# The future of coral reefs is looking bleak:
## Potential areas where assisted colonization of naturally resilient coral species would be most suitable

**Bachelor thesis**

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## Abbreviation list

| | |
|---|---|
| ABH | Adaptive Bleaching Hypothesis |
| ASB | Annual Severe Bleaching |
| CMIP5 | World Climate Research Programme's Coupled Model Intercomparison Project Phase 5 |
| $CO_2$ | Carbon Dioxide |
| DHM | Degrees Heating Moth |
| DHW | Degrees Heating Week |
| IUCN | International Union for Conservation of Nature |
| NOAA | National Oceanic and Atmospheric Administration |
| SST | Sea Surface Temperature |
| UNEP | United Nations Environment Programme |
| WoRMS | World Register of Marine Species |
| WWF | World Wide Fund for Nature |

## Summary

The future of coral reefs is looking bleak. Global warming is causing there to be more frequent and severe coral bleaching events. There are, however, thriving corals that are flourishing in extreme environments. These so-called "super" corals have for instance been able to adapt to extremely high temperatures and will therefore, be less likely to bleach due to the effects of global warming. The increasing threat of global warming should be regarded as a call to action to explore new proactive reef management options, such as assisted colonization. This thesis aims to give an overview of areas in which assisted colonization of naturally resilient coral species occurring in thermally extreme environments will be most suitable. This aim was accomplished by first of all, discerning coral reef 'hotspots' that will be subjected to a prolonged increase in SST in the upcoming decades using climate model output. Thereafter, coral species that are able to thrive in thermally extreme environments were identified and an overview was made of their spatial distributions and the environmental conditions in which they occur. At last, maps of the hotspots were compared with maps of the spatial distributions of the naturally resilient corals in ArcGIS. The Red Sea, east coast of Africa, Madagascar, Taiwan, the Philippines, Papua New Guinea, and Indonesia are identified as suitable areas for assisted colonization. What these areas have in common is that they are mostly situated in developing regions. This means that multi-stakeholder partnerships need to be established to implement assisted colonization in these areas. *Stylophora pistillata* and *Pocillopora damicornis* are identified as suitable coral species to translocate, as they have the highest interaction rate with zooxanthellae of any known coral species. Furthermore, these species are frequently mentioned in literature as corals that are able to withstand high thermal stress and show less suffering as a result of bleaching. Despite the limitations of this research, it is nonetheless important to do additional research in this field of study, as immediate action is necessary to impede extinctions caused by climate change.

# 1. Introduction

Coral reef ecosystems are one of the most diverse natural communities on Earth (Reaka-Kudla, Wilson, & Wilson, 1996). Coral reefs are the habitat for 25% of all marine life. Even though they cover only 0.00063% of the Earth's surface, they harbour more than 250,000 known species (Birkeland, 2015). Next to their source of natural beauty and ecological significance, coral reefs provide a myriad of services to the coastal communities they support, on which 500 million, predominantly poor, people depend (Value of Reefs, 2020; Wilkinson, 2004). These ecosystem services add up to nearly $10 trillion annually (Anthony, et al., 2017), mostly in the form of food, tourism, and coastal protection (Wilkinson, 2004).

These vital ecosystems are under climatic threat. Over the last four decades, the living coral has declined by 53% in the Western Atlantic, 40% in the general Indo-Pacific, and 50% on the Great Barrier Reef (Birkeland, 2015). Greenhouse gases are accumulating in the atmosphere, which results in increasing sea surface temperature (SST) and increasing acidification of the ocean (Camp, et al., 2019). This has led to more frequent and intense thermal-stress events. As a result, there have been unprecedented cases of coral bleaching, disease, and mortality (van Woesik & McCaffrey, 2017). This rapid decline of coral reefs all over the world has been a call to action for researchers to identify or engineer a way to increase resilience in coral populations (Camp, Schoepf, & Suggett, 2018).

Studying and understanding thriving coral species flourishing in extreme environments can prove to be beneficial in creating more resilience for coral reefs threatened by anthropogenic climate change (Camp, et al., 2018). These corals are naturally resilient to extreme conditions (Camp, et al., 2019). Examples of this are the "super-corals" growing in the Gulf of Aqaba (northern Red Sea). These corals will only bleach when the SST is 6 degrees Celsius warmer than their average summer maximum. This is considered to be an extreme thermal tolerance, as most corals will start to bleach when they are subjected to SSTs of 1 or 2 degrees Celsius warmer than their maximum (Grottoli, Tchernov, & Winters, 2017).

Corals thriving in extreme conditions can function as natural laboratories to gain knowledge on how coral reefs will respond to increasing environmental stress. This knowledge could be used to aid decisions that need to be made concerning coral reef resilience (Pratchett, 2020). One way to do this would be to use these super-corals with a high thermal tolerance to restock coral reefs that have been subjected to detrimental bleaching events (Grottoli, Tchernov, & Winters, 2017). A study by Morikawa & Palumbi (2019) reported that creating a nursery with heat-tolerant corals species resulted in two to three times less bleaching than a nursery stock of less heat-tolerant species. Also, these heat-tolerant species showed higher individual genetic diversity, that had been previously accumulated, during the bleaching events (Morikawa & Palumbi, 2019).

A study by Camp et al. (2019) argued that there is a time-critical need to study these naturally resilient coral populations. In this way, a better understanding will be created of which coral species are most capable of surviving multiple stressors and which are the key mechanisms that aid coral survival (Camp, et al., 2019). Although this research by Camp et al. (2019) is very valuable for the understanding of naturally resilient coral populations, it lacks practical ways to implement this knowledge. Camp et al. (2019) mention that it is highly debated whether proactive reef management, like assisted colonization, will be necessary for coral survival.

The debate around assisted colonization is triggered by the uncertainty of whether the favourable traits for coral survival in naturally resilient corals will be conserved or lost when they would be relocated to new environments (Camp, et al., 2019). However, the increasing threat of global warming should be a call to action in exploring new reef management possibilities, including assisted colonization of naturally resilient coral species. This leads to the research question addressed in this thesis:

*Where are the coral reefs situated that would be most suitable for assisted colonization of coral species currently thriving in thermally extreme environments?*

The following sub-questions are addressed:

1. Which coral reefs will experience the most frequent and severe bleaching in the future?
2. Which coral species are currently thriving in thermally extreme environments?
3. How are these coral species spatially distributed and in which environmental conditions do they occur?

The objective of this research is to give an overview of potential areas in which assisted colonization of naturally resilient coral species occurring in thermally extreme environments will be most suitable. To answer the research question, coral reef 'hotspots' that will experience the most severe coral bleaching in the upcoming decades will need to be identified using climate model output. Furthermore, coral species that are able to thrive in thermally extreme environments need to be identified and an overview needs to be made of their spatial distributions. Hotspots need to be compared to the spatial distributions of naturally resilient corals. Consequently, areas that could benefit from assisted colonization can be mapped.

This thesis will be divided into multiple chapters. First of all, in chapter 2, the most important theories and concepts used in this thesis will be clarified. The relations between the theories and concepts will be visualized in a DPSIR framework. Afterwards, in chapter 3, the methods used in this research will be presented. Thereafter, in chapter 4, the results will be presented in the form of maps created using ArcGIS. Then these results will be discussed in chapter 5. At last, in chapter 6, the research will be concluded by giving an answer to the research question.

# 2. Theory and concepts

The most important theories and concepts used in this thesis will be described below. The relations between these concepts will then be visualized in a conceptual framework (Figure 2).

## 2.1 Coral bleaching

Corals are in a mutually beneficial symbiotic relationship with the algae zooxanthellae (Boschma, 1924). In every coral polyp lives one of these single-celled algae. They live together in a relationship that benefits both the coral and the algae. This algae provides corals with photosynthetic pigment, supplying the corals with energy, oxygen, and nutrients. The coral, in turn, offers protection and expels carbon dioxide to aid the photosynthetic process (Boschma, 1924). Coral bleaching is the process under which the coral host will eject its symbiont under thermal stress (Hoegh-Guldberg, 1999).

The presence of the algae also gives the coral its magnificent colours. Thus, when the symbiont is expulsed, the tissue of the coral host will become transparent, which will make the white of the calcium carbonate clearly visible. The coral will eventually starve to death, as the zooxanthellae provide 90% of the coral's energy (Slezak, 2016). Coral bleaching can have various causes: extreme temperatures, high irradiance, long-lasting darkness, reduced salinity, heavy metals and pathogenic micro-organisms (Douglas, 2003). Most bleaching events, however, can be accounted to a prolonged increase of SST together with higher solar radiation (Douglas, 2003).

Global warming causes more frequent and intense coral bleaching events (Hoegh-Guldberg, 1999). Hoegh-Guldberg (1999) estimated that the increase in SST due to global warming will most likely have severe effects on the world's coral reefs within 20 to 30 years. He expected that there will be near-annual bleaching events for most coral reef systems by 2040. A study by Skirving et al. (2019) confirmed that this estimation might become reality in the near future. This research shows that 85.5% of the corals worldwide experienced at least low-level bleaching between 2015 and 2017. It is unknown if this pace will keep up, but the future is looking bleak (Skirving, et al., 2019).

## 2.2 Extreme and marginal locations

Some coral reefs can be considered marginal or extreme relating to one or more abiotic factors, such as seawater pH, temperature, low light, and oxygen (Camp, et al., 2018). Different types of environments have extreme values of one or more of these abiotic factors. Examples include high-latitudinal coral reefs, corals situated next to a $CO_2$ vent, corals in hot seas, mangrove systems, seagrass systems, macro-tidal environments, ojos, upwelling environments, turbid reefs, mesophotic reefs, shallow reefs, and tide pools (Camp, et al., 2018). In this thesis, the focus will be on extreme environments relating to high SST, which are classified as hot seas in the quantitative synthesis by Camp et al. (2018). As corals thriving in these environments have been subjected to extremely high temperatures, they may provide exceptionally promising options for the assisted colonization of thermally resilient coral species.

These hot seas have similar, or have even surpassing, abiotic conditions of predictions for the open-ocean under future global warming (Camp, et al., 2018). Figure 1 shows the abiotic conditions that coral species faced at different extreme or marginal environments. Figure 1(A) demonstrates that there are coral species in hot seas environments that have been able to withstand temperatures above 36 degrees Celsius in summer. This significantly exceeds the thermal maximum of most coral species (Donner, Skirving, Little, Oppenheimer, & Hoegh-Guldberg, 2005).

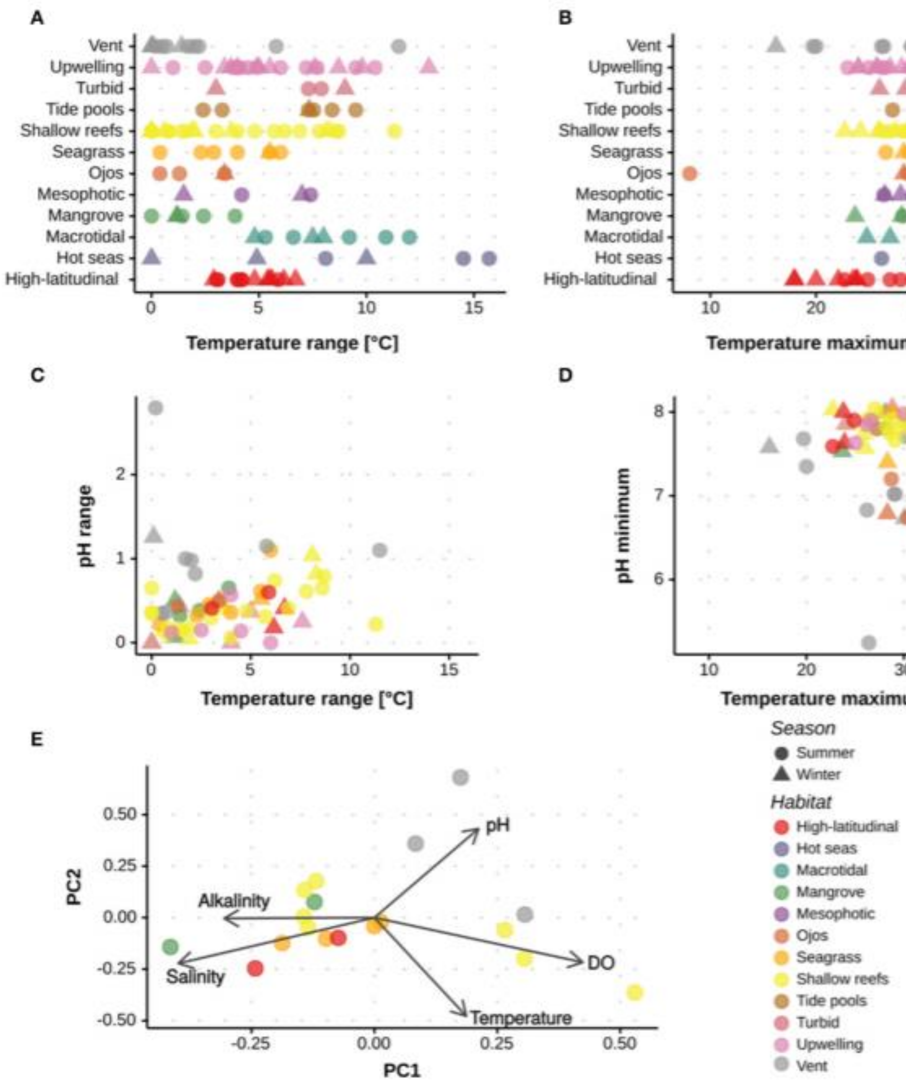


Figure 1: Quantitative assessment by Camp et al. (2018) of the abiotic conditions experienced at the different extreme and marginal environments. Data are shown for studies out of the 285 assessed that reported (A) temperature range, (B) temperature maximum, (C) temperature and pH range, (D) temperature and pH maximum, and (E) temperature, pH, AT, salinity and oxygen. Data are shown per season and environment.

The study by Camp et al. (2018) accounts this survival, or even thriving, under extreme conditions to various adaptive mechanisms of these coral species. In extreme or marginal locations where corals have shown increased thermal tolerance, it is generally due to acclimatization and/or adaptation in the coral host and as well as its symbiont (Camp, et al., 2018). Another crucial response to extreme or marginal environments is the ability of phenotypic plasticity, which is a form of acclimatization (Camp, et al., 2018). This is the change in behaviour, morphology, and physiology by an organism in response to a unique environment (Price, Qvarnström, & Irwin, 2003). Morikawa & Palumbi (2019) claim that in cases of adjusted individuals in different thermal environments by phenotypic plasticity there is significantly less additive genetic variation, compared to adjustments by natural selection. This shows that resistance of coral species to climate stressors acquired by acclimatization may not provide the same tolerance when they are translocated to new places (Morikawa & Palumbi, 2019). Thus, coral species that have been able to adapt genetically to environmental stressors in extreme or marginal environments will be more suitable for assisted colonization.

## 2.3 Assisted colonization

In the scientific community, assisted colonization is increasingly being suggested as a way to conserve and restore biodiversity in the battle against the effects of global warming (van Oppen, Puill-Stephan, Lundgren, De'ath, & Bay, 2014). Other terms for assisted colonization are: assisted migration, managed relocations or managed translocation. These terms are used interchangeably in this thesis. Kreyling, et al. (2011) defined assisted colonization as: ‘‘the intentional movement of focal units to recipient localities, where these focal units are currently absent, and where they cannot be expected to colonize by natural means within a short time frame (i.e., years or decades)’ In the context of this research it will be the movement of heat-stress-tolerant coral species living in extreme or marginal conditions, just outside their species range to places experiencing coral bleaching (National Academies of Sciences, 2019). Assisted colonization of coral species should be a technically feasible measure, but there are information gaps concerning project design (National Academies of Sciences, 2019).

Assisted colonization is considered to be controversial due to knowledge gaps in the risk of the undertaking (Kreyling, et al., 2011). Furthermore, it is considered to be a last resort in creating resilience, as it does not tackle any symptoms. It is a last-ditch effort in saving coral reefs that are experiencing severe bleaching events. It is, however, a serious option to consider, because corals are very close to their thermal limits (Hoegh-Guldberg, Climate change, coral bleaching and the future of the world's corals, 1999). For corals to survive, their thermal tolerance must increase by 0.2-1 degree Celsius per decade over the next 30-50 years to avoid annual bleaching (Donner, Skirving, Little, Oppenheimer, & Hoegh-Guldberg, 2005). However, it is unlikely that corals will be able to adapt or acclimatize at this rate (Donner, Skirving, Little, Oppenheimer, & Hoegh-Guldberg, 2005). Furthermore, current conservation measures may be insufficient in preventing mass-scale species losses in the face of climate change (Hoegh-Guldberg, et al., 2008). Therefore, it is very likely that many coral species will need assisted colonization under a wide range of possible future climates (Hällfors, et al., 2016).

## 2.4 Coral reef resilience

The eventual goal of assisted colonization of coral species living in extreme conditions would be to create more resilient coral reefs against bleaching. The resilience of a system is determined by the balance of positive and negative feedbacks (Holling, 1973). Holling (1973) defines resilience as the ability of a system to recover from perturbations. Typically, coral reefs are dominated by *Scleractinian* corals, which is considered to be a stable coral reef system (McManus & Polsenberg, 2004). After a disturbance, a phase shift can occur, in which the ecosystem will be dominated by algae (McManus & Polsenberg, 2004). These algae are naturally present on the reef in low densities, but can assert their dominance after a perturbation to the system.

McManus and Polsenberg (2004) mention that the coral-algal phase shift is generally believed to be caused by increasing gradual stress, in the form of increased nutrient levels or loss of herbivory, but is commonly the result of a major disturbance like a hurricane, outbreak of coral disease or bleaching event. Throughout their evolutionary history, corals have been able to effectively recover from recurrent perturbations (Hughes, Graham, Jackson, Mumby, & Steneck, 2010). However, recently the resilience of coral reefs has been declining, as coral reefs have been unable to recover from disturbances to the same extent as before (Hughes, Graham, Jackson, Mumby, & Steneck, 2010).

## 2.5 Conceptual framework

Figure 2 shows the DPSIR framework applied to the concepts explained above. This framework makes it possible to give an indication of connections between drivers, pressures, state, impacts, and response (Korte uitleg DPSIR methode, n.d.). The model visualizes the impact of the driving forces and pressure on the state of the environment (Korte uitleg DPSIR methode, n.d.). This impact on the state eventually leads to a response in the form of policies or other solutions (Korte uitleg DPSIR methode, n.d.). This response aims to tackle the drivers, pressures, state, impacts, or a combination thereof (Korte uitleg DPSIR methode, n.d.). In this case, the response only tackles the state and impacts. As this response is considered to be a final option in coral reef management, and thus, it does not tackle the drivers and pressures.

The driver in this framework, global warming, is causing a pressure on the state by means of SST increase. This pressure is in turn causing the state of coral reefs to deteriorate, as the thermal stress threshold will be exceeded by increasing SSTs. The change in state will have detrimental impacts on the coral reef ecosystem, such as coral bleaching, disease, and death. To combat these impacts there needs to be a suitable response. This thesis argues that assisted colonization of naturally resilient corals to threatened reefs will be beneficial in tackling the state and impacts and eventually will cause the affected coral reefs to become more resilient.

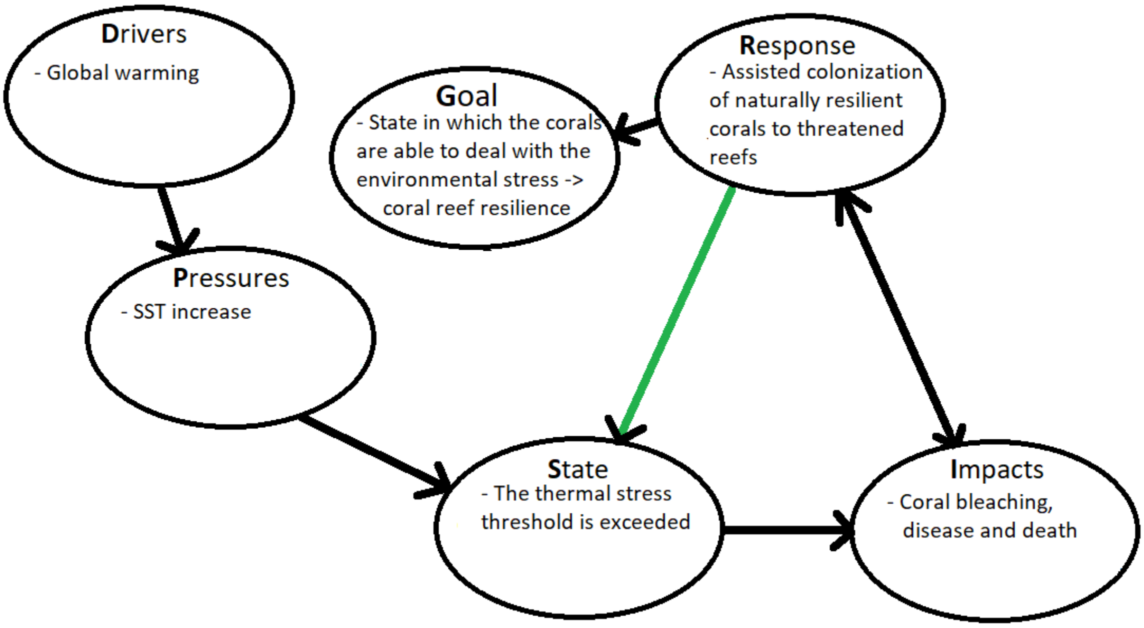


Figure 2: DPSIR framework visualizing the causal relationships between the response, driving forces, pressures, state, and impacts. This leads to the eventual goal of more resilient coral reefs.

# 3. Methods

In the following chapter, the methods will be discussed that will be used to gather and analyse data to answer the research question.

## 3.1 Coral bleaching hotspots

Before it is possible to research the prospect of assisted colonization of naturally resilient corals to threatened coral reefs, it is necessary to research which areas will suffer most from coral bleaching in the future. Therefore, a climate prediction model will be used to indicate the heat stress that coral reefs will experience. These data will be visualized in a map showing hotspots of expected coral bleaching. Using this map it is possible to give an answer to the first sub-question: *Which coral reefs will experience the most frequent and severe bleaching in the future?*

### 3.1.1 Degrees Heating Week (DHW)

To estimate when corals will begin to bleach, Degrees Heating Week (DHW) will be used as an indicator of thermal stress. This is a method designed by Coral Reef Watch, a programme of the National Oceanic and Atmospheric Administration (NOAA), and derived from NOAA satellite data. DHW represents the level of thermal stress accumulation in an area over the last 3 months (NOAA, n.d.). This method states that corals will bleach if they are subjected to temperatures above their bleaching threshold, which is generally 1 degree Celsius higher than the average summer maximum SST. This measurement of the cumulative intensity of heat stress is expressed in the unit degree C-weeks (NOAA, n.d.).

DHW is calculated by using the formula: DHWs = 0.5 * Summation of previous 24 twice-weekly HotSpots (NOAA Coral Reef Watch, 2020). HotSpots values are calculated by subtracting maximum mean summertime SST from the SST in an area. HotSpots values have to be at least 1.0 degrees Celsius to be accumulated in the DHW formula, as this is considered to be the bleaching threshold for corals. The sum of twice-weekly HotSpots data are used in this measurement and is multiplied by 0.5 to get DHW. For example, four DHWs are equal to one week of twice-weekly HotSpots values of 4 degrees Celsius, or two weeks of twice-weekly HotSpots values of 2 degrees Celsius (NOAA Coral Reef Watch, 2020). It is assumed that bleaching will commence once DHW exceeds 4 degrees C-weeks and it will become severe once DHW surpasses 8 degrees C-weeks (Teneva, et al., 2012).

### 3.1.2 Climate prediction model

A study done by the United Nations Environment Programme (2017) will be used to give an indication of the coral bleaching hotspots. In this research, they made downscaled projections of bleaching for coral reefs all around the world. UNEP, together with partners like NOAA and WWF, created a climate model that predicts the occurrence of severe bleaching events happening ten times per decade, or twice per decade (UNEP, 2017). Severe bleaching happens when the thermal stress exceeds 8 DHWs (UNEP, 2017). The research by UNEP uses the ensemble average value of SST from 33 different CMIP5 models. Using these data, UNEP has calculated the Degrees Heating Months (DHM) for each year between 2006 and 2099. DHM is calculated by multiplying DHW by 4.35 (UNEP, 2017). Projections of DHM have been made for both the RCP4.5 scenario and the RCP8.5 scenario (UNEP, 2017). In this thesis, the projection of the severe bleaching events occurring annually under RCP4.5 scenario will be used. This scenario has been chosen, as the “worst-case” RCP8.5 scenario seems increasingly unlikely to happen with each passing year (Hausfather & Peters, 2020). Also, projections of annual bleaching will be used, instead of twice a decade, because coral reefs experiencing annual severe bleaching should have the highest conservation priority (UNEP, 2017). Using the data provided by UNEP (2017) a map will be created using ArcGIS, visualizing which coral reefs will experience the most frequent and severe bleaching.

## 3.2 Coral species thriving in marginal and extreme conditions

### 3.2.1 Literary study

In order to find out which coral species are thriving in thermally extreme conditions, a literature study is carried out. A quantitative synthesis of Camp et al. (2018) gives an overview of research done in natural extreme environments. On the basis of the list of literature used in that research, found in Appendix A, coral species can be identified that are able to survive in conditions that would be considered to have high heat stress. This list of literature will also give an indication of the commonalities between the identified coral species. Using these data it is possible to give an answer to the second sub-question: *Which coral species are currently thriving in thermally extreme environments?*

### 3.2.2 Spatial distribution map and environmental conditions

Based on a database by the World Register of Marine Species (WoRMS) of the occurrence records of coral species, it is possible to create a map of the spatial distribution of these naturally resilient coral species in ArcGIS. It is necessary to know how these naturally thermally resilient coral species are spatially distributed, because assisted colonization will only be used as a measure, if the species can already be found or used to be found on the threatened reef. This ensures that these coral species will be able to survive in their new environment, as they have been able to survive here in the past. Next to the spatial distribution, the WoRMS database also provides data concerning the environmental conditions of these occurrence records. These data will be used to give an indication of the SST, Sea surface salinity, and sample depth of the occurrence records. Using the acquired data, it is possible to answer the third sub-question: *How are these coral species spatially distributed and in which environmental conditions do they occur?*

## 3.3 Areas suitable for assisted colonization

A map will be made of potential areas where assisted colonization of corals species thriving in extreme conditions would be most suitable. This map will be made using ArcGIS. Maps of coral bleaching hotspots and the spatial distribution of coral species will be layered. Overlap between these maps will show coral reefs suitable for assisted colonization of species currently thriving in thermally extreme environments. The outcomes of this overlay can be used to answer the research question: *Where are the coral reefs situated that would be most suitable for assisted colonization of coral species currently thriving in thermally extreme environments?*

# 4. Results

## 4.1 Coral bleaching hotspots

Figure 3 shows the year in which coral reefs will start to be affected by annual severe bleaching (ASB), under the RCP4.5 scenario. This is visualized by colours, ranging from red to blue. With red representing coral reefs that will be affected by ASB the earliest and blue the latest. The red dots are coral reefs that are already experiencing extreme thermal stress or will do so in the near future. This model starts in 2006. The period 2006-2030 are the red dots in figure 3, these can be considered hotspots of coral bleaching. Hotspots can be found in the Caribbean, the Red Sea, Indonesia, and Taiwan.

Furthermore, what figure 3 shows, is that most of the coral reef around the world will experience ASB in the future. There is, however, great variation in the timing of the onset of ASB events, with areas already being affected by ASB currently and areas that will start to experience similar bleaching a lot later, like coral reefs found in the Pacific Ocean around Polynesian islands. Additionally, there is also variation in the timing of the onset of ASB within countries. This can be seen around Indonesia in figure 3, where red and blue dots are situated next to each other. This reveals that some coral reefs are already experiencing ASB right now, while adjacent coral reefs in the same country will start to be affected several decades later.

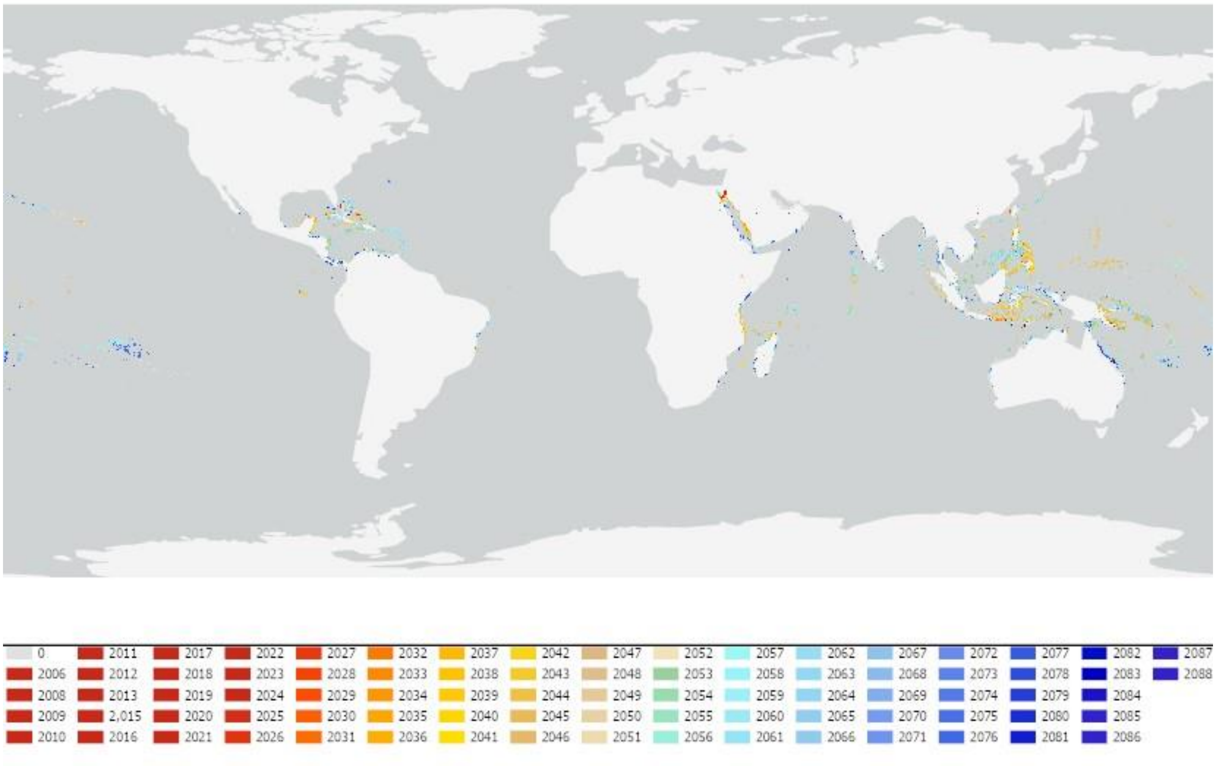


Figure 3: Projection of coral bleaching hotspots under the RCP4.5 scenario, adapted from the data by UNEP (2017)

## 4.2 Coral species thriving in thermally extreme conditions

There are two coral species that are mentioned frequently in literature, as species that are able to withstand high thermal stress and show less suffering from coral bleaching, namely *Pocillopora damicornis* and *Stylophora pistillata*. The quantitative synthesis done by Camp et al. (2018) used 34 papers that concerned coral species living in hotter seas. Of these 34 papers, 8 mention *Pocillopora damicornis* as a coral species that is able to have a high thermal tolerance for coral bleaching, and 6 papers mention *Stylophora pistillata*. This is more than other coral species mentioned in these 34 papers. Of these 8 mentions of *Pocillopora damicornis*, 5 are unique findings and 3 refer to those findings. Of these 6 mentions of *Stylophora pistillata,* 3 are unique findings and 3 refer to those findings.

*Pocillopora damicornis* and *Stylophora pistillata* have been labelled as super-corals by Grottoli, Tchernov, & Winters (2017). The study by Grottoli, Tchernov, and Winters (2017), conducted a bleaching experiment in which three coral species in the Red Sea, namely *Pocillopora damicornis*, *Stylophora pistillata* and *Favia favus*, were subjected to temperatures 6 degrees Celsius higher than their thermal maximum for 37 days. This experiment was equivalent to an exposure of 32 DHW, four times higher than 8 DHW which is critical to coral species (Grottoli, Tchernov, & Winters, 2017). Of these species, *Pocillopora damicornis* was least affected by coral bleaching, as it preserved its total energy reserves and biomass (Grottoli, Tchernov, & Winters, 2017). The research by Grottoli, Tchernov, and Winters (2017) also shows that *Pocillopora damicornis* was not dependent on heterotrophy after being bleached and was still able to calcify in these extreme conditions. *Stylophora pistillata* showed more signs of bleaching in this experiment. However, this species was also able to still preserve its total energy reserves and biomass (Grottoli, Tchernov, & Winters, 2017). Calcification rates of *Stylophora pistillata* declined on the other hand, whilst being exposed to the higher temperatures (Grottoli, Tchernov, & Winters, 2017). Grotolli, Tchernov, and Winter (2017) state that *Pocillopora damicornis* and *Stylophora pistillata* are coral species that will most likely die as a result of bleaching in other areas. Therefore, they mention that these two coral species, currently thriving in the Red Sea, will be relevant to use in restocking other reefs that have been detrimentally affected by coral bleaching.

## 4.3 Spatial distribution and environmental conditions

### 4.3.1 Stylophora pistillata

Using the database of the World Register of Marine Species (WoRMS), the spatial distribution of *Stylophora pistillata* has been visualized in figure 4 (WoRMS Editorial Board, 2017). This coral species is widely distributed and can be found on every continent except for the Americas. Most of the occurrences have been recorded in the Indian Ocean, around the east coast of Africa, the Red Sea, Southeast Asia, Indonesia, and the west coast of Australia. In the Pacific Ocean, many occurrences of *Stylophora pistillata* have been recorded as well, around the east coast of Australia, the Philippines, in the East China Sea, the Marshall Islands, and along the Mariana Through. This dataset contains 2086 different occurrence records of *Stylophora pistillata*, discovered between 1874-2017.

Figure 5 shows the environmental conditions under which these occurrence records of *Stylophora pistillata* have been found. It shows that this coral species can mostly be found in tropical waters with temperatures varying from 25-30 degrees Celsius. Of the 2086 occurrence records, 2054 have documented the SST in which the coral was found. 90% of these 2054 documentations have been recorded in SSTs ranging from 25-30 degrees Celsius. There are some exceptions, 9.6% of occurrence records can be found in SSTs between 20-25 and 0.14% can be found in SSTs ranging from 15-20 degrees Celsius. Furthermore, this coral species can be found in saline water with sea surface salinity ranging between 30-35 PSU. Figure 5 also shows that occurrences of *Stylophora pistillata* have been recorded at a depth of 0-50 meters. The sample depth in meters has been documented in this dataset for 1449 of the 2086 occurrence records of *Stylophora pistillata*. Of these 1449 documentations, 45.7% can be found in shallow waters with a maximum of 10 meters depth. While 33.2% have been documented ranging between 40-50 meters. The remaining 21.1% can be found in depth between 10-40 meters.

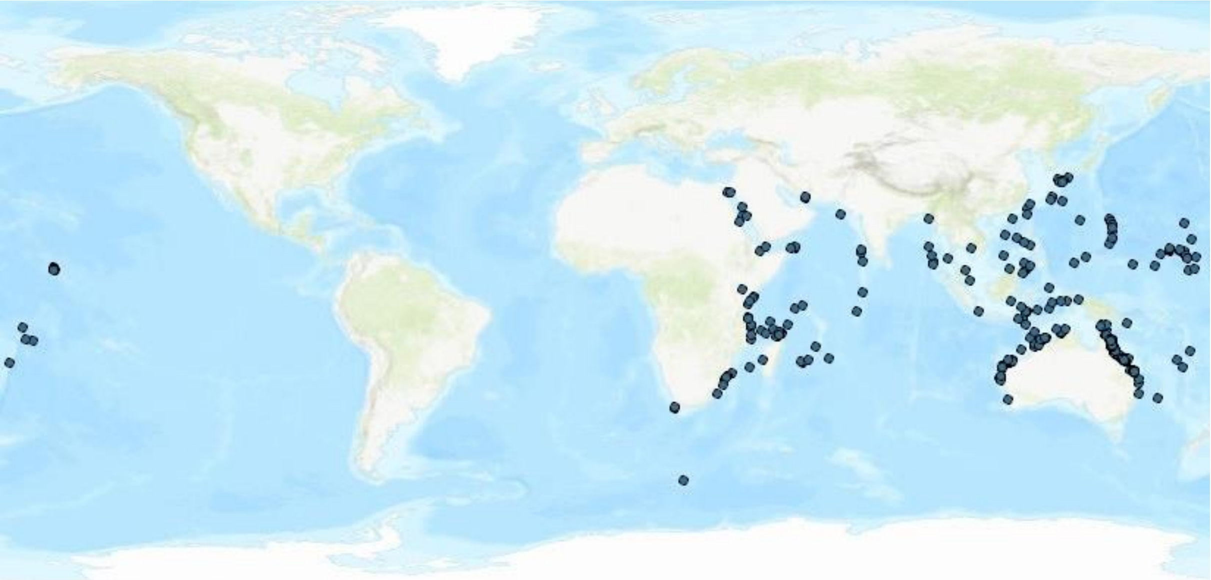

Figure 4: Spatial distribution of *Stylophora pistillata*, adapted from the database by WoRMS (2017)

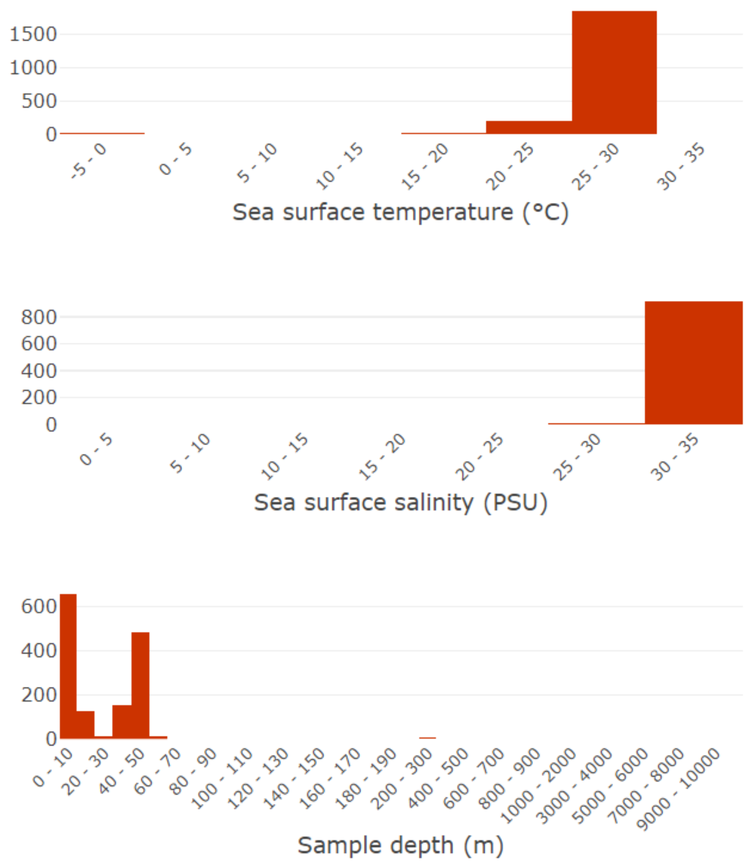

Figure 5: Environmental conditions of occurrence records of *Stylophora pistillata*, taken from the database by WoRMS (2017). Data are shown for occurrence records that reported on: (A) SST in degrees Celsius, (B) Sea surface salinity in PSU, and (C) Sample depth in meters.

### 4.3.2 Pocillopora damicornis

Using the database of the World Register of Marine Species (WoRMS), the spatial distribution of *Pocillopora damicornis* has been visualized in figure 6 (WoRMS Editorial Board, 2018). This coral species is more widely distributed than *Stylophora pistillata* and can be found on every continent. Like *Stylophora* pistillata, most of the occurrences of *Pocillopora damicornis* have been recorded in the Indian Ocean, around the east coast of Africa, the Red Sea, Southeast Asia, Indonesia, and the west coast of Australia. Unlike *Stylophora pistillata*¸ there are also many occurrences of *Pocillopora damicornis* found along the coast of Sri Lanka. In the Pacific Ocean many occurrences of *Pocillopora damicornis* have been recorded as well, around the east coast of Australia, the Philippines, in the East China Sea, the Marshall Islands, along the Mariana Through and Hawaiian ridge. There are also some occurrences documented along the coast of Colombia. This dataset contains 4807 different occurrence records of *Pocillopora damicornis*, discovered between 1875-2018.

Figure 7 shows the environmental conditions under which these occurrence records of *Pocillopora damicornis* have been found. It shows that this coral species can also mostly be found in tropical waters with SSTs ranging from 25-30 degrees Celsius, as 73% of the dataset is documented in this temperature range. This coral species has 26.9% of its occurrences recorded in colder waters with temperatures between 20-25 degrees Celsius, compared to the 9.6% of *Stylophora pistillata* occurrence records in this range. The sea surface salinity levels in which *Pocillopora damicornis* can be found is the same compared to *Stylophora pistillata*¸ varying from 30-35 PSU. Figure 7 shows that *Pocillopora damicornis* occurrences have been spotted up to a depth of 100 meters. However, this coral species can predominantly be found between a depth of 0-20 meters. With 66% of *Pocillopora damicornis* being documented at a depth of 0-10 meters and 24.4% ranging between 10-20 meters.

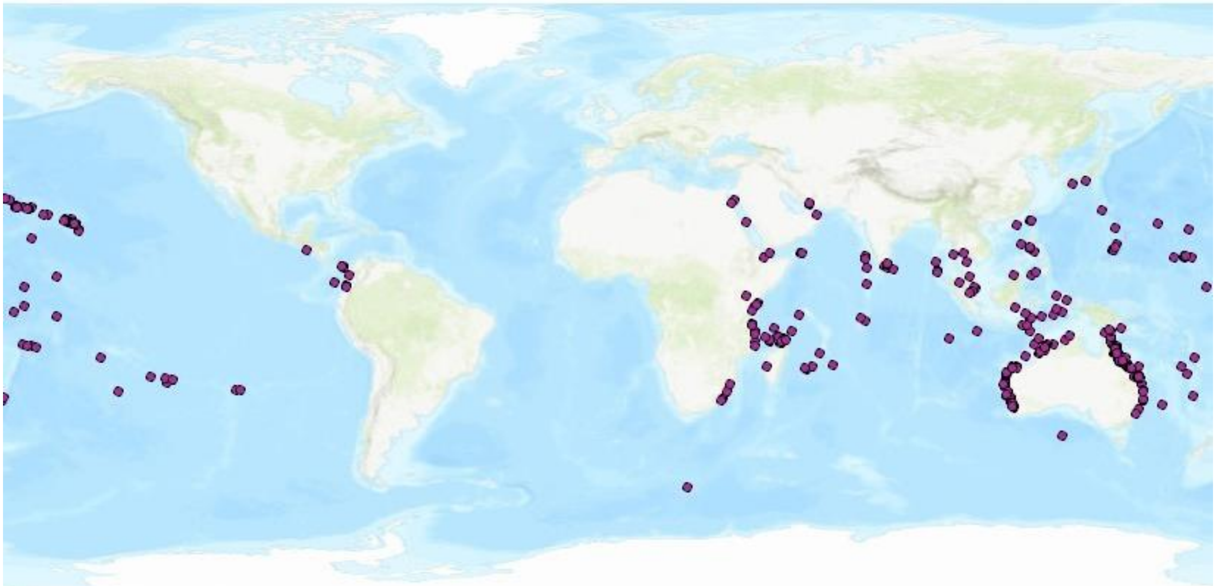

Figure 6: Spatial distribution of *Pocillopora damicornis,* adapted from the database by WoRMS (2018)

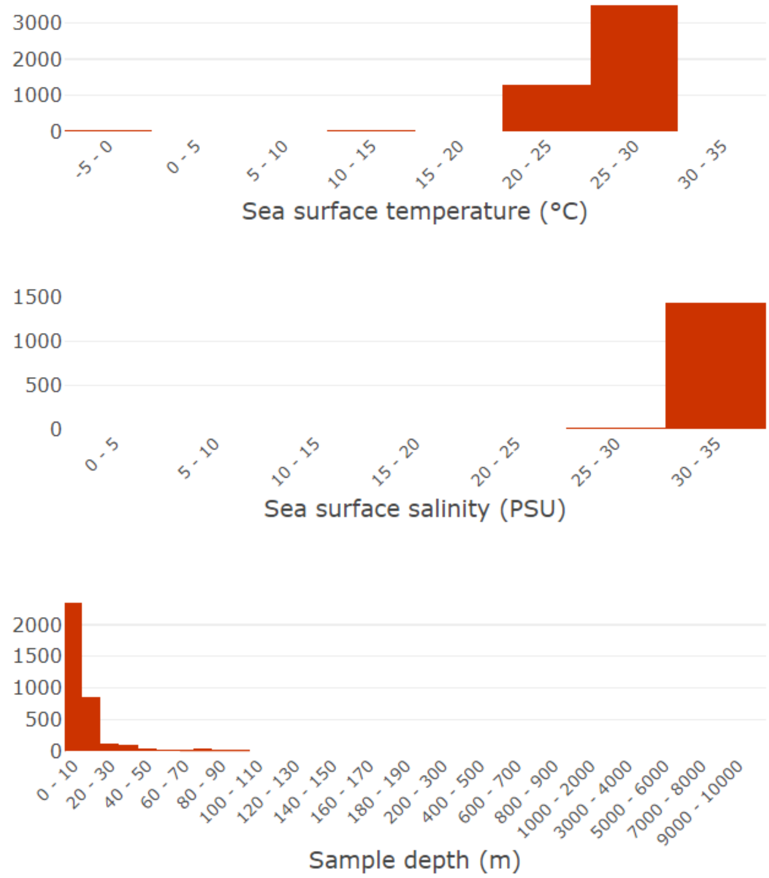


Figure 7: Environmental conditions of occurrence records of *Pocillopora damicornis*, taken from the database by WoRMS (2018). Data are shown for occurrence records that reported on: (A) SST in degrees Celsius, (B) Sea surface salinity in PSU, and (C) Sample depth in meters.

## 4.4 Overlap between spatial distribution and hotspots

Figure 8 shows the hotspots for ASB between 2020-2030. These are the coral reefs that will experience 8 DHW annually, in the 4.5RCP scenario. Figure 8 shows that most tropical areas in the world, have coral reefs experiencing ASB in the period 2020-2030, ranging from the Caribbean to Indonesia. Coral reefs in the Indian Ocean, Polynesia, and along the coast of Australia are less affected by ASB between 2020-2030. As seen in figure 3, these areas will eventually also suffer from ASB in the future. For instance, the coral reefs situated along the coast of Australia will experience ASB in the period 2060-2090, indicated by its blue and light-blue colours. To find out which coral reefs are most suitable for assisted colonization of *Pocillopora damicornis* and *Stylophora pistillata*, maps of the spatial distributions of these coral species were overlapped with hotspots of ASB between 2020-2030 in ArcGIS.

The results are depicted in figures 9 and 10. The overlap between the spatial distribution of *Stylophora pistillata* and hotspots of coral bleaching between 2020-2030 has been visualized in figure 9. This shows coral reefs that contain *Stylophora pistillata* and are threatened by ASB in the period 2020-2030. Out of the 2086 occurrence records of *Stylophora pistillata,* there are 10 cases where this coral species will experience ASB between 2020-2030. This is 0.48% of all the occurrence records. Of these 10 cases, 2 can be found in the Red Sea, 2 along the east coast of Africa, 1 in Madagascar, 1 in Taiwan, 1 in Malaysia, 1 in the Philippines, 1 in Indonesia, and 1 next to Papua New Guinea. Of these coral reefs, 7 are situated in the Indian Ocean and 3 are situated in the Pacific Ocean.

The overlap between the spatial distribution of *Pocillopora damicornis* and hotspots of coral bleaching between 2020-2030 has been visualized in figure 10. Of the 4807 occurrence records of this coral species, there are 8 cases where this coral species will experience ASB between 2020-2030. This is 0.17% of the occurrence records. Of these 8 cases, 1 can be found in the Red Sea, 2 along the east coast of Africa, 1 in Madagascar, 1 in Taiwan, 1 in the Philippines, and 2 in Indonesia. Of these coral reefs, 5 are situated in the Indian Ocean and 3 are situated in the Pacific Ocean.

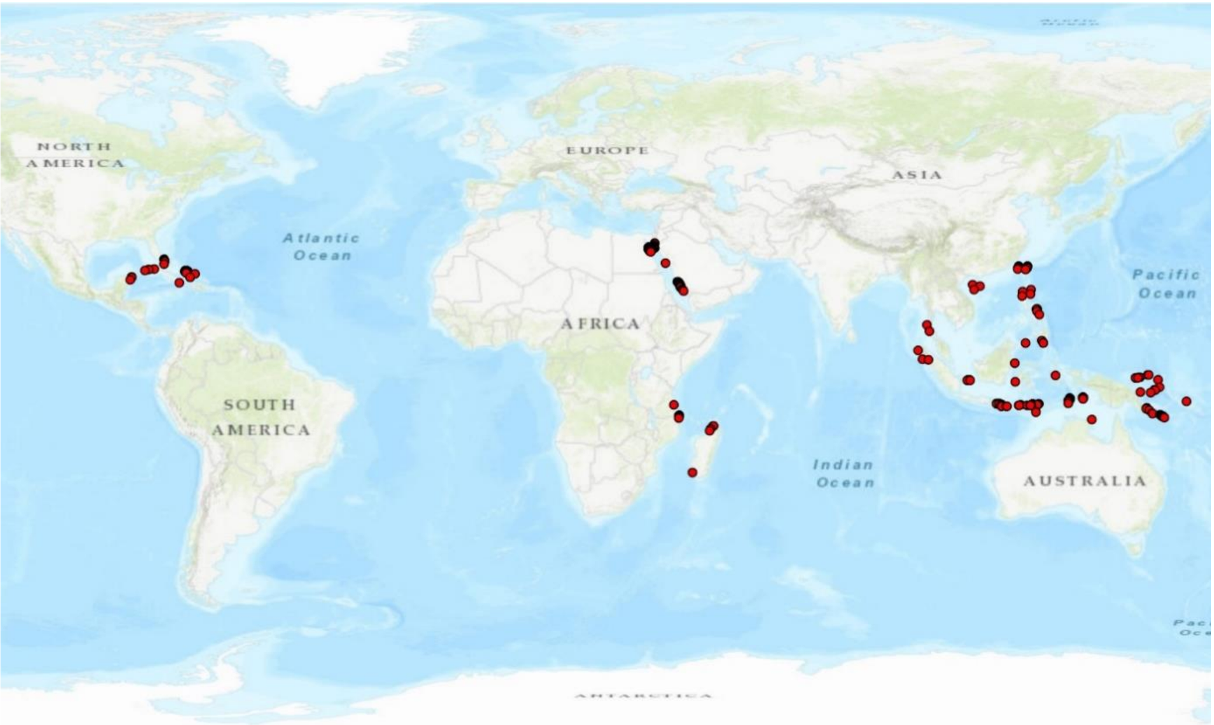


Figure 8: Hotspots of coral bleaching. These areas will experience ASB between 2020-2030


Figure 9: Overlap between spatial distribution of *Stylophora pistillata* and coral bleaching hotspots between 2020-2030


Figure 10: Overlap between spatial distribution of *Pocillopora damicornis* and coral bleaching hotspots between 2020-2030

# 5. Discussion

## 5.1 Interpretation of results

What *Pocillopora damicornis* and *Stylophora pistillata* have in common is that they have the highest interaction rate with symbionts of any known coral species (Franklin, Stat, Pochon, Putnam, & Gates, 2012). These corals are both known to be able to interact with 30 different species of *Symbiodinium* (Franklin, Stat, Pochon, Putnam, & Gates, 2012). According to the adaptive bleaching hypothesis (ABH), this high interaction rate means that these coral species will be more resilient to bleaching (Mostafavi, Fatemi, Shahhosseiny, Hoegh-Guldberg, & Loh, 2007). The ABH states that a coral host can be repopulated with a new symbiont, after the old symbiont is expulsed under thermal stress (Buddemeier & Fautin, 1993). This means that if there are heat-tolerant *Symbiodinium* species in the environment, a recently bleached coral can survive by replacing its old symbiont by the available heat-tolerant zooxanthellae (Mostafavi, Fatemi, Shahhosseiny, Hoegh-Guldberg, & Loh, 2007). *Pocillopora damicornis* and *Stylophora pistillata* have the highest interaction rate with symbionts, meaning that they have a higher chance of survival after bleaching, because there is a higher possibility to find a new, more heat-tolerant, symbiont. This makes these two coral species suitable for assisted colonization. Also, due to the fact that there will be a higher chance of finding a suitable symbiont once these corals have been relocated to their new environment.

It is important to relocate species to places where they have lived before, because then the place where they will be relocated to is a suitable environment for them to grow in. In the sense that *Symbiodinium* species are living there to interact with, and the reef has favourable environmental conditions for these coral species to survive. Furthermore, this will make sure that the species will not become invasive in their new environment. There is a big concern with assisted colonization, that it will trigger detrimental effects on the ecosystem, due to the invasiveness of the translocated species (Chauvenet, Ewen, Armstrong, Blackburn, & Pettorelli, 2013). However, this would be counteracted if the species has a history in this new environment.

The red dots or hotspots in figure 3, should be considered as conservation priorities (UNEP, 2017). These coral reefs will experience ASB in the near future or are already suffering from it. Thus, making them most suitable for assisted colonization of coral species with a high thermal tolerance. The red dots resemble coral reefs that suffer from ASB in the period 2006-2030. In the overlay analysis the period 2020-2030 was chosen because these coral reefs will experience ASB in the near future and thus, there is no time left in tackling the symptoms of bleaching. Therefore, an adaptation strategy, like assisted colonization, is more suitable in this period.

The overlay results show that the coral reefs that will be suitable for assisted colonization can in the case of both *Stylophora pistillata* and *Pocillopora damicornis* be found in similar areas. The results reveal that assisted colonization will be a worthwhile conservation strategy for both corals in the Red Sea, east coast of Africa, Madagascar, Taiwan, the Philippines, and Indonesia. Even though there are differences in the exact location, a pattern can be identified. This can be explained by the fact that these areas will experience detrimental thermal stress earlier than other parts of the world. This can also be seen in figure 3, as the outcome of figure 9 and 10 can be localized in areas which display a red or orange colour in figure 3, meaning that these areas will experience ASB in the near future or are already experiencing it.

Despite there being more than two times as many occurrence records of *Pocillopora damicornis* compared to *Stylophora pistillata*, there are more areas of overlay of *Stylophora pistillata* and ASB hotspots between 2020-2030. This can be explained by the fact that *Stylophora pistillata* grows on coral reefs which are closer to their thermal maximum and thus, are closer to bleaching.

When comparing the environmental conditions of these coral species in figure 5 and figure 7, it becomes clear that 90% of *Stylophora pistillata* occurrences are recorded in waters with SST between 25-30 degrees Celsius. On the other hand, only 73% of *Pocillopora damicornis* occurrence records can be found in the SST range of 25-30 degrees Celsius.

The coral reefs that are suitable for assisted colonization of coral species currently thriving in thermally extreme environments are mostly situated in developing countries, with the exception of two cases, namely the one in the Red Sea and the one in Taiwan. This means that conservation strategies, like assisted colonization, are unlikely to be adopted by these developing nations, as these countries mostly prioritize basic human needs for survival, like food security and housing, over conserving the environment (Bell, Ratner, Stobutzki, & Oliver, 2006). Governments alone, cannot bear the responsibility for managing and conserving coral reefs, especially if these governments have little financial capabilities (Dight & Scherl, 1997). Therefore, multi-stakeholder partnerships should be set up, involving the public and private sectors, the scientific community, NGOs, and local communities (Dight & Scherl, 1997). This way, conservation measures, such as assisted colonization, can become feasible to conduct in developing countries (Dight & Scherl, 1997).

## 5.2 Implications

As stated in the introduction, there is a knowledge gap concerning practical ways to implement knowledge on naturally resilient coral populations (Camp, et al., 2019). Not a lot of research has been done in the field of assisted colonization of coral species. With this research, a contribution has been made to this knowledge gap, as this research identified two naturally resilient coral species, namely *Pocillopora damicornis* and *Stylophora pistillata* that are suitable for the implementation of assisted colonization. Projections of ASB indicate a time-critical need to conserve coral reefs. This research is a call to action for implementing proactive measures, like assisted colonization, to promote coral reef resilience. The findings of this thesis are also a starting signal for more research needed to be done concerning the assisted colonization of coral species that are currently thriving in thermally extreme environments.

## 5.3 Limitations

Despite the useful knowledge obtained for potential areas suitable for assisted colonization of naturally thermally resilient coral species to bleaching, there are limitations of this research. First of all, assisted colonization is a controversial conservation measure, as it is a relatively new measure and therefore, it has yet to be implemented as a measure to conserve coral reefs (McLachlan, Hellmann, & Schwartz, 2007). This means that there are knowledge gaps concerning the risks of assisted colonization (Kreyling, et al., 2011). There are uncertainties in climate projections and in how coral species will respond to a new environment (Kreyling, et al., 2011). These uncertainties can be tackled by increasing our understanding of the habitat requirements and distribution of coral species that are suitable for assisted colonization (Kreyling, et al., 2011). Therefore, Kreyling et al. (2011) claims that it is possible to identify cases in which the risk of assisted colonization is low and where the benefits will significantly outweigh the adverse outcomes.

With these uncertainties in mind, Kreyling et al. (2011) established a decision framework concerning assisted colonization, as visualized in figure 11. Decision step 1 asks if there is a high risk of decline or extinction under climate change. In the case of the assisted colonization of *Stylophora pistillata* and *Pocillopora damicornis,* there is a high risk of decline or extinction under climate change.

Even though they are respectively near threatened and least concern on the IUCN Red List, these coral species will not survive ASB for a prolonged time (IUCN, 2008). Therefore, there will be a high risk of decline or extinction under climate change for these species. Figure 3 has shown that there are many reefs around the world that are already experiencing severe bleaching on an annual basis, and there will be many more in the future. With this magnitude of bleaching, virtually no coral species will be able to survive and *Stylophora pistillata* and *Pocillopora damicornis* would be suitable coral species to use for assisted colonization, due to their high interaction rate with symbionts (Franklin, Stat, Pochon, Putnam, & Gates, 2012).

Step 2 asks whether translocation and establishment of species are technically feasible. As the National Academies of Sciences (2019) pointed out, the measure of assisted colonization can be technically feasible, but there are information gaps in project design. There is no research done on the feasibility of assisted colonization for the coral species discussed in this thesis. Therefore, it is not possible to form a scientific answer on step 2 and more research is needed to be done. The same goes for step 3: do benefits of translocation outweigh the biological and socioeconomic costs and constraints? This is also a point that needs further research.

In the context of this research, the decision framework by Kreyling et al. (2011) does not clearly lead to the step: undertake assisted colonization. However, immediate action is necessary to impede extinctions caused by climate change (McLachlan, Hellmann, & Schwartz, 2007). Continuing and improving conventional conservation approaches will not be enough in the face of climate change and its detrimental effects on coral reefs. Therefore, this thesis can be seen as a starting point for further research conducted in the field of assisted colonization

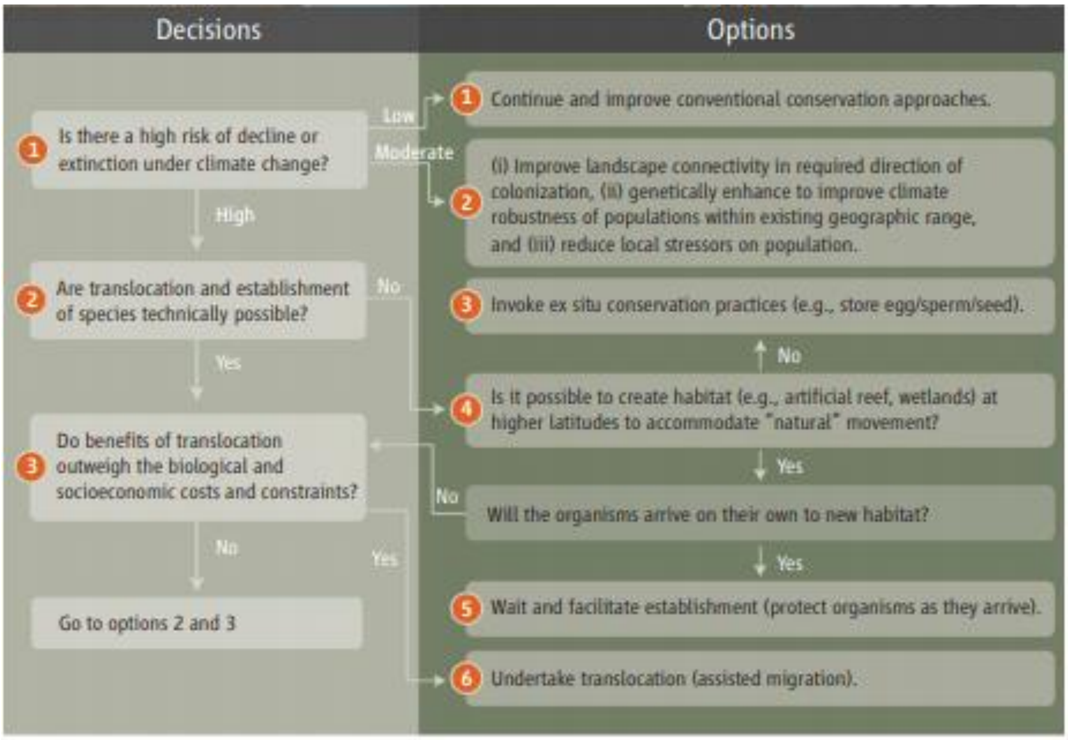


Figure 11: Decision framework for assisted colonization (Kreyling, et al., 2011)

In this thesis, only SST and the spatial distribution of the coral species are accounted for in deciding which coral reefs are suitable for assisted colonization. Accounting for the spatial distribution of the corals suitable for assisted colonization, makes sure that the environmental conditions in the new environment are favourable for these coral species to survive, because these coral species have been living there before. However, this does not account for changing environmental conditions due to climate change. For instance, the accumulation of carbon dioxide in the atmosphere is causing the oceans to acidify (Caldeira & Wickett, 2003). These lower pH values in the ocean are detrimentally affecting coral reefs, as structures made from calcium carbonate are vulnerable to dissolution under these lower values (Caldeira & Wickett, 2003). The results of figures 9 and 10 do not account for this and other changes in environmental conditions and therefore, more research is needed to be done to form a better answer to the research question.

Another limitation is that it is very challenging to decipher the specific adaptations found in corals because corals are a collection of symbiotic species that are connected to each other (Bartz & Brett, 2015). This collection of species is called the *holobiont* and includes the coral animal that forms the skeleton and carbonate structure and the zooxanthellae living in the coral tissue providing photosynthetic capabilities (Bartz & Brett, 2015). Bartz and Brett (2015) argue that because of the inter-connectedness of these species it is hard to discern what caused a coral to adapt to extreme environmental conditions. Therefore, there is an uncertainty in translocating thermally resistant coral species to a new environment, as it is not always known which component of the coral animal caused it to be more resilient to bleaching (Bartz & Brett, 2015). However, recently next-generation sequencing techniques have been evolving and are becoming more financially appealing (Bartz & Brett, 2015). According to Bartz and Brett (2015), this means that there are more opportunities in deciphering the cause of specific genetic developments, which is making assisted colonization more scientifically grounded.

## 5.4 Future research

There are uncertainties and limitations in this research and therefore, future research is necessary. As briefly mentioned in the previous section, there are several assumptions that need to be more grounded in research. First of all, experimental research needs to be done that implements assisted colonization of corals. In this way, a better understanding can be created of the measure assisted colonization and the impacts of translocated species on their new environment. Currently, no implementation of assisted colonization of coral species has been completed.

Furthermore, in future research more environmental conditions need to be taken into account in deciding which areas are suitable for assisted colonization. This thesis only accounts for an increase in SST due to climate change. To make sure that the environmental conditions match the habitat requirements of the introduced coral species, it needs to be analysed how the environmental conditions will change in the face of climate change. Possible fields of study would be, pH change due to ocean acidification and the change in salinity due to the influx of fresh polar water.

## 6. Conclusion

To mitigate the detrimental effects of global warming on the bleaching of coral reefs, new measures of coral reef conservation should be put on the agenda. The future of coral reefs is looking bleak, with many corals already showing signs of severe bleaching and climate models predicting global ASB in the near future. Hence, to put the measure of assisted colonization of naturally thermally resistant coral species on the agenda, this research aimed to answer the following research question: *Where are the coral reefs situated that would be most suitable for assisted colonization of coral species currently thriving in thermally extreme environments?*

It can be concluded that the coral reefs that are most suitable for assisted colonization of coral species currently thriving in thermally extreme environments can be found in the Red Sea, east coast of Africa, Madagascar, Taiwan, the Philippines, Papua New Guinea, and Indonesia. What these areas have in common is that they are mostly situated in developing regions. This means that multi-stakeholder partnerships need to be established to implement assisted colonization in these areas. *Stylophora pistillata* and *Pocillopora damicornis* are suitable coral species to translocate, as they have the highest interaction rate with zooxanthellae. Furthermore, these species are frequently mentioned in literature as corals that are able to withstand high thermal stress and show less suffering as a result of bleaching.

Despite the limitations of this research, it is nonetheless important to do additional research in this field of study, as immediate action is necessary to impede extinctions caused by climate change. The controversial nature of this measure, should not prevent future research, because it could always turn out to be an effective and essential measure in the end. Therefore, to protect coral reefs against the detrimental effects of bleaching and increase their overall resilience, assisted colonization should be considered as a measure worth trying and analysing.

## Acknowledgements

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# Appendix A

Literature list of papers mentioning coral species thriving in hotter seas, compiled by Camp et al. (2018)

| | |
|---|---|
| 1. | Riegl, B. (2002). Effects of the 1996 and 1998 positive sea-surface temperature anomalies on corals, coral diseases and fish in the Arabian Gulf (Dubai, UAE). *Mar. Biol. 140*, 29-40. |
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