as in this experiment, and how would the results differ when applied over various time periods. Much more research, currently in various stages of planning or completion, needs to be accomplished to begin to answer these types of questions more definitively.

3.4.2 Trans-generational Acclimatization

Parental effects are rapid-response mechanisms where the parental environmental exposure impact aspects of offspring phenotype and can contribute to trans-generational acclimatization. Trans-generational acclimatization, such as epigenetics, where there are heritable phenotype changes that do not involve alterations in the DNA sequence, can help offspring mitigate the impact of the environment experienced by the parent. Having the ability to pass on greater heat stress tolerance to offspring could potentially help reduce coral vulnerability and adapt to the predicted environmental conditions of the future (Putnam & Gates, 2015).

Research conducted by Putnam and Gates (2015), sought to explore this relationship in the reef-building coral *Pocillopora damicornis*. The study culminated in the first documented evidence of parental effects in a cross-generational exposure to increased temperature and ocean acidification. While we are only interested in increased temperature effects in this study, increased ocean acidification is consistent with predicted future oceanic conditions, as previously mentioned. This study is significant in that up until this time research into the acclimatization in corals was limited to a single generation.

Parent coral was divided into two groups and subject to either ambient (26.5°C) or elevated (28.9°C) temperature profiles during the larval brooding period which occurs over a period of approximately 1.5 months. There were no indications that exposure to higher temperatures affected the larvae release timing.

Brooded larvae from both adult colonies were each subsequently exposed to ambient and elevated temperature conditions. Measurements of larvae size, dark respiration rate, and dark respiration rate normalized to the size of the larvae were taken and compared between ambient and elevated temperature conditions. The results of the measurements can be seen in figure 8.

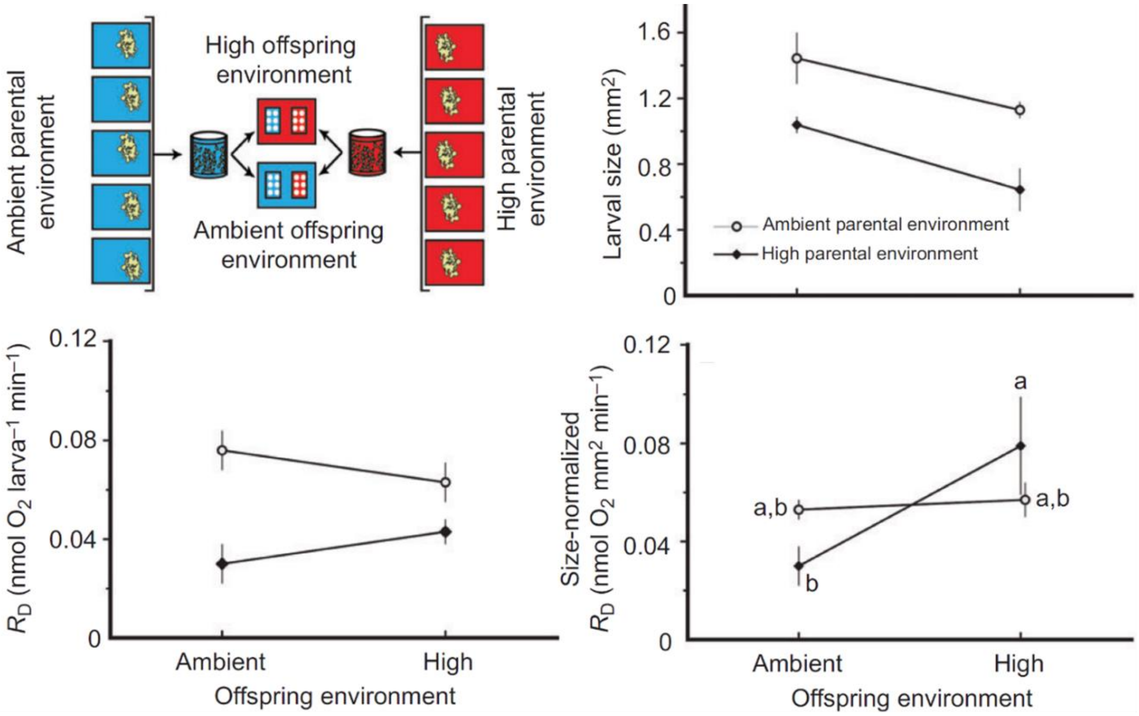

Figure 8 – Measurements of offspring larvae under ambient and elevated conditions (Adapted from Putnam & Gates, 2015)

Larvae measured before the secondary treatment showed a significant size difference with larvae brooded in the elevated temperature of exposed parents being an average of 33% smaller than their ambient counterparts. Additionally, dark respiration rates were shown to be reduced by 43%. Subsequently, when sets of larvae were exposed to a secondary treatment of elevated temperature, there was further size reductions of 38% and 22% in the elevated and ambient temperature brooded larvae, respectively.

However, these results are somewhat deceiving until both sets of larvae were size normalized, exposed to secondary treatment, and measured for dark respiration rates. Upon doing so, results from the ambient brooded larvae showed a negligible difference in respiration rates when exposed to ambient or elevated temperature conditions. Conversely, the elevated temperature brooded larvae displayed a significantly higher dark respiration rate when exposed to conditions identical to brooding conditions versus a low dark respiration rate when exposed to ambient temperatures.

These findings suggest that larvae brooded in heat stressed conditions will physiologically perform better in similar conditions indicating a potential avenue to take advantage of trans-generational acclimatization to breed more heat resistant coral. While this study may offer a glimmer of hope, much more research must be completed to determine the potential capacity of these effects. For example, there has undoubtedly been opportunities for trans-generational effects to occur in the natural environment, yet widespread coral cover decline has continued to take place. Also, this study was completed using one species of coral at a constant specified temperature. Variations on this experiment, such as the inclusion of a variety of coral species that are globally ubiquitous in coral reef systems and employing fluctuating temperatures during the brooding process may yield significant results.

Chapter 4: Conclusions

It is clear that the health of coral reefs is being impacted by anthropogenic activities. Local impacts to coral reefs have been degrading and destroying these important marine ecosystems for decades. However, the greatest threat to the existence of coral reefs on a global scale is the fallout from the climate crisis. By continuing to emit GHGs to the atmosphere, humans are tipping the planet's natural energy balance, and trapping heat within our atmosphere. This steady increase in heat is causing our oceans to warm and the changing climate is causing marine heat waves to occur with greater frequency and intensity.

Corals are quite sensitive to deviations in seawater temperature and can become stressed with just a 1-2°C increase from the mean monthly temperature. When corals are thermally stressed, they expel their resident zooxanthellae with whom they have a symbiotic relationship. If the seawater temperature does not decrease, the coral will not intake any new algae. Corals rely on the photosynthetic capabilities of the algae for energy and sustenance. Consequently, if corals experience sustained thermal stress, they will eventually starve to death.

While coral species grow at different rates, the mortality of long-lived species can take decades to be naturally replaced. The increasing frequency of marine heat waves does not allow enough time for corals to recover from these heat stress events. In order to secure a future for coral reefs, research into assisted evolution is ongoing to help corals naturally adapt to predicted environmental conditions. Acclimatization, an assisted evolution technique, is offering some hope in the efforts to find a way to help corals adapt to rising ocean temperatures.

Results from studies have generated mixed conclusions with some research showing that corals do have the ability to acclimatize to novel environmental conditions, albeit over a long temporal scale, and become more heat stress resistant after recovering from a bleaching event. Conversely, there is research that has indicated being previously subject to bleaching temperatures does not induce acclimatization and that there is no statistically significant change in coral thermal tolerance when subject to warmer environmental conditions.

Research into the potential for acclimatization in corals can indicate different results for a variety of reasons. For example, there are differences between studies in the discrete species of coral being studied, experimental methodologies, equipment setups, temperature regimes, ways of quantifying coral health. Also, subjective bias can be introduced due to data collection techniques such as visual observations. Developing and implementing a standard heat stress testing regime, such as CBASS, that can be used in all scenarios would help reduce the variations in results imparted by study-specific methodologies and provide better data for comparisons. The challenge is to identify species of coral that have a high thermal tolerance or have the capacity for acclimatization to warmer conditions at a rate that at least matches the increasing thermal stress imparted by the climate crisis.

Some research suggests that corals have an easier time adjusting to cooler than normal seawater conditions as opposed to warmer conditions. Also, research indicates that coral may retain their upper thermal tolerance even after acclimatizing to the colder environmental conditions. The implications of coral retaining their upper thermal tolerance are quite significant. Sourcing coral from areas of high heat tolerance and seeding coral reefs in cooler environmental locations through transplantation provides an excellent management tool. As ocean temperatures rise in the cooler locations, coral will already have the necessary thermal tolerance to survive the novel conditions, at least in the short term.

One potential issue is that corals currently residing in thermally extreme environments may have already reached their upper thermal tolerance limit. Increasing their heat stress tolerance may not be possible or acclimatization may not be able to occur fast enough to keep up with the increasing thermal stress imposed upon them. If adaptation is not possible, or there is an upper thermal tolerance limit, the fallout could be disastrous if the current climatic trends continue; however, much more research must be completed before such a claim can be made.

Trans-generational acclimatization is an emerging field of study as most studies up to this point have focused on intra-generational acclimatization. Since corals are long-lived creatures, scientists initially focused on the potential to modify their thermal tolerance during their lifespan. Research is now expanding into the potential of trans-generational acclimatization with a novel study suggesting that there is potential to utilize this approach. The results indicate that trans-generational acclimatization could have a positive affect on the progeny of corals that have experienced heat stress, specifically during the brooding period of offspring development.

What is quite evident from conducting this systematic literature review, is that a significant amount of research in all areas pertaining to acclimatization potential of corals needs to be performed. There appears to be mounting evidence that acclimatization could be a viable methodology to assist corals in increasing their thermal tolerance. However, our current level of knowledge cannot provide a definitive answer as to which coral species are primary candidates or what temporal scale is necessary to produce an upper thermal tolerance comparable to predicted environmental conditions. The evidence indicates that humans are in a race against time to help ensure there is a future for corals. Human innovation, technology, and resources must be employed expeditiously to solve a problem that we have created before it is too late.

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Appendix A

Table A1 – Documents that provide the basis for the systematic literature review project

Source	Year	Purpose	Type of article	Major findings
Coral Reef Decline				
Bruno, J.	2011	To provide an argument as to why the baseline of the Great Barrier Reef (GBR) should be derived from information from indicators prior to 1986 when ecological surveys by the Australian Institute of Marine Science (AIMS) began.	Review Report	Acknowledgement that science cannot definitively provide an accurate baseline for the GBR at this time. However, enough evidence exists that indicates declines began prior to 1986 when ecological surveys began. Thus, the 1986 ecological surveys should not be used as a comparative baseline. There is great difficulty and uncertainty in trying to establish a baseline.
Cramer et al.	2020	To determine when Caribbean corals first began to decline from prehuman levels. Also, to explore the connection between local drivers and initial declines.	Research Report	Declines in dominance from prehuman values began in the 1950's and 1960's long before disease or bleaching began to impact the Caribbean corals. Local human stressors played a significant role in coral declines.
Ecosystem Services				
Scripps Institution of Oceanography	2020	To provide an overview of the connection between coral reefs and oceanic biodiversity and a description of various ways that corals provide qualitative value.	Research Report	Although coral reef ecosystems occupy one tenth of one percent (0.1%) of the earth's seascape, an estimated 25% of marine species are supported by coral reef systems at some point during their lifecycle.
Scripps Institution of Oceanography	2020	To provide a description of various ways that corals provide qualitative value. (web page, no page numbers)	Research Report	Although coral reef ecosystems occupy one tenth of one percent (0.1%) of the earth's seascape, an estimated 25% of marine species are supported by coral reef systems at some point during their lifecycle.
TEEB	2010	The aim is to provide a synthesis of the approach employed by The Economics of Ecosystems and Biodiversity (TEEB). Thus, show how economic concepts and tools can be used to incorporate the values of nature into the decision-making process.	Synthesis Report	There is a need to make nature's value visible, provide a valuation methodology for biodiversity and ecosystem services, account for risk and uncertainty, compare future costs and benefits, provide better management through better measuring of natural resources, include social costs due to impacts on the environment in any valuation, change behaviour through incentives, create more protected areas, enhance ecological infrastructure, and incorporate ecosystem services and biodiversity valuations into economic decision making.

Source	Year	Purpose	Type of article	Major findings
Kiessling et al.	2010	To determine whether evidence indicates coral reefs are drivers of evolution and biodiversity.	Research Report	Results of the study showed 21.6% of candidate genera were positively identified as originating in a reef environment, indicating that coral reefs are cradles of evolution, and that reefs are a significant net exporter of biodiversity.
Climate Crisis				
NASA	n.d.	To provide an overview of global warming and climate change.	Review Report	Observed change in average global surface temperatures and climate change are continuing primarily as a result of anthropogenic activities.
NASA	2017	To provide an overview of the earth's energy budget.	Review Report	Studying the earth's energy budget will identify imbalances, through anthropogenic activities and natural phenomenon, that will affect global warming and weather patterns.
IPCC	2014	To provide a synthesis of climate change information available at that time.	Synthesis Report	Anticipated consequences of climate change include global mean sea level rise, ocean warming, ocean acidification, and heat waves, precipitation events, and hurricanes occurring with more intensity and frequency.
IPCC	2019	To provide an assessment on how climate change will impact the ocean and cryosphere.	Assessment Report	The effects of climate change are predicted to impact many aspects of the ocean and cryosphere including ocean warming resulting in coral bleaching events, increased disease outbreaks, and hypoxia.
Rick and Caldera	2014	To determine the latency period between a release of CO_2 and its maximum warming impact on the environment.	Research Report	The warming effect from a CO_2 emission to the atmosphere can be expected to reach its maximum within approximately a decade from release and persist for longer than a century.
Ocean Temperature Rise				
Guan et al.	2014	To determine the global distribution and environmental tolerances of coral reefs and identify potential reef habitat areas.	Research Report	Coral reefs are currently present in waters with an annual mean temperature between 21.7°C and 29.6°C. The minimum value of aragonite saturation in coral reef waters has decreased from 3.28 to 2.82. Since the modeling did not consider local anthropogenic stressors, the results indicated greater coral cover than currently surveyed.

Source	Year	Purpose	Type of article	Major findings
Oliver et al.	2019	To predict marine heat wave (MHW) frequency and intensity to the end of the 21st century under two GHG emission scenarios, being Representative Concentration Pathways (RCPs) 4.5 and 8.5.	Research Report	MHWs will become more frequent with greater intensities. Global mean MHW intensity will exceed natural variability for RCP 4.5 in the year 2044 and the year 2033 for RCP 8.5. The results predict that globally, there will be MHWs 365 days a year under RCP 8.5 by the year 2100.
<u>Ocean Acidification</u>				
Ocean Chemistry & Acidification	2018	To provide an overview of how acidification of the earth's ocean is caused by changing chemistry due to CO_2 uptake.	Review Report	Buffering can not keep up with the increasing rate of ocean acidification and shell-producing marine organisms are becoming increasingly physiologically stressed as it becomes more difficult to build shells.
Eyre et el.	2018	To determine a tipping point when net accretion of coral reefs will turn to net dissolution due to ocean acidification.	Research Report	$CaCO_3$ dissolution in reef sediments across five globally distributed sites is negatively correlated with the aragonite saturation state of seawater. The years when net accretion of $CaCO_3$ will turn to net dissolution were identified under various scenarios.
TOPT	2018	To provide an overview of the causes and consequences of ocean acidification.	Review Report	Massive amounts of carbon dioxide are dissolving into the ocean at a quicker rate than any time in history. The result is that natural buffering will not be able to keep up which is increasing the acidity of the ocean.
Byrne and Fitzer	2019	To provide an overview of the impacts of ocean acidification on various marine organisms.	Research Report	Ocean acidification imparts physiological stress upon marine organisms that biomineralize their shells.
<u>Coral Bleaching</u>				
NOAA	n.d.	To provide a foundational overview of coral bleaching.	Review Report	Stressors such as temperature, light, and nutrients can result in coral bleaching. Bleaching occurs when coral expel zooxanthellae that live within their tissue. Coral can potentially survive a bleaching event.
Hughes et al.	2018	To examine the shortening intervals between major bleaching events and the resulting impact to the recovery of affected coral reefs.	Research Report	The interval between bleaching events has steadily declined since approximately 1980 with the average time between events currently being only 6 years. This does not allow enough time between events for coral communities to recover.

Source	Year	Purpose	Type of article	Major findings
Eakin et al.	2018	To provide a review of the history of mass bleaching events and an evaluation of the predicted frequency and intensity of such events.	Research Report	The rate of incidence of global bleaching events is increasing dramatically with greater intensity and duration of such events.
Mitigation of Global Climate Crisis Impacts to Coral Reef Systems				
Smith and McCleod	2018	To provide an overview of the history and science behind reef restoration methods and techniques.	Research Report	There have been three distinct periods when different approaches in reef restoration have emerged since the 1970's. The first period involved the addition of artificial reef structures and transplanting of coral. The second period concentrated on both the addition of habitat and removal of invasive algae and predators such as the crown-of-thorns starfish. Finally, the current period, beginning in 2016, has been focussing on incorporating advances in technology into reef restoration efforts.
Liew et al.	2018	To study whether epigenetic mechanisms regulate phenotypic acclimatization in corals when exposed to increased acidification over a long time period.	Research Report	The findings indicate that DNA methylation could fine-tune gene expression in response to changes in the exposed environment. Additionally, the results suggest an epigenetic component in phenotypic acclimatization could help corals adapt to changing environmental conditions.
van Oppena et al.	2015	To provide suggested avenues to evaluate the capacity of coral to develop greater heat stress tolerance through assisted evolution. Also, to analyze risks and benefits associated with assisted evolution.	Review Report	There are four main areas of research in the field of assisted evolution, being acclimatization, modification of microbial symbiont communities, evolution of *Symbiodinium*, and selective breeding, that need to be advanced to determine their feasibility as it applies to the adaptation and acclimatization of corals to climate change. Also, ethical and socioeconomic implications of these approaches should be discussed robustly.
Heat Stress Thresholds				
Jokiel and Coles	1977	To determine how long-term exposure to heat will affect the rate of growth and mortality of Hawaiian corals. (Pg.201)	Research Report	Coral growth is curvilinear as related to temperature. Coral can recover when returned to optimal temperature conditions. Upper lethal limits for the three species of coral tested were consistent with previous research.

Source	Year	Purpose	Type of article	Major findings
Coles et al.	1976	To compare the natural temperature variations and upper thermal limits of tropical and subtropical corals.	Research Report	Corals are exposed to temperatures that are within 1-2°C of their upper thermal limit at both tropical and subtropical locations.
Hoegh-Guldberg, O	1999	To provide an overview of the biochemical, physiological and ecological components of coral bleaching and establish predictions as to the frequency and intensity of bleaching events over the 100 years from when the study was conducted.	Research Report	Most coral reef systems are predicted to experience bleaching events on a nearly annual basis by the year 2040. Some coral reefs are predicted to reach this point by 2020. Corals are living in seawater that is in increasingly closer proximity to their thermal limit in the summer months.
Schoepf et al.	2015	To experimentally assess the heat tolerance of two species of coral, from both intertidal and subtidal environments, located in the Kimberly region of Australia, to variable and elevated water temperatures.	Research Report	Both corals were susceptible to bleaching when their maximum monthly mean temperature was exceeded by just 1°C. Intertidal corals, which experience wide diurnal temperature fluctuations, were less susceptible to bleaching than subtidal corals that inhabit a much more thermally stable environment.
Reef Resilience Network	n.d.	To provide insight into the various mechanisms that produce different levels of susceptibility to bleaching in corals.	Review Report	Characteristics that affect different levels of susceptibility to bleaching in corals include differences in species, genetics, and various other factors (eg. tissue thickness, colony integration)
Voolstra et al.	2020	To assess the ability of short-term acute heat stress assays (18-hours) and long-term heat stress experiments (21-day) approaches to determine thermal tolerance differences of in-situ coral reef thermal tolerance thresholds.	Research Report	The measurements of photosynthetic efficiency using CBASS and the classic long-term setup were found to be comparable. This is important because photosynthetic efficiency during heat stress indicates the ability of the host coral to maintain a hospitable environment for the symbiont algae.
<u>Heat Stress Identification and Monitoring</u>				
Liu et al.	2006	To provide an overview of NOAA Coral Reef Watch (CRW) program's near-real-time satellite global coral bleaching monitoring activities.	Review Report	CRW monitoring includes near-real-time satellite global 50-km nighttime SSTs, coral bleaching HotSpots, coral bleaching DHWs, Tropical Ocean Coral Bleaching Indices webpage, and SST time series. These tools are used to detect the occurrence and monitor the development of thermal stress that can result in a coral bleaching event.

Source	Year	Purpose	Type of article	Major findings
Louis et al.	2016	To provide a review of the current state of knowledge at that time regarding gene expression biomarkers (GEBs) being used to determine heat stress in corals.	Review Report	GEBs have the potential to be utilized by reef managers as a tool to link organism physiology with large-scale climatic conditions. Also, GEBs have the potential to be used proactively to detect sublethal stress, in-situ, before visible signs of stress are observed.
Acclimatization				
Schoepf et al.	2015	To experimentally assess the heat tolerance of two species of coral from the Kimberly region of Australia to variable and elevated water temperatures from intertidal and subtidal environments.	Research Report	Both corals were susceptible to bleaching when their maximum monthly mean temperature was exceeded by just 1°C. Intertidal corals, which experience wide diurnal temperature fluctuations, were less susceptible to bleaching than subtidal corals that inhabit a much more thermally stable environment.
Schoepf et al.	2019	To determine whether naturally heat-resistant coral can maintain their heat tolerance upon larval dispersal or translocation to cooler reefs.	Research Report	The results indicate coral that has been preconditioned to a higher than ambient temperature bleached more quickly and with greater severity during a heat stress test as compared to the control coral. Coral that had been subject to a cooler preconditioning temperature regime showed heat stress tolerance similar to the control coral.
Putnam et al.	2015	To determine if there is evidence of parental effects in reef-building coral as a result of cross-generational exposure to increased temperature and ocean acidification.	Research Report	The findings suggest that larvae brooded in heat stressed conditions will physiologically perform better in similar conditions indicating a potential avenue to take advantage of trans-generational acclimatization to breed more heat resistant coral.
Coles et al.	2018	To determine possible changes in thermal tolerances of coral located in Kānéohe Bay, Hawaii.	Research Report	The results indicate that thermal acclimatization to increased ocean temperature does occur under the experimental conditions used.
Warner et al.	1999	To determine whether thermal stress may disrupt thylakoid membrane stability and proper D1 turnover of the symbiont algae, resulting in damage to photosystem II.	Research Report	The study provides evidence of irreversible damage to photosystem II in heat-stressed symbiotic algae within corals during a natural bleaching event.
Middlebrook et al.	2008	To determine how recent thermal history affects the response of corals and symbionts to thermal stress.	Research Report	The study indicates that recent thermal stress events, 2 weeks and 1 week prior to a bleaching event, provide increased thermal tolerance for coral. Short time-scale thermal adaptation could affect coral bleaching tolerances.

Glossary

Acclimatization

The process by which an organism will respond to being exposed to new environmental conditions (Britannica, 1998).

Anthropogenic

"Relating to or resulting from the influence of human beings on nature" (Merriam-Webster, n.d.-a).

Anthropogenic forcings

Human caused influences on the natural equilibrium of the earth's energy budget that drive changes in the climate (National Oceanic and Atmospheric Administration [NOAA], n.d.-a).

Assisted evolution

Naturally occurring evolution that is assisted through human intervention to increase the speed of the process and enhance desired traits (van Oppena et al., 2015).

Benthic marine invertebrates

Marine organisms that do not have a backbone and live on the ocean floor (Biologica, n.d.).

Biogenic carbonate

Carbonates that are precipitated as a result of biomineralization (Duller, 2015).

Biomineralization

The act of an organism forming biological tissue or structure from the accumulation of minerals (Merriam-Webster, n.d.-b).

Brooding period

Brooding occurs in coral polyps when spawned sperm fertilize eggs within the polyp. Larvae are not released by the polyp until they have undergone substantial development, usually being timed with a lunar cycle (Great Barrier Reef Marine Park Authority [GBRMPA], n.d.).

Calcium carbonate polymorph

Calcium carbonates that are chemically identical but exist in more than one crystal form (Britannica, n.d.-a).

Calyxes

Cavities within which coral polyps reside (Liew et al., 2018).

Carbon sequestration

The capturing and storage of carbon from the atmosphere within a carbon sink (United States Geological Survey [USGS], n.d.).

Carbon sink

A reservoir that absorbs more carbon than it releases and stores the accumulated carbon (National Geographic, n.d.-a).

Carbonate system

The carbonate system is a series of reversible chemical reactions that serve to buffer fluctuations in species concentration while regulating pH levels and flow of CO2 between the atmosphere, hydrosphere, biosphere, and lithosphere (*Ocean Chemistry & Acidification*, 2018).

Coral aquaculture

Also known as coral gardening or coral farming, coral fragments of healthy populations are cultivated in nurseries before being explanted onto reefs with degraded coral cover (Reef Resilience Network, n.d.-a).

Coral bleaching

Coral bleaching occurs when coral polyps expel their colourful resident algae, zooxanthellae, which leaves the coral a striking white colour, and is an indicator that the coral is under stress (NOAA, n.d.-b).

Coral polyps

Coral polyps are clear, soft body animals that produce calcium carbonate protective structures around their bodies which form corals reefs (Coral Reef Alliance, n.d.).

Dark respiration rate

“The rate of oxygen consumption measured in the darkness per unit of skeletal surface area” (Coral Trait Database, n.d.).

Degree heating week

A method to quantify an area’s accumulated heat stress over a 12-week period. A degree heating week is calculated by the addition of temperatures that have exceeded the bleaching threshold in the area of interest during that period (NOAA, n.d.-c).

DNA methylation

DNA methylation is an epigenetic mechanism involving the transfer of a methyl group to DNA. DNA methylation can modify the function of genes thereby affecting gene expression (Moore et al., 2013).

Earth's energy budget

The earth's energy budget consists of the balance between energy radiated by the sun into the earth's atmosphere versus the amount of energy radiated from earth's atmosphere back into space (National Aeronautics and Space Administration [NASA], 2017).

Ecosystem

A geographic area comprised of all living and non-living components and the interrelationships therein (Britannica, n.d.-b).

Ecosystem services

The direct and indirect contributions of ecosystems to human well-being, that benefit the environment, human health, and underpin many economies (The Economics of Ecosystems and Biodiversity [TEEB], 2010).

El Niño

El Niño is a naturally occurring phenomenon named for the warming phase of the El Niño Southern Oscillation (ENSO). It occurs approximately every three to seven years and results in the warming of the surface temperature of the Pacific Ocean. (National Geographic, n.d.-b).

Epigenetics

Epigenetics is the study of how environmental factors can cause changes that affect the way an organism's genes work. Epigenetics can change how your body reads a DNA sequence but do not change your DNA sequence itself and are reversible (Centers for Disease Control and Prevention [CDC], n.d.).

Fluorescence

Fluorescence is the "emission of electromagnetic radiation, usually visible light, caused by excitation of atoms in a material, which then reemit almost immediately. The initial excitation is usually caused by absorption of energy from incident radiation or particles, such as X-rays or electrons" (Britannica, n.d.-c).

Gene expression biomarkers

Biological markers identified through large-scale gene expression profiling (Stransky & de Souza, 2013).

Genera

Genera is the plural of genus, where genus is used to classify a group with similar biological characteristics and is ranked between family and species (Merriam-Webster, n.d.-c).

Genes

Genes are passed from a parent organism to its offspring and allow for the heritable transfer of traits (National Human Genome Research Institute [NHGRI], n.d.-a).

Genomes

An organism's genome contains all the information that would be needed for replication as it is its complete set of DNA or a DNA blueprint (NHGRI, n.d.-b).

Global bleaching event

Global bleaching events take place when mass bleaching events occur within all three ocean basins, being the Atlantic, Pacific, and Indian Oceans, during a given year (Eakin et el., 2018).

Global warming

Global warming the gradual increase of the mean global temperature of the lower atmosphere, typically measured from surface temperatures, over a 30-year period (IPCC, 2018).

Greenhouse gas

Gases that absorb infrared radiation emitted by the earth's surface in response to the shortwave radiation received from the sun. The infrared radiation is absorbed as heat; thus, heat is trapped in the earth's atmosphere that would normally be emitted back into space. Greenhouse gases include water vapour, carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), hydrofluorocarbons (HFCs), perfluorocarbons (PFCs), and sulphur hexafluoride (SF_6) (Environmental Protection Agency [EPA], n.d.-a).

Hypoxia

Hypoxia is low dissolved oxygen content in seawater which is exacerbated by warming seawater. Warmer water decreases the solubility of oxygen, resulting in a reduced capacity to absorb dissolved oxygen as compared to cold water (Altieri et al., 2017).

Intra-generational acclimatization

Intra-generational acclimatization is a rapid-response mechanism where phenotypic changes occur in an organism during its lifetime due to imparted stresses (van Oppena et al., 2015).

Marine heat waves

For the purposes of this study, MHWs are defined as periods when daily temperatures were above a threshold based on the seasonally varying 90th percentile for at least five consecutive days (Oliver et al., 2019).

Modification of symbiont communities

The process of adjusting the composition of coral-associated microbes, within their endosymbiotic communities to increase the stress tolerance of the symbionts (van Oppena et al., 2015).

Phenotype

An organism's observable traits or characteristics (NHGRI, n.d.-c).

Phenotypic plasticity

The ability of one genotype to express varying phenotypes (Liew et al., 2018).

Photochemical efficiency

The fraction of light energy converted into chemical energy during photosynthesis (Warner et al., 1999).

Representative Concentration Pathways

"Representative Concentration Pathways (RCPs). RCPs are scenarios that include time series of emissions and concentrations of the full suite of greenhouse gases (GHGs) and aerosols and chemically active gases, as well as land use / land cover. RCPs provide only one set of many possible scenarios that would lead to different levels of global warming" (Intergovernmental Panel on Climate Change [IPCC], 2019).

Selective breeding

The process of selective breeding involves identifying desirable traits in parent corals that can be bred to produce offspring with these desirable characteristics (Albright, 2018).

***Symbiodinium* evolution**

Symbiodinium evolution looks to modify zooxanthellae through mutagenesis and/or selection processes in a laboratory setting (van Oppena et al., 2015).

Symbiont

A participant in a symbiosis relationship where two organisms from different species form a close biological interaction (Merriam-Webster, (n.d.-d).

Trans-generational acclimatization

Trans-generational acclimatization (eg. epigenetics) involves heritable phenotype changes that do not involve alterations in the DNA sequence (Putnam & Gates, 2015).

Zooxanthellae

Zooxanthellae are photosynthetic algae, in a symbiotic relationship with coral, that reside within coral polyps, give them their vibrant colours, and provide sustenance to survive (NOAA, n.d.-d).